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Maximum flood depth characterizes above-ground biomass in African seasonally shallowly flooded grasslands

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Abstract: Flood depth has been frequently used to explain the distribution of plant species in seasonally flooded grasslands, but its relation with vegetation production has remained ambiguous. The relationship between flooding and above-ground biomass at the end of the flooding season and during the dry season was studied to assess the impact of reflooding on the Logone floodplain, Cameroon. Above-ground biomass of a combination of all species and of the individual perennial grasses *Oryza longistaminata* and *Echinochloa pyramidalis* showed a positive linear relationship with maximum flood depth up to 1 m. The gradient of these relationships became steeper and their fit better during the 2 y following the installation of the flooding, showing the response lag to floodplain rehabilitation. Flood duration only explained the above-ground biomass of the combination of all species and not of the individual species. Above-ground biomass data from other floodplains in the three main African geographic regions showed a similar relationship with maximum flood depth less than 1 m. Dry-season regrowth, important because of its high nutrient quality during forage scarcity, was not directly related to maximum flood depth, possibly because of its dependency on the period of burning and soil moisture. Presented data indicate that a rise of water level of 1 cm corresponds to an increase in above-ground biomass of *c.* 150 kg DM ha^{-1}.

Key Words: above-ground biomass, below-ground biomass, Cameroon, *Echinochloa pyramidalis*, flood depth, floodplain rehabilitation, *Oryza longistaminata*, regrowth, seasonally flooded grasslands, soil moisture, *Vetiveria nigritana*

INTRODUCTION

African seasonally flooded grasslands have drawn widespread attention as source of forage for wildlife (Howell *et al.* 1988, Rees 1978a) and livestock (Breman & de Wit 1983, Hiernaux & Diarra 1983). Flooding intensity characterizes the composition of floodplain vegetation (Ellery *et al.* 1991) as has become apparent by the construction of upstream dams (Marchand 1987, Scholte *et al.* 2000). The raising of water levels by flood releases, as practised in the Logone floodplain in North Cameroon, showed the recovery of the vegetation composition to the pre-dam situation within 10 y (Scholte 2005, Scholte *et al.* 2000). The impact of the flood regime on the productivity of seasonally flooded grasslands remains unknown, as only general productivity characteristics, not linked to flood depth or duration, are reported. In relatively well-studied temperate zones, where flooding often occurs outside the growing season, it is assumed that the lower the inundation the higher the production becomes (Middleton 1999). Although this also holds for forested tropical floodplains (Hughes 1990), scattered data for seasonally flooded grasslands in Africa suggest a higher production with increasing flood depth (Ellenbroek 1987, Francois *et al.* 1989, Hiernaux & Diarra 1983). Tropical seasonally flooded grasslands show low productivity under rapid and deep flooding (Ellenbroek 1987, Junk *et al.* 1989, Morton & Obot 1984).

To assess the impact of increased flooding on vegetation production, I studied the relationship between above-ground biomass at the end of the flooding season and dry-season regrowth of grasses with maximum flood depth in the Logone floodplain (Figure 1). I compared these findings with the main seasonally flooded grasslands in West, North-East and Southern Africa (Denny 1993), excluding depression and stream communities with a maximum flood depth of over 1 m because of their limited occurrence in Logone (Scholte *et al.* 2000). Because of Logone's importance for grazing (Scholte *et al.* 2006), assessments included forage quality parameters allowing a link with monthly nutritional quality assessments of comparable grassland communities in the Sudd marshes

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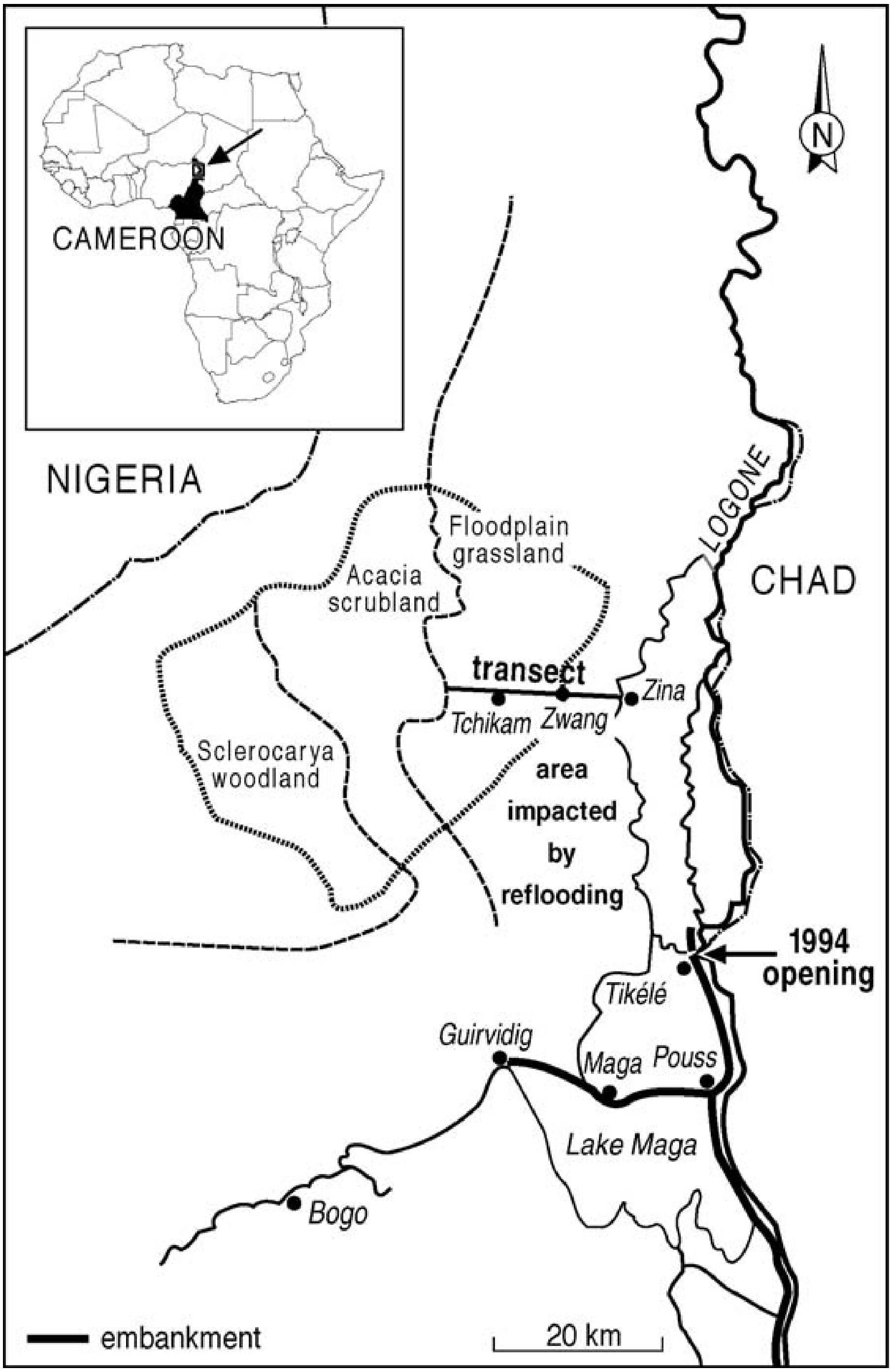

Figure 1. Waza-Logone area and the position of the transect where the study took place.

of Sudan (Howell *et al.* 1988). Soil properties were assessed as they were expected to explain differences in soil moisture and influence (regrowth) production.

METHODS

Study site

The Logone floodplain has a Sahelo–Sudanian climate, with an average annual rainfall of 650 mm that falls from June to September. In the study period 1994–1996, annual rainfall in Zina (Figure 1) was 691, 656 and 761 mm respectively.

The eastern and central parts of the area are subject to flooding, from September until December, by the Logone River. The area is extremely flat, with a difference in altitude of only a few cm per km, intersected by poorly developed watercourses. Most of the flooding occurs over the land surface, still saturated by the rains, called creeping flow (Howell *et al.* 1988).

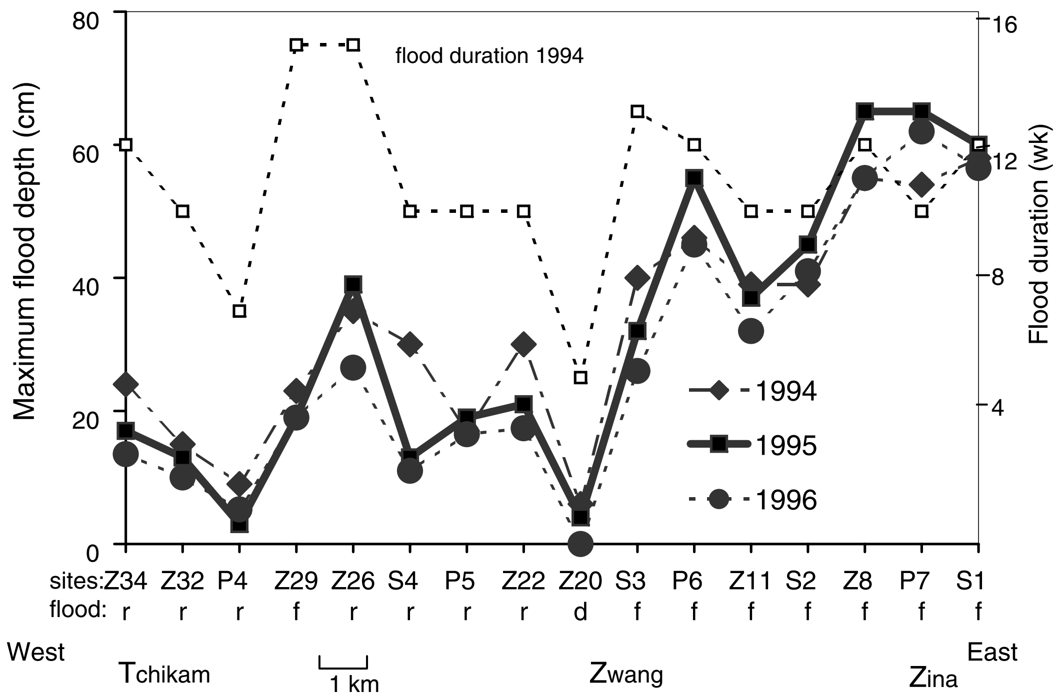

Figure 2. Maximum flood depth and flood duration in the transect Zina–Zwang–Tchikam. For position, see also Figure 1. Flood situation: f: flooded (before and after 1994), r: reflooded from 1994 onwards, d: dry (before and after 1994).

The Logone floodplain was severely degraded when it was cut off from its main water supply through the construction of a dam upstream in 1979 (Figure 1). This dam has caused the disappearance downstream of the perennial floodplain vegetation in an area of 1500 km^2 with a negative impact on livestock, fisheries and wildlife (Drijver *et al.* 1995, Scholte 2005). To counter the ongoing degradation, an embankment was breached in 1994, opening a watercourse that had been closed off since 1979 (Figure 1). This brought back the annual floods in an area of 180 km^2 and triggered recovery of perennial floodplain vegetation that dominated the reflooded area again in 2003 (Scholte 2005).

In 1985, a 16-km transect was established starting at Tchikam in Waza National Park (Figure 1). Prior to the construction of the Maga dam, the vegetation in the western transect was dominated by *Vetiveria nigritana* subsequently replaced by *Sorghum arundinaceum*, *Ischaemum afrum* and *Panicum anabaptistum*. This area has been reflooded since 1994 (Figure 2), and was gradually colonized by the rhizomatous grasses *Oryza longistaminata* and *Echinochloa pyramidalis* (Scholte *et al.* 2000). Zwang village, situated on a rise on the border of Waza National Park (Figure 1), separates the reflooded western from the eastern part of the transect that has always been flooded. The transect ended near Zina, in the well-inundated floodplain, dominated by *Oryza longistaminata* and *Echinochloa pyramidalis* (Figure 1).

Water and soil

In 1994, 1995 and 1996, water depth was assessed with a measuring tape attached to a stick, at a fixed location at each observation site, twice a month during the flooding period from mid-August till mid-November. In 1994, every second week flood duration was assessed, but was discontinued in subsequent years because of the inaccessibility of the western part of the transect, especially in the beginning and end of the flooding season.

In 1995, at the end of the dry season, eight soil pits were dug along the transect, described (cf. FAO 1977) with observations on the micro-relief (cf. Blokhuis 1993) (Table 1). Soils were classified as Eutric Vertisols (FAO 1988). Of four pits, soil texture, pH-KCl, organic matter and $CaCO_3$ were analysed for each distinguished horizon at BLGG laboratories (The Netherlands). The upper soil layers had high organic matter contents and low associated pH values (Table 1), respectively higher and lower than usually observed in vertisols (Blokhuis 1993, Bunting & Lea 1962), but comparable to vertisols in the Kafue Flats, Zambia (Ellenbroek 1987, Rees 1978b). Soil moisture was determined at 20–40 cm, 60–80 and 120 cm. In 1996, soil moisture content was determined in February, mid-dry season, in 16 plots at 20–40 cm. The 110-ml samples were oven-dried for 24 h at 110 °C; soil moisture was expressed as percentage of dry weight.

Table 1. Differentiating soil characteristics of sampled sites in Waza–Logone, Cameroon.

Site[1]	Micro-relief[2]	Rhizome layer (cm)	OM[3] top-sub soil (%)	pH KCl	Surface cracks	Depth of cracks (cm)	$CaCO_3$ nodules in layer (cm)	Soil moisture ratio mid/end dry season
S1	1:50	0–10	9.2–0.5	3.9–5.5	rare	60	10–60	1.36
P7	1:50	0–10	–	–	rare	60	60–120	1.67
S2	1:50	0–10	–	–	rare	72	no	1.57
P6	1:15	0–15	6.1–0.6	4.5–6.2	rare	100	no	2.54
S3	1:15	none	6.4–0.3	5.0–6.8	common	65	no	5.21
P5	1:25	none	–	–	common	65	no	3.34
S4	1:25	none	–	–	common	70	no	3.01
P4	none	none	6.4–0.5	4.7–6.3	common	40	no	2.01

[1]see Figure 2 for position and flooding status.
[2]wavelength : amplitude (Blokhuis 1993).
[3]Organic matter.
– : not determined.

Biomass

Above-ground biomass at the end of the flooding season. In 1994, 32 sites were sampled at equal distances along the transect, reduced to eight and 16 equidistant sites in 1995 and 1996 respectively. Immediately after the floods receded, in each site randomly selected 1-m^2 samples of above-ground biomass were hand clipped at ground level. The difficulties in reaching the western part of the transect in 1994 allowed only four samples to be taken and four additional replicates in each site to be visually estimated after cutting, corrected following a double-sampling weight-estimate ('t Mannetje 1987). In 1995 and 1996, 10 samples in each selected site were cut. In the laboratory, clipped biomass was separated according to species (nomenclature following Van der Zon 1992). Samples were oven-dried at 65 °C for 48 h and expressed as dry weight percentage. The average of the above-ground biomass per site was used for comparison with maximum flood depth, below-ground biomass, regrowth and soil moisture. Comparison of biomass between years was based on the individual samples in each site.

After the retreat of the floods, above-ground biomass dropped because of the passing of fire or the flattening of the large grasses that subsequently decomposed. As only a limited amount of dead above-ground biomass (< 5%) was observed, I assumed that biomass sampled when sites dried up was also the maximum above-ground biomass of the growing season.

Above-ground biomass in the dry season after burning (regrowth). In 1995 and 1996, eight and 16 sites respectively adjacent to the soil moisture and below-ground biomass assessment sites were burnt in mid-February. In each of the sites burned in 1995 and 1996, 12 and 8, respectively, 1-m^3 wire-netted exclosures were placed to prevent grazing. In April regrowth turned brown and was hand cut at ground level, irrespective of species composition. For comparison we took 10 random samples outside the exclosures at each site and treated as described above.

Below-ground biomass. In 1996, 3 mo after the recession of the floods, eight below-ground biomass samples of 0.5 litres were taken horizontally at depths of 0–15 cm and 15–50 cm respectively in each of the 16 pits used for the assessment of soil moisture. Roots and rhizomes with a diameter larger than approximately 0.2 mm were separated by hand from the firm soil and oven-dried for 48 h at 65 °C. No distinction was made between living and dead below-ground biomass, as the latter was estimated to be less than 10%.

Forage quality. In 1994 and 1995, 30 oven-dried samples were selected, targeting sites dominated by the six dominant grass species (see above). The entire plants were sampled (cf. Mefit-Babtie 1983), allowing a comparison with the monthly measurements in the Sudd (Howell *et al.* 1988) and an assessment of total N yield (N% × biomass). N concentration was analysed at BLGG laboratories (The Netherlands).

Data analysis

Above-ground biomass observations from the same plots were compared amongst years, depending on normality, assessed with Kolmogorov–Smirnov test, with t-tests or Mann–Whitney U-tests. The calculations of correlation coefficients, Pearson's or Spearman's and linear regressions followed SPSS for Windows, release 9.0.

RESULTS

Maximum flood depth and flood duration

In 1994, flooding lasted 5–15 wk, prolonging the rainy season that started with the first rains in June that ponded periodically on the surface from July onwards. The rains ended in early October, when floodwater had reached all sites. Some sites dried up in the first week of November,

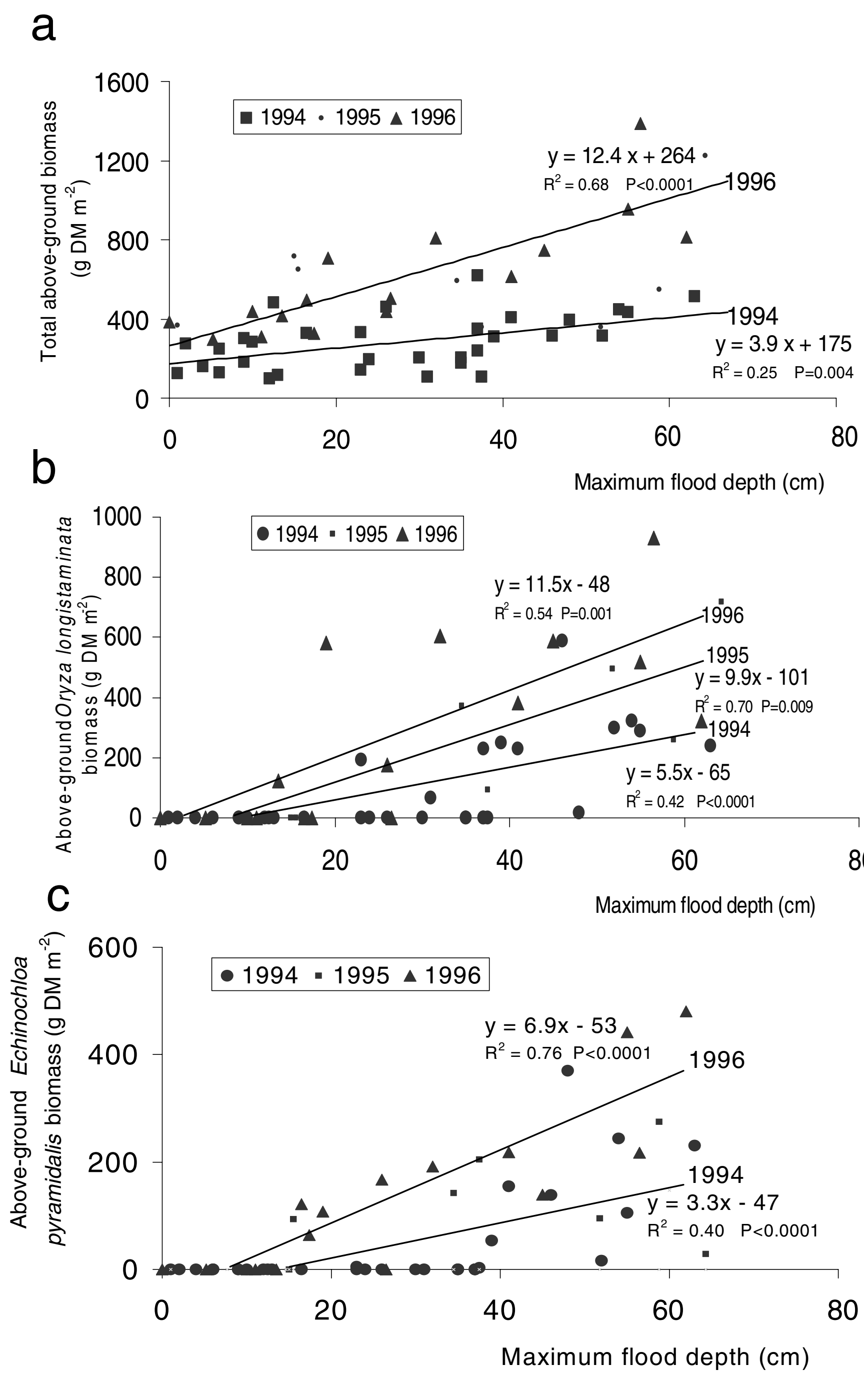

Figure 3. Relation between maximum flood depth and above-ground biomass of a combination of all species (a), *Oryza longistaminata* (b) and *Echinochloa pyramidalis* (c) in Waza–Logone (Cameroon), after increase in water levels from 1994 onwards (0–65 cm max. flood depth).

most of the others in the last week of November; the remaining three sites, at the western end of the transect, during the second week of December.

Maximum flood depth followed a comparable pattern in the three observation years but in 1996 was 5.2 cm and 4.4 cm lower than in 1994 and 1995 respectively (Figure 2). Flood duration was correlated with maximum flood depth ($R = 0.55$, $P < 0.001$), but with limited amplitudes, partly due to the 2-wk interval of flood duration measurements (Figure 2).

Above-ground biomass at the end of the flooding season

Total above-ground biomass, combining all species (Figure 3), increased with increasing maximum flood

Table 2. Correlations between maximum flood depth, above-ground and below-ground biomass and intermediate soil parameters in Waza–Logone, Cameroon.

			Maximum flood depth	Above-ground biomass wet season	Above-ground biomass dry season	Perennials %	Below-ground biomass 0–15 cm	Below-ground biomass 15–50 cm
Maximum flood depth		r [1] 1995						
		r 1996						
Above-ground biomass	wet	r 1995	0.49*					
		r 1996	0.83*					
	dry	r 1995	0.60	0.41				
		r 1996	0.20	0.16				
Perennials	%	r 1995	0.70	0.46	0.49			
		r 1996	0.69*	0.63*	0.44			
Below-ground biomass	0–15 cm	r 1995	–	–	–	–		
		r 1996	0.49	0.56*	−.011	0.63*		
	15–50 cm	r 1995	–	–	–	–	–	
		r 1996	0.69*	0.59*	0.072	0.75*	0.86*	
Soil moisture	20–40 cm	r 1995	0.54[2]	0.49[2]	0.88*[2]	0.24[2]	–	–
		r 1996	0.53*[3]	0.42[3]	0.33[3]	0.53*[3]	0.66*[3]	0.59*[3]

[1] Pearson Correlation Coefficient.
[2] soil moisture at the end of the dry season (May).
[3] soil moisture half-way the dry season (February).
–: not determined *: $P < 0.05$.

depth. In 1996, in the third year of the reflooding, the gradient of this linear relationship had increased and its fit improved compared to the first year, 1994. In 1995 the number of observations was too limited for such calculation. Total above-ground biomass in both 1996 and 1995 was higher than in 1994 (respectively $t = 5.2$, $df = 198$, $P < 0.0001$ and $t = 5.5$, $df = 123$, $P < 0.0001$) and in 1995 equal to 1996 ($t = 0.42$, $df = 172$, $P = 0.64$).

Among the dominant grass species, *Sorghum arundinaceum*, an annual reed-like grass that had invaded the desiccated floodplain, produced substantial above-ground biomass up to a maximum flood depth of 38 cm, in 8 out of 32 reflooded sites in 1994. In 1996, its occurrence was reduced to 2 out of 16 reflooded sites with maximum flood depth less than 15 cm. For wild rice, *Oryza longistaminata*, above-ground biomass was a function of maximum flood depth in 1994, a relationship of which the gradient became steeper in subsequent years (Figure 3). In 1994, above-ground biomass of *Oryza longistaminata* was lower than in 1995 ($t = 3.5$, $df = 82$, $P = 0.001$ and in 1996 ($t = 5.6$, $df = 118$, $P < 0.0001$) and in 1996 slightly higher than in 1995 ($t = 2.1$, $df = 108$, $P = 0.045$). *Echinochloa pyramidalis*, co-dominant, also showed an increasing gradient and better fit of its relationship with maximum flood depth (Figure 3). In 1995, the limited number of observations did not allow such a calculation. In 1994, above-ground biomass was lower than in 1995 and 1996 (respectively $P = 0.002$ and $P < 0.0001$) and in 1995 not significantly different to 1996 ($P = 0.50$).

Flood duration, assessed in 1994, characterizes total above-ground biomass comparable to maximum flood depth ($R^2 = 0.28$, $P = 0.002$), but did not explain above-ground biomass of *Oryza longistaminata* ($R^2 = 0.1$, $P = 0.078$) nor of *Echinochloa pyramidalis* ($R^2 = 0.033$, $P = 0.32$). These two dominant species had a maximum above-ground biomass at a flood duration of 10–12 wk.

Above-ground biomass in the dry season after burning (regrowth)

Regrowth was higher inside than outside the exclosures ($P < 0.05$) in one site (S1) in 1995 and in 1996 in five sites (S1, Z8, Z11, P6, Z22). With one exception (Z22), these sites were situated in the well-flooded eastern part of the transect, outside Waza National Park (Figure 2). The following presentation will be limited to the exclosure data. In 1995 regrowth was correlated with soil moisture still present at the end of the dry season at a depth of 20–40 cm (Table 2) but not with soil moisture at 60–80 cm and at 120 cm. The 1996 data indicated that regrowth was hardly influenced by mid-dry-season soil moisture. Both mid-dry-season soil moisture and soil moisture at the end of the dry season were influenced by maximum flood depth (Table 2). A positive correlation existed between maximum flood depth, below-ground biomass and % perennials, but these parameters had little influence on regrowth that was only correlated with soil moisture at 20–40 cm (Table 2).

Below-ground biomass

In the topsoil (0–15 cm), below-ground biomass varied from 8 g DM m^{-2} (Z32, with annual vegetation) to

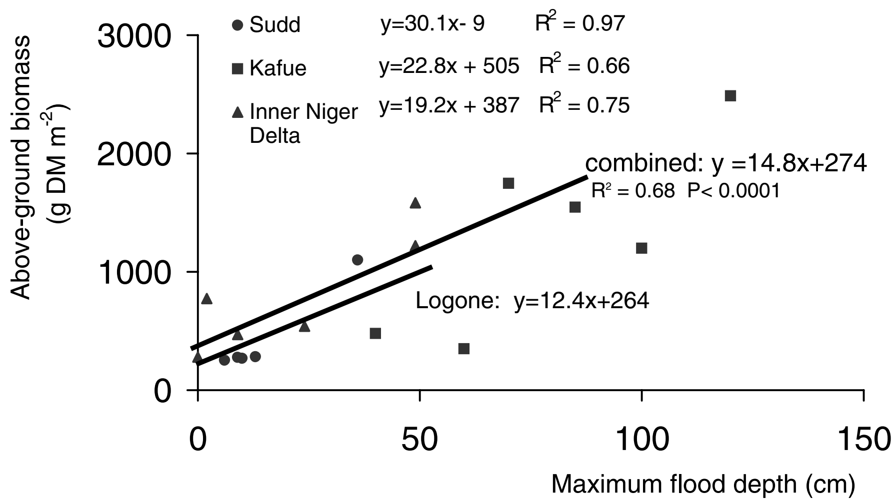

Figure 4. Relation between maximum flood depth and total above-ground biomass in the seasonally flooded grasslands of the Sudd, Sudan (Mefit-Babtie 1983), Kafue Flats, Zambia (Ellenbroek 1987) and Inner Niger Delta, Mali (Hiernaux & Diarra 1984a). Biomass measurements are based on 10 (Sudd), an unknown (Kafue Flats) and 24 (Inner Niger Delta) samples of 1-m^2 collected at the end of the flooding season.

2750 g DM m^{-2}, double the above-ground biomass (Z29, with a dense rhizome layer of *Oryza longistaminata*). In the 15–50-cm layer, below-ground biomass was reduced to 3–165 g DM m^{-2}. The shoot/root ratio was negatively correlated with the percentage of perennials ($R = -0.60$, $P = 0.014$). Maximum flood depth was correlated with below-ground biomass at 15–50 cm (Table 2). Below-ground biomass at both 0–15 and 15–50 cm was correlated with above-ground biomass, with the percentage of perennials and soil moisture at 20–40 cm, but not with dry-season regrowth (Table 2) nor with soil moisture at lower depths.

Forage quality and N yield

N concentration of above-ground biomass at the end of the flooding season was between 0.38–0.74%, with minor differences between species and not correlated with biomass ($R = -0.051$, $n = 23$, $P = 0.82$), nor with maximum flood depth ($R = -0.27$, $n = 23$, $P = 0.21$). N yield was not correlated with maximum flood depth either ($R = 0.26$, $n = 9$, $P = 0.50$). Regrowth had a N concentration between 0.9 and 2.2%; the limited number of observations tend to have a negative correlation with above-ground biomass ($R = -0.55$, $n = 7$, $P = 0.21$).

DISCUSSION

Comparison with other African seasonally flooded grasslands

Although long-term rainfall was 150 mm higher in the Sudd marshes (Sudan) than in Logone, the species composition was comparable with *Oryza longistaminata* and *Echinochloa pyramidalis* as dominant species and *Hyparrhenia rufa* and *Vetiveria nigritana* occurring on the edges of the floodplain (Howell *et al.* 1988). In the Kafue Flats (Zambia) with a somewhat higher rainfall of 880 mm y^{-1} and comparable soils, *Echinochloa stagnina* and *Vossia cuspidata* dominated the deeply flooded parts (> 1 m), as in Logone. However the shallowly flooded area (< 1 m) had a different vegetation composition from Logone with only occasionally *Oryza longistaminata* (Ellenbroek 1987). In the Inner Niger Delta (Mali), with a low rainfall of 380 mm y^{-1}, *Oryza longistaminata* dominated the parts with a maximum flood depth of about 50 cm, with *Echinochloa stagnina* and *Vossia cuspidata* occurring at a maximum flood depth of 1–2.8 m, occasionally up to 5 m (Hiernaux & Diarra 1983, 1984a). Above-ground biomass measurements in these three areas generally followed the methodology described for Logone, although flood depth was often measured only twice during the flooding season, probably underestimating its maximum value.

In this sample of seasonally flooded grasslands from the three main African geographic regions, above-ground biomass measured at the retreat of the floods was a function of maximum flood depth as well (Figure 4). Together with the Logone 1996 data, a comprehensive relation for African seasonally flooded grasslands, with a maximum flood depth of less than 1 m was found: above-ground biomass (g DM m^{-2}) = 14.8 (max. flood depth) (cm) + 274 ($R^2 = 0.68$, $P < 0.0001$).

The African seasonally flooded grasslands have only one main growing season (Denny 1993), and with a relatively low regrowth production after the passing of fires, above-ground biomass at the end of the main flooding season approaches total annual production.

Flood duration versus maximum flood depth

In addition to flood depth, flood duration has been considered a main determinant of vegetation composition in wetlands (Ellenbroek 1987, Thompson 1985). In Logone, there was no linear relationship between flood duration and above-ground biomass of the individual grass species. In the Inner Niger Delta (Hiernaux & Diarra 1984a), maximum flood depth was more strongly correlated with flood duration than in Logone ($R = 0.94$, $P < 0.0001$ versus $R = 0.55$, $P < 0.001$). I attribute this difference to the large number of deeply inundated sites in the Inner Niger Delta as well as to the large number of fish canals in Logone that accelerate drainage (Drijver *et al.* 1995). Maximum flood depth was not only a better but also a more practical parameter to measure than flood duration, for which a long presence in the (inaccessible) field is necessary.

Floodplain rehabilitation

In 1995 and 1996, above-ground biomass of all species together, as well as of the individual species *Oryza longistaminata* and *Echinochloa pyramidalis*, were higher than in 1994, the first year of reinstatement of flooding. The correlation coefficient between maximum flood depth and biomass also increased after 1994, showing the 2-y time lag in reaction of vegetation production to increased flooding. Scholte *et al.* (2000) reported this initial vegetation stress, due to the sudden rise of the water level, leading to the lack of flowering in *Oryza longistaminata* and its limited increase in cover as well as of *Echinochloa pyramidalis* compared to subsequent years. In 1994, *Sorghum arundinaceum* was still widespread and attained a high production in the re-flooded sites, but gradually disappeared in following years (Scholte *et al.* 2000). Contrasting these changes in species composition and production was the lack of any noticeable impact on the morphological characteristics of the (top) soils within this 3-y study period (Table 1). The impact of soil properties on (regrowth) production therefore remained unclear as concluded by Tobias & Vanpraet (1981) and Ellenbroek (1987).

Regrowth after burning

Dry-season regrowth was very limited, but not neglected by herbivores as shown by the difference in biomass in and outside the exclosures. The equation of Breman & de Ridder (1991) that relates above-ground biomass at the end of the main growing season with regrowth after burning, would imply a regrowth of 42–147 g DM m^{-2} with a maximum flood depth of 20–60 cm. This is considerably more than the observed maximum regrowth measurements of 10 g DM m^{-2} (1995) and 27 g DM m^{-2} (1996). Moreover, dry season regrowth was not correlated with above-ground biomass at the end of the flooding season, nor with below-ground biomass (Table 2). Regrowth in the Sudd, under similar flood depths, did not exceed 17 g DM m^{-2} (Mefit-Babtie 1983). Substantial regrowth (> 90 g DM m^{-2}) is only produced with a maximum flood depth exceeding 50–100 cm and early dry-season burning (Ellenbroek 1987, Hiernaux & Diarra 1984b), contradicting the linear biomass-regrowth relationship of Breman & de Ridder (1991). The role of above- and below-ground biomass and soil properties in the production of regrowth remains to be clarified.

Biomass forage quality

The observed N concentration of regrowth and of above-ground biomass at the end of the flooding season of *Oryza longistaminata* and *Echinochloa pyramidalis* correspond to the extremes of the year-round biomass-nutritional quality relationship of Howell *et al.* (1988). Herbivores select, however, the more nutritious parts of the grasses and target nutritious regrowth, maintaining a N concentration of 0.66% in their diet in the Inner Niger Delta (Hiernaux & Diarra 1984b).

Wet-season growth was N-limited, as hardly any of the above-ground biomass samples surpassed the physiological threshold of 0.5% N (Breman & de Ridder 1991). The lack of correlation between N concentration and above-ground biomass at the end of the flood season also points to this. In contrast, dry-season regrowth has been largely water limited, although irrigation experiments in the Inner Niger Delta showed that with higher regrowth (> 110 g DM m^{-2}), production was enhanced by NP fertilization (Hiernaux & Diarra 1984a).

The N-growth limitation notwithstanding, results of this study did not support a link between N-yield and maximum flood depth or with the position on the transect, a measure of the distance water travelled and potentially an indication of sediment load (Breen *et al.* 1988, Scholte *et al.* 2000).

Explanation of the linear relationship between maximum flood depth and above-ground biomass

The difference in intercept between 1994 and 1996 of *Oryza longistaminata* and *Echinochloa pyramidalis*

(Figure 3) can be partly explained by the 5-cm difference in maximum flood depth (Figure 2). The Rain-Use Efficiency, based on the 0-intercept of maximum flood depth with total above-ground biomass (Figure 3), was with 2.5 and 3.5 kg DM ha^{-1} y^{-1} mm^{-1} in 1994 and 1996 respectively, well in line with the 1.5–6 kg DM ha^{-1} y^{-1} mm^{-1} range noted for the Sudano–Sahelian transition subzone (Le Houerou 1989). The established linear relationship between above-ground biomass and maximum flood depth was not reached by coincidence. The good fit, probably underestimated as the micro-relief was not included in the 1-m^2 sample plots, and steep gradient of the relationship between maximum flood depth and above-ground biomass in 1996 (Figure 3) also suggest a causal relation.

Junk *et al.* (1989) emphasized the local character of a possible flood depth–production relationship, arguing that differences in inundation rates regularly disturb this relationship. The time lag in vegetation production and species recovery (Scholte *et al.* 2000) to the start of reflooding is illustrative for such disturbances. Catling (1992), based on a large number of field measurements, concluded that most floating rice species are adapted to an optimum flooding regime at which their full grain yield potential is expressed. In Logone *Oryza longistaminata* and *Echinochloa pyramidalis* had a maximum above-ground biomass with a flood duration of 10–12 wk, contrasting with the linear increase of above-ground biomass with maximum flood depth.

Flooding drives adapted plants to keep pace with the rising water-level (Blom & Voesenek 1996, Breen *et al.* 1988, Cronk & Fennessey 2001). This shoot elongation is practised by the deeply flooded *Vossia cuspidata–Echinochloa stagnina* communities with relatively weak stems that, supported by the buoyancy of the water, may reach 250 cm or more with a height of the aerial parts of about 80–100 cm at all seasons (Ellenbroek 1987). The linear relationship between maximum flood depth and above-ground biomass as well as the N concentration that reached physiological threshold values suggest a comparable shoot elongation in the studied communities where inundation levels were lower. *Echinochloa pyramidalis* has strong fibrous shoots, however, that rise at the start of the flood season above the approaching floodwater, challenging this explanation. In addition, *Oryza longistaminata*, the only important C3 grass on the floodplain, is known to photosynthesize under reduced light conditions and relatively low ambient temperatures underwater (Cronk & Fennessey 2001, Ellenbroek 1987).

After the rainy and flooding season, the growth period extends into the dry season when small quantities of regrowth are produced, related to soil moisture (20–40 cm) and below-ground biomass (Table 2). Neither above-ground biomass at the end of the flooding season, nor below-ground biomass, did, however, correlate with dry-season regrowth, suggesting different causal chains: from maximum flood depth and soil moisture (20–40 cm) to below-ground biomass on one hand and to dry-season regrowth on the other hand.

CONCLUSION

Flood depth is a well-known environmental determinant of species distribution in wetlands (Ellery *et al.* 1991) and was also the main environmental factor explaining above-ground biomass production in the shallowly flooded Logone floodplain. Based on data from Central as well as West, North-East and Southern Africa, I showed that a rise in maximum flood depth of 1 cm, to a maximum of 1 m, is likely to correspond to an increase in above-ground biomass at the end of the flood season of approximately 150 kg DM ha^{-1}. Dry-season regrowth after burning possibly increases as well, but only becomes substantial once maximum flood depth exceeds 50–100 cm. The factors, influenced by maximum flood depth, that determine plant production such as length of growing season, soil moisture and induction of shoot elongation, have to be further clarified. An experimental follow-up of this study should also take into account the relation of maximum flood depth with sediment load and micro-relief.

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LITERATURE CITED

BLOKHUIS, W. A. 1993. *Vertisols in the central clay plain of the Sudan.* PhD Thesis, Wageningen University, Wageningen.

BLOM, C. W. P. M. & VOESENEK, L. A. C. J. 1996. Flooding: the survival strategies of plants. *Trends in Ecology and Evolution* 1:290–295.

BREEN, C. M., ROGERS, K. H. & ASHTON, P. J. 1988. Vegetation processes in swamps and flooded plains. Pp. 223–247 in Symoens, J. J. (ed.). *Vegetation of inland waters*. Handbook of Vegetation Science 15/1. Kluwer, Dordrecht.

BREMAN, H. & DE RIDDER, N. 1991. *Manuel sur les pâturages des pays sahéliens*. Karthala, Paris. 485 pp.

BREMAN, H. & DE WIT, C. T. 1983. Rangeland productivity and exploitation in the Sahel. *Science* 221:1341–1347.

BUNTING, A. H. & LEA, J. D. 1962. The soils and vegetation of the Fung. *Journal of Ecology* 50:529–558.

CATLING, D. 1992. *Rice in deep water*. IRRI. The Macmillan Press Ltd, London. 542 pp.

CRONK, J. K. & FENNESSY, M. S. 2001. *Wetlands plants. Biology and ecology*. Lewis Publishers, Boca Raton. 462 pp.

DENNY, P. 1993. Wetlands of Africa: introduction. Pp. 1–31 in Whigham, D., Dykyjova, D. & Hejny, S. (eds.). *Wetlands of the World: inventory, ecology and management*. Handbook of Vegetation Science Volume 15/2. Kluwer, Dordrecht.

DRIJVER, C. A., VAN WETTEN, J. C. T. & DE GROOT, W. T. 1995. Working with nature: local fishery management on the Logone floodplain in Chad and Cameroon. Pp. 29–45 in Van der Breemer, J. P. M., Drijver, C. A. & Venema, L. B. (eds). *Local resource management in Africa*. John Wiley & Sons, Chichester.

ELLENBROEK, G. A. 1987. *Ecology and productivity of an African wetland vegetation*. Junk Publishers, Dordrecht. 267 pp.

ELLERY, K., ELLERY, W. N., ROGERS, K. H. & WALKER, B. H. 1991. Water depth and biotic insulation: major determinants of black-swamp plant community composition. *Wetlands Ecology and Management* 1:149–162.

FAO 1977. *Guidelines for soil profile description*. FAO, Rome. 66 pp.

FAO 1988. FAO/UNESCO *Soil Map of the World, revised legend*. World Resources Report 60. FAO, Rome. 119 pp.

FRANCOIS, J., RIVAS, A. & COMPÈRE, R. 1989. Le pâturage semi-aquatique à *Echinochloa stagnina* (Retz.) P.Beauv. Etude approfondie de la plante "bourgou" et des bourgoutières situées en zone lacustre du Mali. *Bulletin des Recherches Agronomiques de Gembloux* 24:145–189.

HIERNAUX, P. & DIARRA, L. 1983. Pâturages de la zone d'inondation du Niger. Pp. 42–48 in Wilson, R. T., de Leeuw, P. N. & de Haan, C. (eds.). *Recherches sur les systèmes des zones arides du Mali: résultats préliminaires*. Rapport de recherche 5. ILCA, Addis Abeba.

HIERNAUX, P. & DIARRA, L. 1984a. Is it possible to improve the traditional grazing in the flood plain of the Niger river in Central Mali? Pp. 201–204 in Joss, P. J., Lynch, P. W. & Williams, O. B. (eds.). *Rangelands: a resource under siege. Proceedings 2nd International Rangeland Congress*. International Rangeland Congress, Adelaide.

HIERNAUX, P. & DIARRA, L. 1984b. Savanna burning, a controversial technique for rangeland management in the Niger floodplains of Central Mali. Pp. 238–243 in Tothill, J. C. & Mott, J. C. (eds.). *Ecology and management of the world's savannas. International Savanna Symposium*. Australian Academy of Science, Canberra.

HOWELL, P., LOCK, M. & COBB, S. 1988. *The Jonglei canal. Impact and opportunity*. Cambridge University Press, Cambridge. 450 pp.

HUGHES, F. M. R. 1990. The influence of flooding regimes on forest distribution and composition in the Tana river floodplain, Kenya. *Journal of Applied Ecology* 27:475–491.

JUNK, W. J., BAYLEY, P. B. & SPARKS, R. E. 1989. The Flood Pulse concept in river-floodplain systems. Pp. 110–127 in Dodge, D. O. (ed.). *Proceedings of the International large river symposium (LARS)*, Honey Harbour, Ontario, Canada, Canadian Special publication of Fisheries and Aquatic Sciences 106, Department of Fisheries and Oceans, Ottowa.

LE HOUEROU, H. N. 1989. *The grazing land ecosystems of the African Sahel*. Ecological studies 75, Springer-Verlag, Berlin. 282 pp.

MARCHAND, M. 1987. The productivity of African floodplains. *International Journal of Environmental Studies* 29:201–211.

MEFIT BABTIE 1983. *Development studies in the Jonglei canal area*. Technical assistance contract for range ecology survey, livestock investigations and water supply. Final report. volume 2, background and volume 3. Vegetation studies.

MIDDLETON, B. 1999. *Wetland restoration. Flood pulsing and disturbance dynamics*. John Wiley & Sons, New York. 400 pp.

MORTON, A. J. & OBOT, E. A. 1984. The control of *Echinochloa stagnina* (Retz.) P.Beauv. by harvesting for dry season livestock fodder in Lake Kainji, Nigeria – a modelling approach. *Journal of Applied Ecology* 21:687–694.

REES, W. A. 1978a. The ecology of the Kafue lechwe: the food supply. *Journal of Applied Ecology* 15:177–191.

REES, W. A. 1978b. The ecology of the Kafue lechwe: soils, water levels and vegetation. *Journal of Applied Ecology* 15:163–176.

SCHOLTE, P. 2005. *Floodplain rehabilitation and the future of conservation & development. Adaptive management of success in Waza-Logone, Cameroon*. Tropical resource management papers 67. Wageningen University and Research Centre, Wageningen, The Netherlands. 344 pp. Available at: http://hdl.handle.net/1887/4290.

SCHOLTE, P., KIRDA, P., ADAM, S. & KADIRI, B. 2000. Floodplain rehabilitation in North Cameroon: impact on vegetation dynamics. *Applied Vegetation Science* 3:33–42.

SCHOLTE, P., KARI, S., MORITZ, M. & PRINS, H. 2006. Pastoralist responses to floodplain rehabilitation in North Cameroon. *Human Ecology* 34: 27–51.

'T MANNETJE, L. 1987. Measuring quantity of grassland vegetation. Pp. 63–95 in 't Mannetje L. (ed.). *Measurement of grassland vegetation and animal production*. CAB International, Wallingford.

THOMPSON, K. 1985. Emergent plants of permanent and seasonally-flooded wetlands. Pp. 43–107 in Denny, P. (ed.). *The ecology and management of African wetland vegetation*. Junk Publishers, Dordrecht.

TOBIAS, C. & PRAET VAN, C. 1981. Notes d'écologie Soudano-Sahelienne. Quelques relations sols-végétation dans le parc national de Waza (Nord Cameroun). *Revue Science et Technologie* 1:51–81.

VAN DER ZON, A. P. M. 1992. Graminées du Cameroun. *Wageningen Agricultural University Papers* 92(1):1–557.