

**Aquatic ecosystem responses to fire and flood size in the Okavango
Delta - Natural experiments on seasonal floodplains**

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Abstract

The frequency of fires in the Okavango Delta is positively correlated with the frequency of flooding and floodplains are commonly burnt each 3-5th year. A burnt seasonal floodplain in the aquatic phase had oxygen levels well above saturation 100-200%, while the levels in the un-burnt control were below saturation and during night could go down to 10-40% saturation. The total phosphorous and total nitrogen concentrations were about the same on both floodplains and considerably higher than in inflowing water.

Zooplankton biomass was very high but there was no significant difference between the two systems while the abundance of fish fry was 10 times higher on the un-burnt floodplain. Sub sequent during a low flood year the un-burnt floodplain water had very high nutrient levels, high primary production, high methane emission and high uptake; and a high zooplankton biomass. The very high flood the following year was basically opposite with much lower levels of all these parameters. The abundance of fish was however much higher during the high flood year. Macrophytes and litter provide direct shelter for fish fry as well as through low oxygen levels, while large flooded areas cause high fish production by removing obstacles related to congestion. Compared to inflowing water the seasonal floodplains had usually 20-50 times higher total phosphorous concentrations, in all likelihood released from the flooded soil-sediment. This mechanism may be crucial for the maintenance of high biological productivity both in the aquatic and terrestrial phase, in a very nutrient poor wetland landscape.

Key words:

Seasonal floodplain, fire, flood pulse, Okavango Delta, nutrients, zooplankton biomass,
fish productivity

Introduction

Emergent aquatic macrophytes, usually aquatic grasses and sedges, visually often dominate the environment where they grow due to their height and density. Large numbers of studies have been done (e.g. Graig et al. 1991, Ellery et al. 1993, Grosshans and Kenkel 1997, Bragazza and Gerdol 1999, Bonyongo et al. 2000, Seabloom and van Der Valk 2003, Koning 2005, Meringliano 2005, Lenssen et al. 2006) on their aut-ecology, on their successions and zonations, as indicators and for the typology of wetlands, but less on their role for aquatic biota that are in one way or another depend on them. They have usually a high biomass with a high growth rate and a fast turnover of biomass that result in large amounts of dead leaves and stems in various stages of decomposition often forming a peaty substrate. They have therefore the potential to significantly modify the aquatic environment (Wetzel 2001, Mitsch and Gosselink 2007) in many ways. First they may remove nutrients from the water and store it for long time periods and by that (out)-compete phytoplankton and attached algae. They also create a shady aquatic environment that is less favorable for phytoplankton and attached algae.

The large production of dead organic matter may under its decomposition cause high bacterial production and thus favor detritus-based heterotrophic food chains which subsequently will reduce oxygen saturation in the sediment and water. The stems and leaves of live and senescent plants also form a substrate for attached aquatic life such as periphytic algae and a range of heterotrophic organisms that explore this habitat for

food and shelter (crustaceans, mollusks, insect larvae). Plants thus provide them with a much larger substrate area than would otherwise be available. Finally the dense stands of aquatic plants provide structural complexity to the aquatic habitat, which protects against predators but can also be used as hideouts by predators.

In the Okavango Delta fires are very common. Heinl et al (2006) and Heinl et al (2007) analyzed satellite images for a 6100 km² area of the southern Okavango Delta over a 15 year period 1998-2003 and showed that the fire frequency was very low on dry land; none or one fire over the study period, while the floodplains had been burnt from two up to ten times during the same period. On floodplains there was also a positive correlation between mean frequency of flooding and the frequency of fires up to a level of seven flooding years and three fires (Fig. 1) after which the fire frequency dropped. 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 for fire frequency (Heinl et al. 2006): fire is less likely where flood frequency is greater than seven years in fifteen because the increased wetness reduces the possibility of burning. The high fire frequency in the Okavango Delta seems to be typical for many large tropical and sub-tropical wetlands in the world such as Kakadu in Northern Australia, Pantanal in South America and the Everglades in Florida. The fires will temporarily remove the grass-sedge-litter matrix and by that fundamentally affect physical conditions like O₂-saturation, nutrient fluxes and productivity, habitat structure and thus the entire ecosystem properties during flooding as outlined above.

The coupling between flooding and fire frequency on floodplains means that during a period of increased flooding caused by either higher inflow or by a shift in flood distribution (Ellery et al 2003, Wolski and Murray-Hudson 2006) there will be dramatic shifts in life conditions for all kinds of aquatic biota. With increased flooding frequency there will be more buildup of macrophyte biomass each season but also larger chances that it will burn during the dry season. From year to year this may cause large shifts in the magnitude of autotrophic and heterotrophic processes and dependent food chains, up to a point when the flooding frequency and wetness becomes too high for fires. Then there will be a continuous buildup of detritus from year to year and more heterotrophic conditions will prevail for longer periods. Overlaid on this pattern come the large variations in flooding from year to year in the Okavango Delta that might be typical for wetlands in the sub-tropics around the Tropics of Cancer and Capricorn, where the amount of rainfall has very large variability.

The consequences on aquatic biota of these coupled flooding-fire sequences have not been studied in the Okavango Delta. Here we will try to piece together a likely picture of major effects on biota by assessing comparative studies on the effects of two major “natural experiments” on two seasonal floodplains. The first trial is a removal experiment of macrophytes by fire where we compare basic ecosystem properties in burned and unburned habitats, while the second trial is a flooding experiment where conditions during an extremely high flooding season are compared with a very low one.

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 extent of flooding extension) these can lead to a number of ecosystem responses as outlined above and have cascading effects. Nevertheless, the kind of observed responses and their magnitude can give valuable insights about the basic ecological functions of the flooding-fire coupling and the importance of variability in the magnitude of flooding. In particular in the large tropical and sub-tropical wetland systems, with considerable socio-economic importance such as the Okavango Delta, and where these ecosystem interactions are poorly known, a better understanding of them can be of great importance for management and conservation.

Methods

The study area

In most years the seasonal flooding in the Okavango Delta, which usually lasts for 3-6 months, is caused by a pulse of high water flow in the inflowing Okavango River that results from rainfall on the Angola highlands during the period November – February and arrives at the Delta inlet in the period January – March after which it moves as a slow wave across the wetland landscape until it reaches the distal parts in July. Occasionally however, heavy rainfall over the Delta itself (such as in beginning of years 2000 and

2008) can cause early flooding of plains in January – March. The seasonally flooded area varies from a minimum of 6000 km² to a maximum (flooded at least once in a decade) including permanent swamps and islands of 14 000 km² (Gumbrecht et al. 2004). Due to shifts in flooding distribution over time periods of decades and decennia the Okavango Delta with typical features such as flood plains and islands is about 28 000 km² (Ramberg et al. 2006).

While the flooding between years on the Delta scale can vary by a factor of 2, individual floodplains can experience a much larger relative variation. In the study area (Fig. 2) during the 12 year period 1996 – 2007 Phelo Floodplain has low floods covering about 0.1 km² in the years 1996, 1998 and 2003 while the maximum is more than 0.4 km² in 2004.

The study area along the Boro River (Fig. 3) has typical vegetation gradients caused by small differences in elevation that in turn determines the duration of flooding (Bonyongo 1999). The permanent swamps along the river are dominated by *Phragmites australis* (Cav.) Steud. When the flood arrives in the area usually in the period mid-May to mid-June it flows over the river banks and moves through a system of channels and small pools into the floodplains. These deepest parts of the floodplains are kept open by habitual movements of hippopotamus and have floating leaved vegetation such as *Ludwigia stolonifera* (Guill.&Perr.) P.H. Raven and *Nymphaea nouchali* Burm. On

slightly shallower water follows dense stands, almost mono-specific, of the sedge *Cyperus articulatus* L. 1-1.5 m high. These two deepest zones are often flooded for 4-8 months. Then follow perennial grasslands with typical species like *Panicum repens* L. and *Paspalidium obtusifolium* (Delile) N. D. Simpson. This zone on slightly higher elevation is usually flooded for 1-3 months and is often heavily grazed by large mammals. Between this area and the riparian woodland are stands of tall perennial grasses such as *Imperata cylindrical* (L.) Rueusch. that are flooded only during years with exceptional high flooding. This typical zonation that can be several hundred meters wide occupies a total vertical depth gradient of about one meter (Bonyongo 1999).

In the study area a number of studies have been done since 1996 on the two seasonal floodplains, Lechwe Floodplain and Phelo Floodplain. Both floodplains receive their water from Boro River and their water chemistry is therefore similar. They have the same vegetation zonation as described above and are on similar substrate- Kalahari sand – that makes up the whole Delta as well as the river basin and is very homogenous. It is also a very nutrient poor substrate and the biota in rivers and the lagoons in the Delta is in limnological terms oligotrophic.

The comparative studies

In April 1998 a large fire swept through the southern part of the area including the Lechwe Floodplain but not Phelo Floodplain (Meyer 1999). Due to several very dry years the fire was very hot and consumed not only all dry debris but also the green above

ground stands of *Cyperus articulatus* and the whole floodplain was covered with a 1-4 cm ash layer. During the following flooding this floodplain had practically no emergent macrophytes. The flooding this year was small, similar to 2003 (Fig. 2 and 3) and was confined to the *Ludwigia* and *Cyperus* zones. (The following year the typical vegetation zonation described above was re-established). By comparing it with Phelo Floodplain this gave us an opportunity to study the effect of fire on aquatic biota.

Fairly intense limnological studies were done on Phelo Floodplain in 2003 and 2004 (Lindholm 2006). The first year the flooding was small, went only into the *Cyperus* zone and lasted for about six months. In this situation all aquatic biota was confined to the small area of open water and the *Cyperus* habitat. The flooding the following year was very big and went up into the rarely flooded *Imperata* zone and lasted for ten months. A large predominantly terrestrial area was flooded and became accessible for aquatic biota.

Sampling and analytical methods

Sampling was done during three periods; at rising water level in end of May – June; at peak water levels in July – August and during receding flood in September –October.

Water samples for analysis of total N, total P, chlorophyll and zooplankton biomass were taken on five stations in the deepest open water pool-channel system from the inlet to the innermost part of the floodplains. Temperature and oxygen were measured to assess diurnal variations on the same sites *in situ*. Pelagic primary production was measured

2003-04 by the standard C-14 method. During the 1998 campaign, fish fry were sampled on ten randomly selected sites in the *Panicum* zone with a ring-net 1.33 m in diameter 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 2003-04 floods was done with a standardized set of gillnets and the fish abundance calculated as CPUE. Standard analytical procedures were used throughout; for details see Lindholm (2006) and Lindholm et al. (2007).

Macrophyte data on species composition and biomass are taken from Bonyongo (1999) and from Murray-Hudson (unpublished) while water chemical data for the Boro River, usually sampled fortnightly, are taken from HOORC environmental monitoring databases.

Results

Macrophyte and litter biomass

The macrophyte biomass on Phelo Floodplain year 1997 has a variation between zones and sampling periods from 36 to 570 g DW m⁻² but most data are between 200-400 g DW m⁻² (Table 1). The *Cyperus articulatus* zone has usually the highest biomass but the difference with the *Imperata* zone is small. The peak biomass for the grasses usually occurs after the rainy season in first half of March while the more aquatic *Cyperus* zone

peaks towards the end of the flooding season. As indicated above the size of flooding has a pronounced effect on the biomass production on floodplains and the difference in biomass of *Cyperus* between a high and a low flood can be four fold (Murray-Hudson unpublished). This will cause a large variation in litter production not only between years but also within a single year as flooding causes a fast decomposition; as much as an 80% reduction (Table 1). Noteworthy is that the Total-P concentration in sediments is 4-5x higher in the deepest part of the floodplain.

Effects of fire

Fires on floodplains in the Okavango Delta remove as a mean 78% of litter (Rutz 2005) with a large variation dependent primarily on wetness and fuel load. The fire on Lechwe Floodplain occurred after a several year long drought and was of the high severity kind (DeBano et al. 1998). It burnt not only the litter but also the green stands of *Cyperus articulatus* and *Schoenoplectus corymbosus* leaving only an ash layer 1-4 cm thick.

The diurnal oxygen saturation showed large differences between the burnt and the un-burnt floodplain (Fig. 4). The burnt Lechwe floodplain had maximum oxygen saturation during midday between 160 and 200% and was never under 100%; not even during early morning reflecting high primary production and low respiratory activities from heterotrophs. The un-burnt Phelo Floodplain on the other hand had very low oxygen saturation, 10-40% during early morning and it was, with one exception, never above 100% during day time reflecting a low production:respiration ratio.

Total N and total P declined from the onset of the flood becoming asymptotic throughout the flooding period (see Hogberg et al. 2002). There is however no significant difference between the mean values for both elements for the burnt and un-burnt floodplains (Table 2). The P: N ratio by weight is close to the optimal of 1: 7 for plants (eg. Wetzel 2001) for both floodplains.

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 in end of June. In second half of July *Daphnia leavis* dominated and by the end of the season there was a burst of *Chydoris sp* (Lindholm 2006). There was no significant difference in the biomass of zooplankton between the burnt and un-burnt floodplains (Table 3). It was very high in beginning of the flooding season approaching 1 mg DW l⁻¹ and declined during the receding phase to 2% or less (2-20 µg DW l⁻¹).

In contrast to the other measured - apart from oxygen – there was a significantly higher abundance (15x) of fish fry on the un-burnt floodplain (Table 3).

Effects of flooding and flood size

When the dry litter is flooded it decays very fast. On Phelo Floodplain there was as a mean 1025 DW gm⁻² of litter when the flood arrived on 17th May 2001 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 CO₂, 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 DOC was introduced with incoming flood water from upstream ecosystems.

The total N concentration in Phelo Floodplain the low flood year 2003 and the high flood year 2004 was similar, 1.3 mg l⁻¹ and 1.0 mg l⁻¹ as means for the whole season (Table 2) and is not significantly higher than from the Boro River from where the water is coming. The total P concentrations on the other hand were very different with 0.4 mg l⁻¹ the first year, which is 7x higher than in Boro River. During the following high flood year on the other hand total-P was as low as 0.009 mg l⁻¹ on the floodplain and consistently below 0.01 mg l⁻¹ in Boro River. This has pronounced effects on the P: N quotients that are 1: 3.2 respectively 1: 110 for the two years.

Discussion

All water to the floodplains is supplied by the Boro River and has low concentration of nutrients, for total-N typically around 1.0 mg l^{-1} and for total-P $0.07\text{-}0.01 \text{ mg l}^{-1}$ (Table 2). These data are similar to data from Cronberg et al (1993 table 13) for years 1991-92 for Boro river with mean for inflow of $0.36 \text{ mg total N l}^{-1}$ and for outflow $1.12 \text{ mg total N l}^{-1}$ and for total P 0.023 respectively 0.055 mg l^{-1} . For year 1999 when HOORC started analyzing total P in Boro River the mean value is 0.039 mg l^{-1} and thus very similar to the earlier values. The total N concentration on both floodplains year 1998 are about twice as high as the likely concentration in Boro River while the values for 2003 and 2004 are close to those in the river. Similarly the total P values, with exception of Phelo Floodplain 2004, are 20-50 times higher than in Boro River. As the turnover time for water on Phelo Floodplain is only 5-6 days and about 80-90% of the inflow infiltrate to the groundwater (Ramberg et al 2006) the high values cannot be caused by evaporative concentration. There must be processes on the floodplains that cause an enrichment of both nitrogen and phosphorous.

The significantly higher total P on floodplains, 7-20-50x, as compared to Boro River for both floodplains in 1998 and on Phelo Floodplain in 2003 can perhaps only be caused by dissolution from the wetted soils that if this is the case must have a considerable storage capacity. This has been shown by Mubyana et al (2003) for soils in the study area. While dry land top soils had available P concentrations around 0.1% floodplains had

considerably higher concentrations: 0.6-1.0% before the flood in March, which after flooding decreased to about 0.1%. It can be calculated that this loss from the sediment could cause an increase (if all dissolved at once) of total P in water to 1.8 g l^{-1} and thus readily explain the observed high total P values in floodplain waters. Losses to groundwater and a gradual dissolution process explain the lower observed values. The release of phosphorous when the water arrives might be triggered by development of anoxic conditions in accordance with the classic Mortimer process. 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. The high water levels and extensive open water areas might have caused better mixing of the water column and prevented anoxia from developing. Another explanation is simple dilution by Boro River water that this year had consistently very low total P levels (below 0.01 mg l^{-1}) and that the soils on higher ground as shown by Mubyana et al (2003) had very low concentrations of available phosphorous. This is somewhat surprising as the flooding of terrestrial river valleys caused by constructed dams, such as Lake Kariba on the Zambezi River (and not far from the Okavango), usually have an eutrophic first phase caused by leaching of accumulated nutrients from the inundated soils (Balon and Coche 1974). In the Okavango situation this is not the case probably because the time from one high flood to the next is too short for substantial nutrient accumulation to happen, or that the nutrients are stored in vegetation and not readily leached, similar as the case in tropical forests.

The fire on Lechwe Floodplain 1998 seems not to have had any effect on the concentrations of total-N and P in floodplain waters. The nitrogen in the litter and *Cyperus* stands probably volatilized at the high temperatures that must have prevailed as indicated by the formation of a thick ash layer (DeBano et al 1998). This did not cause any lower nitrogen levels in the water and supports the probability that nitrogen fixation usually is sufficient to keep the P: N ratio around the optimal 1:7. The exception is Phelo Floodplain during the low flood year 2003, which seems to have been nitrogen limited the whole season. An unknown factor here is the extent of de-nitrification. Anoxic conditions are likely as there was a considerable production of methane year 2003 but not 2004 (Lindholm 2007), probably produced in the decaying litter. It is therefore likely that de-nitrification came into play as well, as this process occurs at considerably higher redox potential than methanogenesis (eg Wetzel 2001 pg 639). As the total N concentration both years 2003 and 2004 is similar this suggests that both nitrogen fixation and de-nitrification were higher 2003 than 2004 and resulted in a low P: N ratio indicating nitrogen limitation. Next year however the situation was the opposite with phosphorus limitation that in this case was caused by extremely low total P concentrations for reasons discussed above.

It seems clear that removal of macrophytes and litter by fire causes a significant increase in oxygen concentration (Fig. 3). The function of macrophyte produced litter can in this regard, by lowering oxygen levels, have a number of effects, in this environment both on the solubility of phosphorus and on de-nitrification. At higher trophic levels however the

high oxygen levels might have been a disadvantage for example for fish fry which avoid predation by tolerating low oxygen levels (Kolding 1993). This might have made the burnt floodplain more accessible for predators where they could stay also during night and feed effectively the whole day. The lack of protective macrophyte refugia on the burnt floodplain made the fish fry even more exposed.

The importance of macrophytes for protection against predators is also illustrated in the flood size experiment. During the high flood year the pelagic primary production was only 42% and the zooplankton biomass 1% of that during the low flood year. Although zooplankton is the most important fish food on the floodplain (Lindholm 2006), the fish abundance during the low flood year was only 35% of that during the high flood year. The high flood is likely to cause a dilution effect on prey; during both years there were emergent macrophytes over the whole flooded area and the area during high flood was three times larger than during the low flood year (Fig. 2). During the high flood year small fish occurred everywhere in abundance up to the waters edge among perennial grasses. The floodplain habitat for fish was thus 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) as well as for African floodplain fisheries where there is a positive relationship between fish yield and flood size (Wellcomme 1979) as also seems to be the case in the Okavango Delta. Most of the fish predators are also large; with fishes like *Clarias spp.*, fish-eating birds of which there are more than 40 species in the Delta and otters and crocodiles. They have in comparison with their prey long life

cycles and cannot respond through increase in reproduction to sudden outbursts in food availability.

Seasonal floodplains in the Okavango Delta are thrown in an unpredictable way between environmental extremes from one year to the next. Low and high oxygen concentrations, low and high nutrient concentrations, low and high predation on fish and fish fry are driven by these variations (Table 5). Hence the year-to year predictability is very low in such systems that resemble chaotic systems yet with some local stability that keeps the system within certain boundaries. This is probably mainly a function of the soil- sediment matrix. During dry periods rhizomes and long lived seeds are stored here and protected as well as 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 dissolution of phosphorus. The seed bank and resting stages respond immediately on the flooding as well and the aquatic biota is re-established within a very short time. The biodiversity is therefore fairly similar between years when it comes to for instance aquatic macrophytes and zooplankton. The seasonal floodplains seem to be ecosystems under intermediate disturbance *sensu* Connell where both terrestrial and aquatic life forms can exist and provide for great productivity in the long run. They have thus a specific identity in the Okavango landscape.

From a management perspective it seems as if a single fire has small effects on nutrient dynamics but frequent fires might reduce the organic content of the soil/sediment matrix and by that in the long run causes a decline in productivity. In addition fires seem to be directly detrimental for fish productivity. Both these results require further corroboration but if confirmed it might be wise to try to restrict floodplain fires. In particular as most are man-made (Heinl et al 2006) and occur probably with much higher frequency than otherwise.

It seems clear that the seasonal floodplains have a considerable ability to accumulate phosphorous, the main limiting nutrient in the Delta. Nitrogen can usually be produced in sufficient quantities by nitrogen fixation as long as the seasonality of flooding is maintained. Phosphorous is brought into the floodplains by the seasonal flood, assimilated by aquatic biota and then stored during the dry phase in the soil-sediment matrix, except what is found in perennial semi-aquatic grasses and used by herbivores during this period. It is the switches between aerobic and anaerobic conditions that accumulate and release phosphorous. Permanently dry or permanently wet conditions will probably not create this dynamic. Likewise changes in flooding regimes that cause more stable hydrological conditions with more semi-permanent or permanent swamps will increase accumulation of litter: - lower oxygen levels – increase de-nitrification – and cause nitrogen limitation in both terrestrial and aquatic phases. This is in essence the probably most important consequence of the flood pulse *sensu* Junk et al (1989) in the Okavango Delta. The seasonal floodplains are therefore the generators of biological

productivity. In a very nutrient poor wetland landscape the processes that create such nutrient rich hot spots are important to understand because they don't only create high productivity in the aquatic phase but during the dry season they are important grazing areas for large mammals. In conclusion there is a very close link between nutrient dynamics and productivity in the terrestrial and aquatic parts of the Delta, meaning that these dynamically integrated parts of the Delta always should be studied and managed together.

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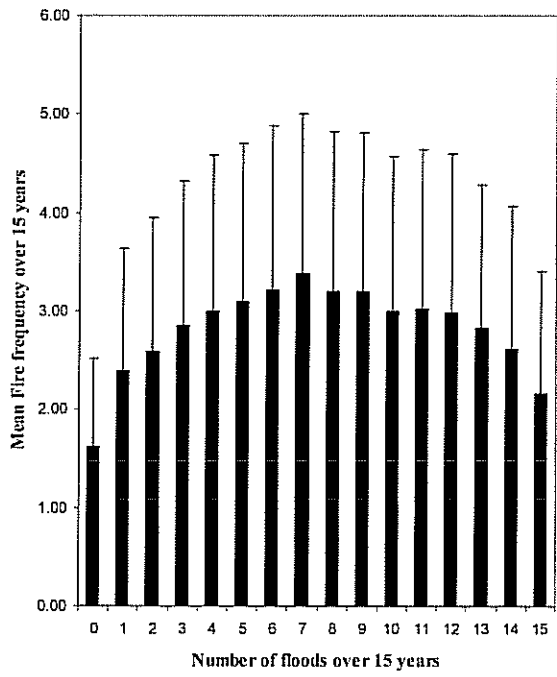
Figures

Fig. 1. Mean fire frequency in floodplains by number of floods over 15 years (based on analysis of satellite image pixels).

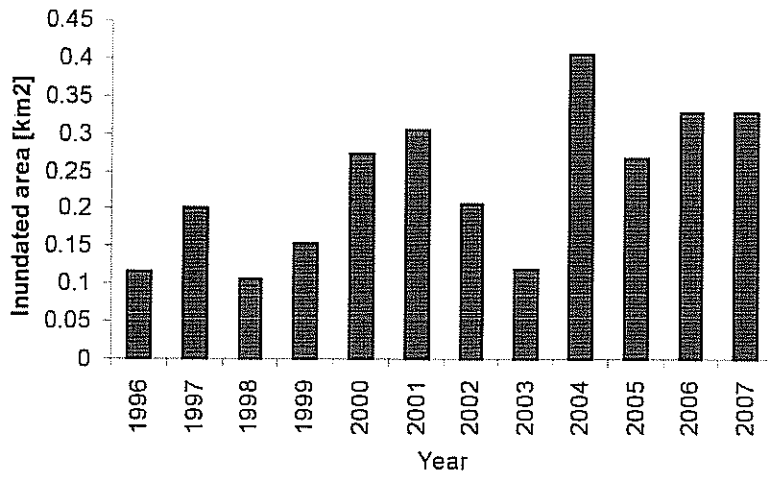
Fig. 2. The study area with the extent of the low flood 1998 and 2003 and the high flood 2004.

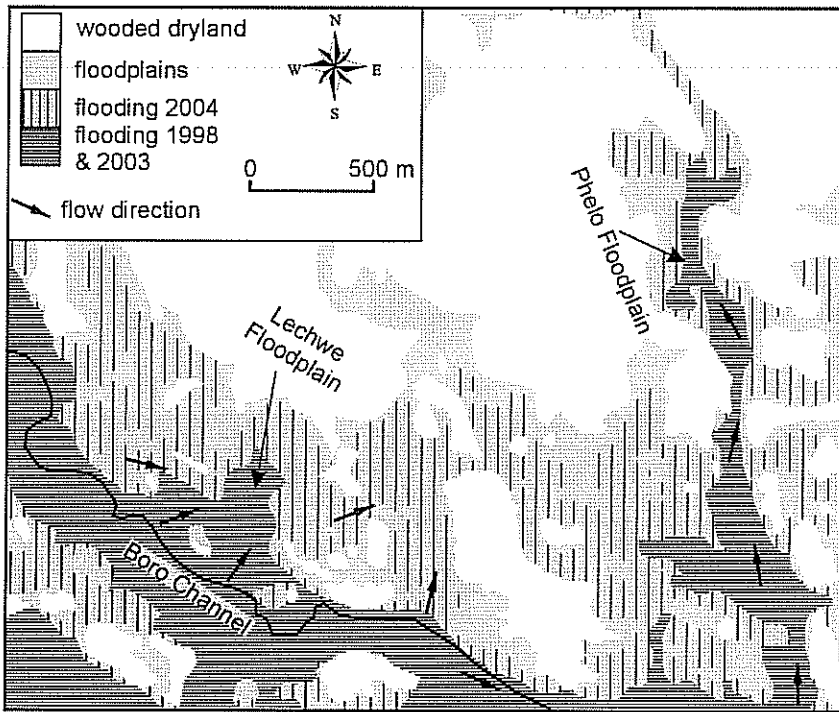
Fig. 3. Maximum annual flooded area 1996-2007 on Phelo floodplain.

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



Phelo's floodplain inundation





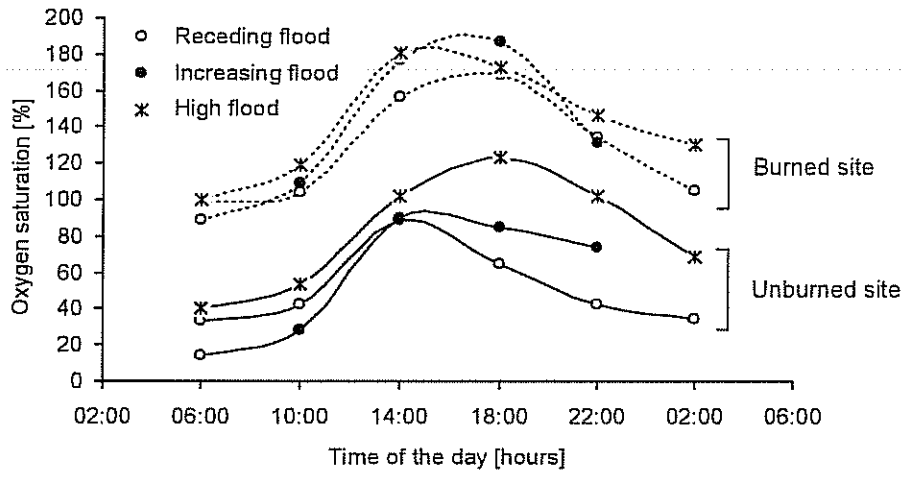


Table 1. Mean elevation above bottom of Boro River (= 0m), total phosphorous in flooded sediment and biomass (gram DW m⁻²) for vegetation zones on Phelo Floodplain 1997 with the data from Bonyongo (1999) and for Cyperus biomass and litter from various sources as indicated below. Biomass data from March 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	Flooding weeks	March	June	November	Total P mg kg ⁻¹
Ludwigia	0.90 (1)	23	-	-	-	21.12
Cyperus	1.19	16	430 (2)	180 (2)	570 (3)	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 (4)	205 (4)	
Cyperus litter			300 (2)	360 (2)	300 (3)	

(1). Derived by regression from table 4.1 in Bonyongo (1999).

(2). Year 2005 from M. Murray-Hudson (unpublished).

(3). Year 2004 from M. Murray-Hudson (unpublished).

(4). Year 2001 from Mladenov et al. (2007).

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 whole flooding season.

	Lechwe burnt	Phelo un-burnt	Phelo low flood	Boro River	Phelo high flood	Boro River
Year	1998	1998	2003	2003	2004	2004
Tot. N	2.0	2.3	1.3	1.05	1.0	0.90
Tot. 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	

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

	Lechwe fl. pl. Burnt (mg DW l ⁻¹)	Phelo fl.pl. 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 4. Pelagic primary production, zooplankton biomass and fish abundance on Phelo Floodplain during low flood year 2003 and high flood year 2004 as mean values for the flooding period.

	Primary production mg C m ⁻² d ⁻¹	Zooplankton mg DW l ⁻¹	Fish abundance CPUE
2003 Low flood	204	7.4	6.4
2004 High flood	85	0.066	18.4
Compared period	High water	Increasing & high water	Whole period

Table 5. General characteristics of the aquatic ecosystem 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