Aquatic ecosystem responses to fire and flood size in the Okavango Delta: observations from the seasonal floodplains

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Abstract The frequency of fires in the Okavango Delta seasonal floodplains peaked at an intermediate frequency of flooding. Floodplains are commonly burnt every 3–5 years. This study showed fundamental changes in ecosystem properties due to burning. A burnt seasonal floodplain in the aquatic phase had oxygen levels well above saturation, 100–200%, while the levels in the un-burnt control site were below saturation and, at night, could decline to 10–40% saturation. The total phosphorous and total nitrogen concentrations were similar on both floodplains but considerably enriched relative to inflowing water, due to nutrient release from the flooded soil-sediment and animal droppings. Zooplankton biomass was very high in both systems although the abundance of fish fry was ten times higher on the un-burnt floodplain. In a low flood year the un-burnt floodplain water had high nutrient levels, primary production, methane emission, and subsequent uptake of methane in biota, as well as a high zooplankton biomass. The very high flood the following year showed the opposite with much lower production at all levels owing primarily to greater dilution of nutrients. The abundance of fish, however, was much higher during the high flood year. Macrophytes and litter provide direct shelter for fish fry but also promote low oxygen levels when decaying. Large flooded areas result in high fish production by removing obstacles related to congestion. This interplay between hydroperiod and fire may be crucial for the maintenance of high biological productivity both in the aquatic and terrestrial phases in a very nutrient poor wetland landscape. Understanding these interactions is crucial for optimal management.

Keywords Seasonal floodplain · Fire · Flood pulse · Macrophyte · Okavango Delta · Nutrients · Zooplankton biomass · Fish productivity

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Introduction

Seasonal flooding of the Okavango Delta in Botswana, which usually lasts for 3–6 months, is caused by a pulse of water in the Okavango River that results from rainfall on the Angola highlands during the period November–February. This pulse arrives at the

inlet to the Delta during January–March, after which it moves as a slow wave across the wetland landscape until it reaches the distal parts in July–August. While the flooding extent between years on the scale of the whole Delta can vary by a factor of two, individual floodplains can experience a much larger relative variation. For example, in the area investigated in this study (Fig. 1) during the 12 year period 1996–2007, the minimum inundation extent was less than a quarter of the maximum flood extent (of greater than 0.4 km² in 2004) (Fig. 2).

Fires are common in the Okavango Delta. Heinl et al. (2006, 2007) analyzed satellite images for a 6100 km² area of the southern Okavango Delta over the period 1988–2003 and showed that the fire frequency was very low on dry land (0–1 fires in 15 years), while seasonally flooded areas experienced 2–10 fires in the same period. On such floodplains there is a positive correlation between mean frequency of flooding and the frequency of fires up to a threshold level of seven flood years and three fires (Fig. 3), after which the fire frequency drops. These trends are readily explained by the increase of aquatic macrophyte primary production caused by higher flooding frequency and the resulting higher fuel load as a determinant of fire frequency (Heinl et al. 2006). Fire is less likely where flood frequency is greater than seven in fifteen years because the increased wetness reduces the possibility of burning.

The consequences for aquatic biota of these flooding-fire sequences have previously not been
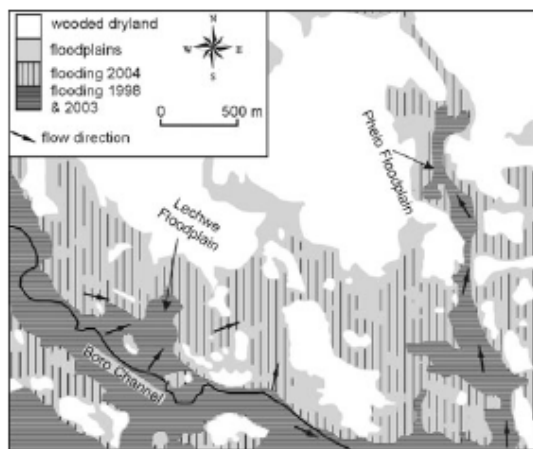

Fig. 1 The study area with the extent of the low-level floods in 1998 and 2003 and the high-level flood in 2004
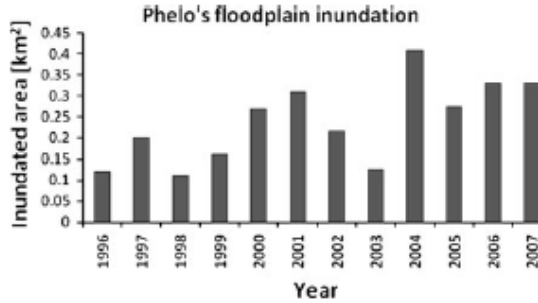

Fig. 2 Maximum annual flooded area 1996–2007 on Phelo floodplain
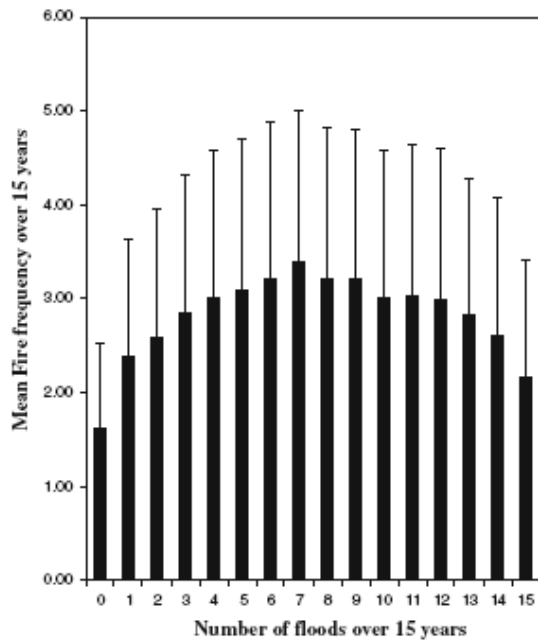

Fig. 3 Mean fire frequency on floodplains by number of floods over 15 years 1988–2003 (based on analysis of satellite image pixels) (adapted from Heinl et al. 2006)

analyzed in the Okavango Delta. Here, we consider the major effects on biota by comparing the effects of two major "natural experiments" on two seasonal floodplains. The first assessment involves the removal of macrophytes by fire in which we compare basic ecosystem properties in burned and un-burned habitats, while the second assessment is a flooding experiment where conditions during extremely high and very low flooding seasons are compared.

These kinds of natural experiments are of course not comparable with controlled experiments. Although

only two changes are made—(i) removal of macrophytes and detritus, and (ii) a switch from very low water levels to very high water levels (with consequent higher duration and greater extent of flooding), these drivers can lead to a number of ecosystem responses that may have cascading effects. Nevertheless, the nature of observed responses can provide some valuable insights to the basic ecological functions of the flooding-fire coupling and the importance of variability in the magnitude of flooding. In particular, large tropical and sub-tropical wetland systems often have considerable socio-economic importance. A better understanding of the interplay between the two major drivers of these ecosystem processes, namely flooding and fire, is a prerequisite for improved management of these important systems.

Methods

The study area

The study area along the Boro River (Fig. 1) has typical vegetation gradients caused by small differences in elevation which determine the duration of flooding (Bonyongo 1999). The permanent swamps along the river are dominated by *Phragmites australis* (Cav.) Steud. When the flood arrives in this area (usually in the period mid-May to mid-June), water extends out over the river banks and moves through a system of channels and small pools onto the floodplains. The deepest parts of the floodplains are characterized by floating leafy vegetation such as *Ludwigia stolonifera* (Guill & Perr.) P.H. Raven and *Nymphaea nouchali* Burm, and are kept open by habitual movements of hippopotamus. In slightly less deep water, almost mono-specific dense 1–1.5 m high stands of the sedge *Cyperus articulatus* L. exist. These two deepest zones are often flooded for 4–8 months. In the shallower areas, perennial grasslands with typical species like *Panicum repens* L. and *Paspalidium obtusifolium* (Delile) N. D. Simpson occur. These slightly elevated zones are usually flooded for 1–3 months and are often heavily grazed by large mammals. Between this raised area and the riparian woodland are stands of tall perennial grasses such as *Imperata cylindrica* (L.) Rueusch, which are inundated only during years with exceptionally high flooding. This typical zonation can be several hundred meters wide, yet occupy a total vertical depth gradient of only about one meter (Bonyongo 1999).

Since 1996, a number of studies within the study area have been undertaken, particularly on the two seasonal floodplains, Lechwe Floodplain and Phelo Floodplain. Both floodplains receive their water from the Boro River and their water chemistry is therefore similar. They have the same vegetation zonation and are on a similar substrate, Kalahari sand, which comprises the whole Delta, as well as the greater river basin, and is very homogenous. It is also a very nutrient poor substrate and the biota in rivers and the lagoons of the Delta can be described as oligotrophic.

In April 1998 a large fire swept through the southern part of the study area including the Lechwe, but not the Phelo, floodplain (Fig. 1) (Meyer 1999). Due to several preceding dry years, the fire was hot and consumed not only all the dry debris but also the green above-ground stands of *Cyperus articulatus*. As a result the whole floodplain was covered with a 1–4 cm ash layer and very few emergent macrophytes were present in the Lechwe Floodplain at the time of its next flooding. This next flood was relatively small (similar to the one experienced in 2003, ~0.1 km^2) and was confined to the deeper *Ludwigia* and *Cyperus* zones. The following year the typical vegetation zonation described previously was re-established in the Lechwe Floodplain, making it structurally similar to the un-burnt Phelo Floodplain and providing an opportunity to study the effect of fire on aquatic biota. It must be acknowledged, however, that differences in nutrient loading between the two floodplains exist, owing to differences in the input of fecal matter from grazing mammals that had favoured the Phelo Floodplain in previous years, as well as differences in dilution.

In 2003 a small flood event in the Phelo Floodplain extended only into the *Cyperus* zone and lasted for about six months. In this situation, all aquatic biota were confined to the small area of open water and the *Cyperus* habitat. The flooding the following year was much greater; it extended into the rarely flooded *Imperata* zone and lasted for ten months. A large, predominantly terrestrial area was flooded and became accessible to aquatic biota. These two years thus offered the opportunity to assess for effects of flooding size. A series of limnological studies were conducted on the Phelo Floodplain in 2003 and 2004, including studies on nutrient dynamics, primary and

secondary production, food web interactions, and methane dynamics (Lindholm 2006).

Sampling and analytical methods

Sampling was undertaken during three periods, (1) during rising water level at the end of May–June; (2) at peak water levels in July–August, and (3) during the receding flood in September–October. Water samples for analysis of total nitrogen, total phosphorus, chlorophyll *a* and zooplankton biomass were taken at five locations in the deepest open water pool-channel system from the inlet to the innermost part of the floodplains. Temperature and oxygen were measured in situ at these same locations to assess diurnal variations. Pelagic primary production was measured during 2003–2004 by the standard ^{14}C method. During the 1998 field work, fish fry were sampled at ten randomly selected sites in the *Panicum* zone, using a 1.33-m-diameter ring-net, with a floating top ring and a heavy metal ring at the bottom that was thrown out and emptied by a hand net. Fishing during the 2003–2004 floods was done with a standardized set of gillnets and the fish abundance calculated as catch per unit effort (CPUE). Standard analytical procedures were used throughout and are detailed in Lindholm (2006) and Lindholm et al. (2007). Macrophyte data on species composition and biomass were taken from Bonyongo (1999) and from Murray-Hudson

(unpublished), while water chemistry data for the Boro River, usually sampled fortnightly, were taken from environmental monitoring databases held within the Harry Oppenheimer Okavango Research Centre (HOORC) at the University of Botswana.

Results

Macrophyte and litter biomass

In 1997, the macrophyte biomass on Phelo Floodplain had a variation (between zones and sampling periods) of 36–570 g DW m^{-2}, but most data were between 200 and 400 g DW m^{-2} (Table 1). The *Cyperus articulatus* zone had the highest biomass on two sampling occasions and was closest in biomass to the *Imperata* zone. The peak biomass for the grasses usually occurred after the rainy season in the first half of March while the biomass of the more aquatic *Cyperus* zone peaked towards the end of the flooding season. The size of flooding can have a pronounced effect on the biomass production on floodplains; the difference in biomass density of *Cyperus* between a high and a low flood can be four fold (Murray-Hudson, unpublished). This causes a large variation in litter production not only between years but also within a single year, as flooding causes fast decomposition; as much as a 80% reduction in biomass has

Table 1 Mean elevation above bottom of Boro River (= 0 m), total phosphorous in flooded sediment and biomass (gram DW m^{-2}) for vegetation zones on Phelo Floodplain 1997 with the data from Bonyongo (1999), Bonyongo et al. (2000) and for *Cyperus* biomass and litter from various sources as indicated below. Biomass data from March represents likely maximum values at the end of the rainy-growth season, for june just before flooding and for November just after flooding

Vegetation zone	Elevation (m)	Flood duration weeks	Macrophyte biomass			Total P (mg kg^{-1})
			March gram DW m^{-2}	June gram DW m^{-2}	November gram DW m^{-2}	
Ludwigia	0.90[a]	23	–	–	–	21.12
Cyperus	1.19	16	430[b]	180[b]	570[c]	3.44
Panicum	1.61	9	255	165	36	5.99
Eragrostis	1.83	5	231	225	154	4.37
Imperata	2.20	0	421	401	316	4.52
Cyperus litter	–	–	–	1025[d]	205[d]	–
Cyperus litter	–	–	300[b]	360[b]	300[c]	–

[a] Derived by regression from table 4.1 in Bonyongo (1999)

[b] Year 2005 from M. Murray-Hudson (unpublished)

[c] Year 2004 from M. Murray-Hudson (unpublished)

[d] Year 2001 from Mladenov et al. (2007)

been recorded (Table 1). Noteworthy is that the total-P concentration in sediments is $4–5\times$ higher in the deepest part of the floodplain.

Effects of fire

Fires on floodplains in the Okavango Delta remove around 78% of the litter (Rutz, 2004) with a large variation dependent primarily on wetness and fuel load. The fire on Lechwe Floodplain occurred after a long drought of several years and was of high severity (DeBano et al. 1998). It burnt not only the litter but also the green stands of *Cyperus articulatus* and *Schoenoplectus corymbosus*, leaving only a 1–4 cm thick ash layer.

One key feature of such a fire is the mineralization of organic matter as it strongly affects oxygen dynamics. The diurnal oxygen saturation of the flood waters showed large differences between the burnt and the un-burnt floodplain (Fig. 4). The burnt Lechwe floodplain had a maximum oxygen saturation during midday between 160 and 200% and never fell below 100%, not even during the early morning diel minima, reflecting the high primary production and low respiratory activities of heterotrophs. The un-burnt Phelo Floodplain, on the other hand, had low oxygen saturation during the early morning
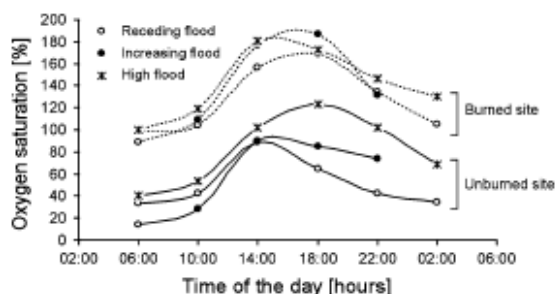
(10–40%) and reached super-saturation only on one occasion (during a high flood) in the day time. This reflected the low production-respiration ratio due to the high amount of decaying biomass and the resultant microbial respiration.

Total nitrogen and total phosphorus concentrations declined from the onset of the flood becoming asymptotic from the flood peak through the decline (Høberg et al. 2002). There was, however, no significant difference between the mean concentrations of these key nutrient elements between the burnt and un-burnt floodplains (Table 2). The P:N ratio by weight was close to the optimal of 1:7 for plants for both floodplains, suggesting that sources of N and P other than those from mineralized plant litter were more dominant.

The zooplankton community was completely dominated by pelagic filter feeding cladocera on both floodplains, and these showed a pronounced succession during the season. Immediately after arrival of the flood, *Moina micrura* occurred in very high numbers followed by *Ceriodaphnia* spp. that peaked at the end of June. In the second half of July, *Daphnia laevis* dominated and towards the end of the season there was a burst of *Chydorus* sp. There was no significant difference in the biomass of zooplankton between the

Fig. 4 Diurnal variation in oxygen saturation on the burnt Lechwe floodplain and un-burnt Phelo floodplain in 1998

Table 3 Zooplankton biomass and fish fry abundance on burnt Lechwe- and un-burnt Phelo floodplains as mean values during flooding year 1998

	Lechwe burnt (mg DW l^{-1})	Phelo un-burnt (mg DW l^{-1})
Zooplankton biomass (high water)	0.685	0.365
Zooplankton biomass (receding water)	0.004	0.008
Fish fry abundance (high water)	0.02	0.29

Table 2 Total-N and Total-P (mg l^{-1}) and P:N quotients by weight on Lechwe burnt and Phelo un-burnt floodplain, and high and low flood, as mean values for the entire flooding season

	Lechwe burnt	Phelo un-burnt	Phelo low flood	Boro River	Phelo high flood	Boro River
Year	1998	1998	2003	2003	2004	2004
Total-N	2.0	2.3	1.3	1.05	1.0	0.90
Total-P	0.20	0.29	0.4	0.072	0.009	<0.01
P:N	1:10	1:8.0	1:3.2	1:14.6	1:110	–

burnt and un-burnt floodplains (Table 3). The biomass was very high at the beginning of the flooding season (approaching 1 mg DW l^{-1}) and declined during the receding phase to between 2 and 20 µg DW l^{-1}, ≤2% of the maximum. In contrast to the other measured parameters, with the exception of oxygen, there appeared to be a significantly higher abundance (15×) of fish fry on the un-burnt floodplain (Table 3).

Effects of flooding and flood size

When dry litter is flooded it decays very fast. On Phelo's Floodplain, when the 2001 flood arrived on 17th May, there was a mean DW of 1025 gm^{-2} of litter that, after 3.5 months, had been reduced by 80% to 205 gm^{-2} (Table 1). Through microbial processes it was converted to dissolved organic carbon (DOC) of which 51% was further oxidized to CO_2, 26% infiltrated to groundwater, and 22% was lost through outflow which (unusually) occurred during this high flood year (Mladenov et al. 2007). In spite of these processes the concentration of DOC remained fairly similar during the flooding season with 10–15 mg C l^{-1}. A contributing reason for this, however, was that 65% of the DOC was introduced with incoming flood water from upstream sources.

The total-N concentration in Phelo Floodplain during the low flood year of 2003 and the high flood year of 2004 was similar (1.3 mg l^{-1} and 1.0 mg l^{-1}, respectively) for the whole season and appeared to not be significantly higher than the source Boro River water (see Table 2). The total-P concentrations on the other hand seemed very different with 0.4 mg l^{-1} in the first year, 7× higher than the total P concentration in the Boro River. However, during the high flood year, the total-P concentration was as low as 0.009 mg l^{-1} on the floodplain and was consistently below 0.01 mg l^{-1} in the Boro River. This has a pronounced effect on the P:N quotients that were 1:3.2 and 1:110, respectively, for the two years.

Discussion

Fires

The fire on Lechwe Floodplain in 1998 seemed not to have had any effect on the concentrations of total-N and total-P in floodplain waters. The nitrogen in the litter and within *Cyperus* stands probably volatilized at the high temperatures that prevailed as indicated by the formation of a thick ash layer (DeBano et al. 1998). This did not result in lower nitrogen levels in the water and supported the idea that nitrogen fixation alone is usually sufficient to keep the P:N ratio around the optimal of 1:7.

The removal of macrophytes and litter by fire caused a significant increase in oxygen levels (Fig. 4). The litter accumulation, by lowering oxygen levels, may have a number of effects on water quality by affecting both the solubility of phosphorus and the de-nitrification process. For higher trophic levels, however, the elevated oxygen levels might be a disadvantage. For example, some species of fish fry avoid predation by tolerating low oxygen levels (Kolding 1993). The saturated oxygen concentrations might have made the floodplain more accessible for ambush predators allowing them to remain during the night and feed effectively the whole day. The lack of protective macrophyte refugia on the burnt floodplain may make the fish fry even more exposed as discussed below.

Flooding

All water supplied to the floodplains was provided by the Boro River which typically has a low concentration of nutrients of around 1.0 mg l^{-1} for total-N and 0.07–0.01 mg l^{-1} for total-P (Table 2). These data were similar to those from Cronberg et al. (1996) for the years 1991–1992 for the Boro river, with a mean concentration of the inflow being 0.36 mg total-N l^{-1} and 0.023 mg total-P l^{-1} and the outflow being 1.12 mg total-N l^{-1} and 0.055 mg total-P l^{-1}. In 1999, when the HOORC started analyzing total-P in the Boro River, the mean value was 0.039 mg l^{-1} and was thus very similar to the earlier values. The total-N concentrations for 2003 and 2004 were close to those in the Boro River. On the other hand, the total-P values, with exception of Phelo Floodplain in 2004, were 20–50 times higher than those in the river. As the turnover time for water on Phelo Floodplain was only 5–6 days and about 80–90% of the inflow infiltrated to the groundwater (Ramberg et al. 2006), the high values cannot be caused by evaporative concentration alone. There must be other processes on the floodplains that cause an enrichment of

phosphorous, as commonly seen in many wetlands (Mitsch and Gosselink 2007). This may be caused by dissolution from the wetted sandy soils. Noe and Hupp (2007) found large releases of N and P on flooding in a short-hydroperiod floodplain. If this is the case, then these soils must have a considerable storage capacity, as suggested by Mubyana et al. (2003) who showed that dry-land top-soils in the Delta had available P concentrations around 0.1%, while floodplains had considerably higher concentrations of 0.6–1.0%. After the flood in March, these decreased to about 0.1% (op. cit.). It may be calculated that this loss from the sediment, if all dissolved at once, could cause an increase of total-P in the water up to 1.8 g l^{-1} and could thus readily explain the observed initial high total-P values in floodplain waters. The release of phosphorous when the water arrives might be triggered by development of anoxic conditions in accordance with the Mortimer process (Pearsall and Mortimer 1939). This could also explain the low total-P concentrations on Phelo Floodplain (around 0.01 mg l^{-1}) during the whole high flood year of 2004. During that time, the high water levels and extensive open-water areas might have caused better mixing of the water column and prevented anoxia from developing. In addition, the low concentrations might simply be the result of both dilution by the Boro River, which had consistently low total-P levels (below 0.01 mg l^{-1}), and the fact that soils on higher ground have low concentrations of available phosphorous (Mubyana et al. 2003) which, when flooded, contribute little to the concentration in water.

The P:N ratio was usually above the optimal 1:7 (Table 2) indicating that in general, the floodplains were predominantly P limited with the exception of Phelo Floodplain during the low flood year of 2003, which seemed to have been nitrogen limited for the whole season. This was in contrast to Ogden et al. (2007), who found that N was limiting in a large semi-arid floodplain in Australia. In their situation, however, the catchment geology contained rocks with high to moderate concentrations of P. The siliceous Kalahari sands, which comprise the catchment and Delta of the Okavango, are very nutrient poor (Mubyana et al. 2003). An unknown factor here is the extent of denitrification. Anoxic conditions were likely, as there was a considerable production of methane within the decaying litter during 2003 but

not 2004 (Lindholm et al. 2007). It is, therefore, likely that denitrification was a significant process, as it occurs at a considerably higher redox potential than methanogenesis (e.g., Wetzel 2001).

The importance of macrophytes for protection against predators, as previously alluded to, is also illustrated in an assessment of flood sizes. During the high flood year, the pelagic primary production was much reduced to only 42% of that during the low flood year, while zooplankton production was down to only 1%. Conversely, the fish abundance during the low flood year was only 35% of that during the high flood year, although zooplankton are the most important nutrient source for fish fry on the floodplain (Lindholm 2006). The high flood is likely to have caused a dilution effect on prey. During both years, emergent macrophytes occurred over the entire flooded area, but the available habitat area during the high flood was three times larger that of the low flood year (Fig. 2). During the high flood year, small fish occurred everywhere in abundance, even close up to the water's edge among the perennial grasses. The floodplain habitat for fish was therefore much larger and fish predators could not use the advantages of prey congestion. Habitat shortage is an important factor in fish egg survival (Hilborn and Walters 1992). The positive relationship between fish yield and flood size for African floodplain fisheries (Welcomme 1979) also seems to pertain in the Okavango Delta. Most of the fish predators are also large: fishes like *Clarias* spp., fish-eating birds of which there are more than 40 species in the Delta, as well as otters and crocodiles. They have long life cycles in comparison with their prey, however, and cannot respond through a rapid increase in reproduction to the sudden outbursts of food availability.

Years of low flood events on un-burned floodplains imply high abundance of decaying plant litter and thus low oxygen levels. This, in turn, promotes methane production and has at least two important implications. Firstly, methane emissions are likely to make this huge delta area a significant source of atmospheric methane. Secondly, as revealed by stable isotope studies (Lindholm 2006; Lindholm et al. 2007), methane may be a significant source of carbon for the aquatic food web via methanotrophic bacteria being consumed by the dense biomass of filter-feeding cladocerans—that also serve as an important food source for fish fry.

Synthesis and conclusions

Seasonal floodplains of the Okavango Delta are subject to limnological extremes, which are unpredictable and vary in timing and magnitude from one year to the next. Low and high oxygen concentrations, low and high nutrient concentrations and low and high predation on fish and fish fry are driven by these variations (Table 4). While the year-to year predictability is very low in such systems, some local processes provide an element of stability to keep the system within certain boundaries. This is most likely a function of the soil-sediment matrix. During dry periods rhizomes and long lived seeds are stored and protected, together with the resting stages of bacteria, algae and zooplankton. These soils have also a considerable phosphorous and organic content that, when flooded, turns more or less anaerobic facilitating nitrogen fixation and the dissolution of phosphorus. The seed bank and resting stages respond immediately on the flooding and the aquatic biota are re-established within a very short time (Lindholm and Hessen 2007). The biodiversity therefore remains fairly similar between years in terms of aquatic macrophytes and zooplankton.

The synergism between flooding and fire on the seasonal floodplains is expressed in several ways. High flooding frequency causes a higher fire frequency up to a certain level. Fires reduce anaerobic processes and limit heterotrophic food chains. This results in high oxygen concentrations in the water, which affects nutrient cycling, in particular of phosphorous. In addition, fires make these floodplains accessible to organisms with high oxygen demand. Fires also result in a low abundance of fish fry, to a certain extent irrespective of hydroperiod. Most fires are caused by humans (Heinl et al. 2006) and occur probably with much higher frequency than natural, and this might have long term effects on Delta biodiversity and productivity.

However, the amount of seasonal flooding has a larger ecosystem impact than fires and is the primary factor in the wetland's productivity It is not only decisive for the frequency of subsequent fires but also has a much larger effect than fire on nutrient accumulation and mobilization. This view is consistent with other studies that demonstrate, through artificial fire experiments on floodplains, that flooding is the primary factor which determines plant species composition (Ishida et al. 2008).

It seems the seasonal floodplains have a considerable ability to accumulate phosphorous, the main limiting nutrient in the Delta. Phosphorous is brought into the floodplains by the seasonal flood. It is assimilated by aquatic biota and then stored during the dry phase in the soil-sediment matrix, except for that which is found in perennial semi-aquatic grasses and that used by herbivores during this period. It is the switching between aerobic and anaerobic conditions that accumulates and releases phosphorous. Permanently dry or permanently wet conditions will not create these dynamics. Likewise, changes in flooding regimes which cause more stable hydrological conditions with more semi-permanent or permanent swamps will increase accumulation of litter, promote lower oxygen levels, increase denitrification rates, and cause nitrogen limitation in both terrestrial and aquatic phases. These two processes (phosphorus accumulation in the sediment and dissolution; organic matter accumulation and decomposition) are in essence probably the most important consequences of the flood pulse (sensu Junk et al. 1989) in the Okavango Delta.

These seasonal floodplains seem to be subject to intermediate disturbance (sensu Connell 1978) where

Table 4 General characteristics of aquatic ecosystems on seasonal floodplains after fire, low-, and high floods

Attribute	Fire	Low flood	High flood
P:N ratio	Balanced	N limitation	P limitation
Oxygen saturation	Very High	Low	High
De-nitrification	Low	High	Low
Dominant food chains	Autotrophic	Heterotrophic	Autotrophic
Pelagic primary production	High	High	Low
Zooplankton production	High	High	Low
Fish production	Very Low	Low	High

both terrestrial and aquatic life forms can co-exist under temporal separation, and which provide for greater productivity on an annual basis and in the long run (Lindholm et al. 2009). They have a specific identity in the Okavango landscape. Thus, there is a close link between nutrient dynamics and productivity in both the terrestrial and aquatic phases of floodplains that are likely to be decisive for the total aquatic and terrestrial productivity of the Delta. These dynamically integrated parts should therefore be managed together, which is a challenge in a country like Botswana where management of water, wetlands, and dry lands is guided by fragmented legislation under the administration of different government ministries.

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