

Effects of soil water regime and grazing on vegetation diversity and production in a hyperseasonal savanna in the Apure Llanos, Venezuela

Guillermo Sarmiento¹, Marcela Pinillos, Marta Pereira da Silva and Dimas Acevedo

Instituto de Ciencias Ambientales y Ecológicas, Universidad de los Andes, Mérida, Venezuela
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Abstract: Soil water content and above-ground biomass accumulation, above 10 cm high, were measured monthly in a flooded savanna ecosystem under grazing pressure and under cattle exclusion, during two growth cycles. Near-to-the-ground and below-ground biomass were measured three times during this period. Besides, composition, species richness and diversity were obtained through a floristic inventory. Despite a relatively high floristic richness and diversity, *Panicum laxum* is the dominant species throughout the study area, while three other perennial grasses, *Paspalum chaffanjonii*, *Leersia hexandra* and *Axonopus purpusii*, also reach high values of cover and biomass. Each of them reacts specifically to flooding, drought and grazing conditions. This ecosystem shows a strongly seasonal behaviour, with primary production, mortality and decomposition sharply timed by soil relative water content. Both drought and water excess seem to limit plant production, even more during wet years when the savanna might remain flooded for up to 4 mo. Some structural and functional differences between the grazed and the protected systems are demonstrated, but under the actual, relatively low stocking rate, the grazed savanna produces as much forage as the ungrazed one.

Key Words: cattle grazing, grasses, hyperseasonal savanna, primary production, tropical grassland, seasonal drought, water excess

INTRODUCTION

Despite the widespread occurrence and the economic importance of inundated savannas, they remain one of the least known tropical ecosystems. The Colombo-Venezuelan Llanos, a Quaternary plain of about 500 000 km², is mostly covered by different types of savanna ecosystem (Blydenstein 1967, Etter 1998, FAO 1964, Sarmiento 1983). In Apure State, in the south-western Venezuelan Llanos (Figure 1), flooded savannas extend over hundreds of km², being only interrupted by the narrow gallery forests that border the many creeks and rivers. Similar seasonally flooded savannas occur in other tropical and subtropical South American regions (Sarmiento 1983, 1990).

Two key environmental constraints act upon these flooded grasslands, first an almost rainless dry season up to 6 mo long, and second, fires that nowadays sweep

the vegetation almost yearly, towards the end of the dry period. The sharp seasonality caused by the dry and wet tropical savanna climate is reinforced by an extended period in which the soil stays saturated or even flooded. This is caused by the huge amount of water falling during the rainy season, coupled with the negligible slope of the plains and the generalized occurrence of mostly impermeable clay-pans. We named this type of tropical ecosystem hyperseasonal savanna because it shows a reinforced seasonality where four, or even five, contrasting seasons follow each other through the year: one extended dry season, then a short period when soil water ranges between the permanent wilting point (PWP) and field capacity (FC), then a long season when the soil remains saturated, that may include a period of waterlogging or flooding, and finally another short period when the soil is neither dry nor water-saturated, that will be followed by the dry season in a new, iterative annual cycle (Sarmiento 1984).

Hyperseasonal savannas in the Apure plains are almost pure grasslands where the nearly continuous grass layer attains 50 cm or more, although livestock grazing may

¹ Corresponding author. Address: Departamento de Botânica, CCS Bloco A, sala 100, Ilha do Fundão, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

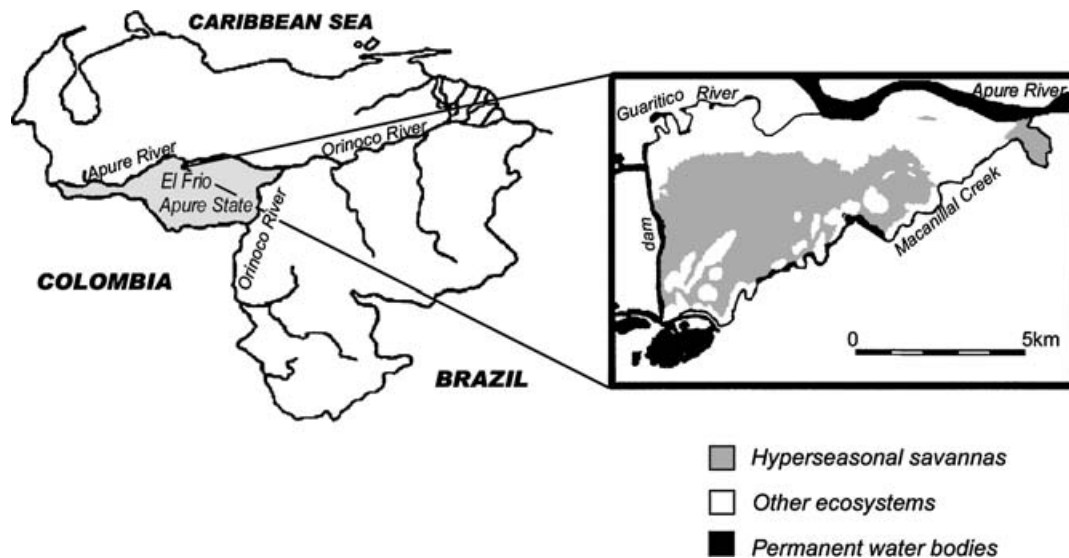


Figure 1. Location of El Frío, within Apure State and Venezuela, showing the study area, downstream from a dam, and between two water courses: Guaritico River and Macanillal Creek, and the distribution of the major vegetation units.

maintain the grass sward closer to the ground. In some cases a few species of small tree and palm form an open woody layer. As in many other regions of tropical and subtropical America where these seasonally waterlogged ecosystems occur, three perennial grasses, *Axonopus purpusii*, *Panicum laxum* and *Leersia hexandra*, appear as important plant species. A fourth grass species quite conspicuous in the Apure lowlands, *Paspalum chaffanjonii*, seems instead to be restricted to the savannas of northern South America.

For more than two centuries these seasonally flooded ecosystems have been used as extensive rangelands. Cattle graze freely throughout the year, profiting from the topographic gradient from seasonal savannas on the highest, non-flooded positions, to the semi-seasonal savannas and related wetlands in the bottomlands, and the hyperseasonal savannas in between. The free movement of the herd from dry to wet sites ensures its feed all year, despite the harsh conditions imposed by the alternation of drought and flood periods (Sarmiento & Pinillos 2000). In the last few decades, the livestock industry started a modernization process to increase its productivity, largely based on replacing the natural grasses by more productive species. In the seasonally flooded savannas, as these managed pastures cannot be established, one alternative to improve the rangelands was the building of low, earth dams to retain surface water, thus keeping savanna grasses green for longer. The environmental and ecological consequences of water management through this system of dykes have yet to be fully evaluated.

An international project sponsored by the European Union has aimed to better understand the behaviour

of flooded ecosystems in the Venezuelan Apure Llanos and in the Brazilian Pantanal. As a part of this programme, the regional ecology of the Apure Llanos was considered in a previous paper (Sarmiento & Pinillos 2001), where we emphasized the high hydrological and ecological variability of this region, linking it with a whole set of interconnected geological, climatic and palaeoclimatic processes. Four Quaternary cycles of deposition and erosion have been distinguished. On the two youngest depositions, along the actual flood plains, named Q_{0a} and Q_{0b} , rain forests, semi-seasonal savannas and permanent wetlands occur. Over the two other sedimentary materials and land forms, Q_1 from Late Pleistocene, and Q_2 from Middle Pleistocene, inundated savannas and seasonal wetlands prevail. We showed that hyperseasonal savannas extend over Middle Pleistocene (Q_2) overflow mantles, of silty textures, where alfisols and ultisols have evolved, in such a way that soil evolution, through the development of an almost impervious illuvial horizon, reinforced the annual cycle of drought and waterlogging.

Continuing the same line of research, the objectives of this study are, first, to quantify the seasonal courses of soil moisture, delimiting the periods of water deficiency and excess. Second, to quantify plant species diversity and primary production in relation to soil moisture and to the occurrence of flooding/drought spells. And third, to test the effect of grazing on composition, primary production and on the availability of forage to livestock. We want to test the hypothesis that both the dry season and the waterlogged period represent major stressors to savanna grasses, regulating biomass accumulation and decomposition, and handicapping primary production.

STUDY AREA

A large tract of uninterrupted flooded savanna of about 5000 ha, was selected on a private ranch: Hato El Frío, in Apure State, Venezuela (Figure 1). Hato El Frío is a typical, large ranch devoted to cattle raising, where a system of earth dykes to control run off was built in the 1970s. The study area is located below one of these dykes. It appears on remote images as a typical extent of seasonally inundated savanna located between two water courses: the Guariquito River in the north and the Macanilla Creek in the south (Figure 1), each of them bordered by a gallery forest. Semi-seasonal savannas and permanent wetlands extend between the gallery forest of the Guariquito River and the large area of hyperseasonal savanna where we carried out our sampling and laid out the permanent plots. Several small, isolated patches of seasonal savanna occur on slightly higher topographic positions. This area is permanently grazed by a herd of around 2000 cattle, mainly 1–2-y-old steers with an average live weight of 300 kg, equivalent to a stocking rate of 0.4 head ha⁻¹, or 120 kg live weight ha⁻¹. This low animal charge suggests that the major effects of grazing will be due to direct intake, while the effects on the soil by trampling and dung deposition will be unimportant. The savanna is burnt each year, towards the last days of the dry season, in order to promote a rapid regrowth of the grasses from the start of the rains.

METHODS

Field and laboratory methods

The study was carried out at two different scales. First, the scale of the aforementioned continuous tract of flooded savanna corresponding to a unit of hydrological and livestock management, since in this unit, downwards from a dam, the same herd grazes the whole year. The study area was delimited on aerial photographs (scale 1:50 000). Then 22 sampling sites were randomly located. The number of samples was a trade-off between representativeness and the real possibility of making vegetation and soil inventories in an area of difficult accessibility, during the short period of the wet season when plant species can be identified and soil samples can be taken with a hand auger. In each sampling site one 10 m × 10-m plot was delimited, and within the plot ten 1-m² sampling units were randomly chosen. In each of these 10 quadrats a complete floristic list was produced, and the cover of each species was estimated visually. Additionally, one soil sample was obtained with an auger in each quadrat, at depths of 0–20, 20–40 and 40–60 cm. The field data were collected in November 1997, that is towards the end of the growth cycle of

the dominant grasses, and when the entire savanna was accessible by vehicle. The 10 soil samples from each sampling site were used to determine relative water content (RWC) by gravimetry, while soil texture was determined in a composite sample by the international method of mechanical analysis. These textural analyses were performed in the Soil Laboratory of the University of Los Andes.

The second and more punctual scale is at the level of experimental plots within the larger area. The biomass and productivity studies were carried on in four permanent 10 m × 20-m plots, randomly chosen within the large study area, but having vehicle accessibility during most of the year. For statistical analysis each of these plots was considered as a block with two treatments, one grazed and the other fenced in November 1995, to exclude grazing by cattle. Vegetation was sampled before fencing, determining initial plant cover with the point-quadrat method (Bonham 1989), in 100 randomly chosen points, in each of the four plots. This sampling was repeated in the 2 following years at the same date. From the onset of rains in May 1996, a monthly sampling was started, harvesting plant biomass in four random 0.25-m² quadrats inside each of the four exclosures, as well as in the same number of quadrats in equivalent areas outside the fences. The biomass was clipped with a knife, at 10 cm high. Then the vegetation in the entire plots was clipped at the same height and the clipped material thrown away from the experimental plots. The plant samples of each 0.25-m² quadrat, within and outside the exclosures, were separated according to the four main grass species, while all other species were lumped together. Each fraction was divided into live and dead biomass, oven dried and weighed. The sum of the values for the four 0.25-m² quadrats was taken as the plant biomass per m², either for each species or for the total, green and dead biomass, thus obtaining a single value for treatment, block and sampling date.

The crown biomass, that is the above-ground plant material below 10 cm high, was sampled at the end of three growth cycles (November 1995, 1996 and 1997), and at the start of the cycles of 1996 and 1997. As these last two values, taken immediately after burning, were negligible, the crown biomass at the end of the growth cycle was considered to be crown production. This fraction of the above-ground biomass, obtained by clipping four random 0.25-m² quadrats, first at 10 cm high and then at the soil level, in the grazed and the protected savannas, was not divided by species. The four samples were summed up to obtain a single value for 1 m². The separation of the above-ground biomass above and below 10 cm was done to determine the amount of forage potentially available to livestock under conditions of moderate grazing pressure, considering the fraction above 10 cm as the forage on offer. The annual amount of forage available to livestock,

a fraction of the ANPP, was calculated as the sum of the positive biomass increments for each grass species and for all other species together, along the whole growing season.

ANPP was estimated as the sum of the forage available to livestock plus the yearly increment in crown biomass. Moreover, in the grazed plots the estimation of cattle feed intake was added to the ANPP value. A rough estimation of above-ground mortality was obtained as the sum of the positive increments in dead biomass for each species. Decomposition was estimated as the sum of the decrease in dead biomass between two consecutive sampling dates. Feed intake by livestock was estimated by taking as a base a daily intake equivalent to 6% of the animal live weight (Pearson & Ison 1987). With a stocking rate of 120 kg live weight ha⁻¹, the daily intake would be 7.2 kg ha⁻¹. The herd grazed in the hyperseasonal savanna for 5 mo during the wetter year of 1966 and 6 mo in 1997, since cattle avoid both the flooding and the dry periods, when they move either to the uppermost parts occupied by non-flooded savannas or to the bottomlands where semi-seasonal savannas stay green during most of the dry season. Therefore, the estimated yearly intake reached 108 g m⁻² in 1996 and 130 g m⁻² in 1997.

Below-ground biomass, 0–20 cm depth, was determined through four 10-cm × 10-cm samples inside and outside each enclosure, at the same dates when the 0–10-cm above-ground biomass was sampled. The biomass of the four 0.01-m² samples were summed and multiplied by 25 to obtain a single value of root biomass per m². Additionally, 10 random soil samples were taken from the topsoil (0–10 cm) to determine RWC by gravimetry. To describe and sample the soil profile, a trench was opened in one of the four permanent plots. The chemical analyses were performed at the Soil Laboratory of the University of Los Andes, with the standard methods of soil analysis.

Two-way analyses of variance (ANOVA) were used to examine general relations among variables, testing the significance of inter-block variability against all other variation factors. Thus, we tested for the effect of site (experimental plots) on crown and below-ground

biomass at the different sampling dates and under the two treatments. ANPP by species was tested for differences between blocks and 20 sets of data, according to species (5), treatment (2) and year (2). Total ANPP was tested for differences among blocks and 12 sets of data according to year (2), treatment (2) and the method by which ANPP was obtained (3). We also used two-way ANOVA to test for the effects of treatment and year on either total annual production or production by species, taking the four blocks as replicates in these cases. Furthermore, pairwise comparisons of crown and below-ground biomass, and of differences in above-ground production by species were evaluated through Student's t-tests. All statistics were performed with the Microsoft Excel[®] data analysis software.

RESULTS

Soil and soil water regime

The soil profile (Table 1) shows sandy loam (0–27 cm), covering the illuvial B horizon. From 48 cm downwards, the soil becomes extremely hard, even during the rainy season, roots are totally absent, and it has a strong yellow and red mottling, with abundant Fe and Mn concretions. This soil has been classified as an ultaquic tropalf (Ecosa 1980, Schargel & González 1972). Because of its slow internal drainage, it remains water saturated during the rainy season and dries up during the rainless season. Hence the generalized mottled and the indurated iron and manganese concretions. Besides, it is an extremely infertile soil, since at the rooting depth of grasses the cation exchange capacity is very low, total nitrogen and base saturation are low, while the amount of soluble phosphorus is negligible.

The field capacity (FC) and the permanent wilting point (PWP) of the two uppermost soil horizons respectively attain about 12% and 5% (Table 1), thus leaving about 7% of available soil water, whereas in the deeper layers both values are higher, with the available water ranging

Table 1. Physical and chemical characteristics of the soil profile in the exclusion plots. The soil is an ultaquic tropalf, with an illuvial B horizon forming a claypan at 40 cm depth. FC, field capacity; PWP, Permanent wilting point; sl, sandy loam; l, loam; cl, clay loam; scl, sandy clay loam.

Depth (cm)	Texture (%)				Water retention (%)		pH H ₂ O	Organic C (%)	Total N (%)	P (ppm)	CEC (cmol kg ⁻¹)	Base saturation (%)
	Sand	Clay	Silt	Text. Class	FC	PWP						
0–12	60	6	34	sl	12.61	5.08	4.80	1.91	0.11	20	3.41	28.7
12–27	66	10	24	sl	12.14	5.19	4.73	0.83	0.05	18	1.89	29.6
27–41	44	20	36	l	20.29	10.68	5.29	0.54	0.05	12	5.68	6.9
41–48	46	26	28	l	21.54	11.83	5.63	0.54	0.05	12	6.81	11.0
48–65	40	30	30	cl	23.29	14.86	6.00	0.54	0.05	8	8.71	20.9
65–120	46	30	24	scl	21.74	4.35	7.28	0.20	0.04	12	11.36	35.6

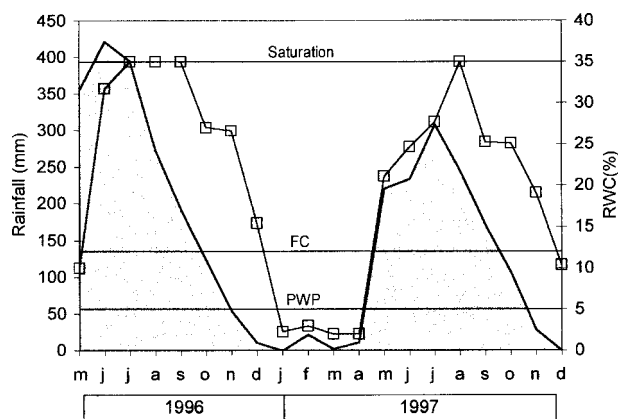


Figure 2. Monthly rainfall in El Samán, 20 km NE from El Frío, and soil relative water content (□) (RWC 0–10 cm, mean of 10 samples in each of the four experimental plots), from May 1996 to December 1997. FC, field capacity; PWP, permanent wilting point.

from 8% to 10%. The RWC of the wholly saturated soil attained 34%, therefore when water input is higher than this capacity, the soil becomes waterlogged or flooded. The topsoil relative water content in the permanent plots (RWC 0–10 cm), together with the monthly rainfall during the period of measurements at the nearest meteorological station (El Samán, 20 km away from El Frío), appears in Figure 2. As soil humidity did not differ significantly between the fenced and the grazed plots, all data were pooled in this figure. Notice how about 95% of the annual rainfall occurs during the rainy season, the 5-mo dry season being almost rainless. In the year before the onset of this study (1995), rainfall, at 1206 mm, was well below the long-term average (1969–1996, 1466 mm). In contrast, rainfall was 350 mm above the mean in 1996, while in 1997 it was 100 mm below the mean. The heavy rainfall in 1996 produced a large accumulation of rain water upstream from the dam that led to its breaching, causing an exceptional flood in the study area, from July to September, when the savanna stayed under water to a depth of 50 cm. As we will see later, this flooding had a conspicuous influence upon the ecosystem's composition and productivity.

Soil texture varied somewhat across the study area, ranging from sandy loam to silty loam. This textural heterogeneity is a normal feature of alluvial plains where the dynamics of deposition may suddenly change over short distances. The high proportion of silt strongly suggests that the area originated as an overflow alluvial plain, where fine sand and silt were deposited almost throughout by the overflowing waters, with localized sandy banks and a few cubettes in the bottomlands, where clay sedimentation took place (ECOSA 1980, Sarmiento & Pinillos 2001). The clay content increases with depth everywhere, often to about 30% or more, forming a well-developed illuvial B horizon. Vertical drainage is quite

Table 2. Frequency and mean cover (%) of the perennial grasses, considering the 22 sampling sites.

Species	Frequency	Mean cover (%)
<i>Panicum laxum</i> Sw.	1.00	51
<i>Paspalum chaffanjonii</i> Maury	0.68	9
<i>Leersia hexandra</i> Sw.	0.68	9
<i>Axonopus purpusii</i> (Mex.) Chase	0.18	2
<i>Elyonurus tripsacoides</i> H.B.K.	0.18	1
<i>Sporobolus indicus</i> (L.) R.Br.	0.18	1

slow as this clay-pan is one of the key factors responsible for the flooding of the savanna during the rainy season.

Floristic composition and species cover

In the 22 sampling sites (in ten 1-m² quadrats per site), the mean number of species and its standard deviation was 22.4 ± 4.2 , whereas in the total area sampled, that is in 220 m², 122 species were listed, most of them occurring in just one or a few sites. The Shannon Index H' for each site, obtained on the basis of species frequency, ranged from 2.44 to 3.26, with a mean of 2.83. The frequency and mean grass cover (Table 2) showed that *Panicum laxum* was the dominant species, being present in all sites and attaining a mean cover above 50%. *Paspalum chaffanjonii* and *Leersia hexandra* occurred in about two thirds of the sites and their mean cover was 9%. The other three grasses are minor components of the savanna.

In the four permanent plots, before grazing exclusion, a total of 34 species were found in 400 point-quadrats, with a mean of 18.5 species per plot and a diversity of 2.06. Both richness and diversity fell in 1996, probably due to the exceptional flood, to recover the following year (Table 3).

Biomass and productivity

At all sampling dates, *Paspalum chaffanjonii* reached an above-ground biomass well above that of the other three grasses (Figure 3). All the species had a similar seasonal

Table 3. Species richness (total number of plant species per 50-m² plot), and diversity (Shannon index H' calculated on the basis of plant cover). Means for the four experimental plots before fencing, and for the grazed and the ungrazed savannas in the following 2 y.

Year	Richness		Diversity (H')	
	Grazed	Ungrazed	Grazed	Ungrazed
1995	18.5	–	2.06	–
1996	12.0	8.0	1.23	0.94
1997	19.0	24.0	2.00	2.17

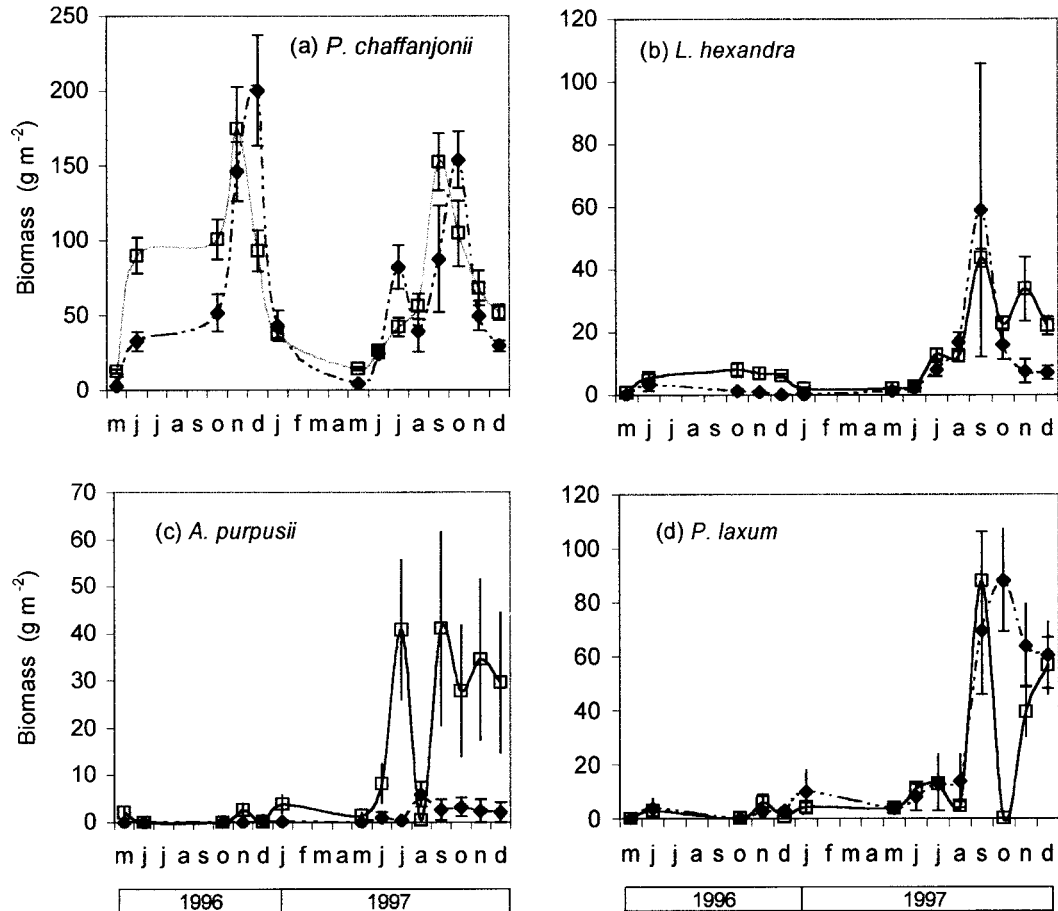


Figure 3. Biomass of the four dominant grasses, in the grazed (◆) and the protected plots (□), during the two growth cycles.

growth pattern, attaining their peak of biomass towards the end of the rainy season, to almost disappear during the 4-mo period of drought. At most dates, each species reached a lower biomass under grazing, but this effect was more evident in *A. purpusii*.

The green biomass peaked about 2 mo after the start of grass growth, to decline thereafter in the waterlogged soil, and recuperate somewhat after flooding in 1996, while in 1997 it reached its maximum after waterlogging to steadily decline with the end of the rains (Figure 4). The standing dead matter accumulates slowly during the rainy season to peak at its end. In both cases, only small differences between grazed and exclusion plots were apparent at each date. Both the accumulation of standing dead plant material and its decomposition are sharply seasonal processes. Dead plant material starts to accumulate 3 or 4 mo after the start of plant growth, with a rapid increase thereafter, to reach a peak towards the end of the rainy season (Figure 4). Decomposition is rapid during the rainy season, but stops when the dry season starts to impose severe limitations to the process (Figure 5). This means high decomposition

rates, 3–5 g d⁻¹, and this just considering the above-10-cm plant biomass.

The 0–10-cm above-ground biomass varied over the 3 y of sampling, sharply decreasing during the year of high flooding. This decrease continued in the exclusion plots in the following growth-cycle (Table 4). We are assuming that the crown-biomass peaks in November, at the end of the rainy season, as does forage on offer and, therefore that this peak corresponds to the annual production of this layer since the starting point, after burning, is negligible.

It is widely known that the sequential harvest method is not good enough to estimate below-ground production (Lauenroth 2000). However, with the few data available (Table 4), we can say that annual BNPP was almost two-fold higher in 1997 than in 1996, being in both cases greater than the initial value recorded at the end of the former wet season (November 1995). These figures certainly underestimate the real BNPP, since below-ground decomposition was not taken into account. However they suggest that, as occurs in most grasslands, in this flooded savanna more than half the primary production is allocated to below-ground plant structures.

Table 4. Above-ground biomass (0–10 cm) and below-ground biomass (0–20 cm). Means and standard errors for four plots. The pre-exclosure (November 1995) values are the starting points for both treatments. According to t-test, values followed by at least one similar letter are not significantly different at $P \leq 0.05$.

	1995	1996		1997
	November	May	November	November
Above-ground biomass (g m^{-2})				
Grazed	348 ± 23^a	–	116 ± 20^b	173 ± 13^b
Ungrazed	–	–	153 ± 19^b	59 ± 8^c
Below-ground biomass (g m^{-2})				
Grazed	723 ± 64^e	981 ± 65^e	815 ± 71^e	1634 ± 120^d
Ungrazed	–	1113 ± 173^{de}	838 ± 31^e	1573 ± 64^d

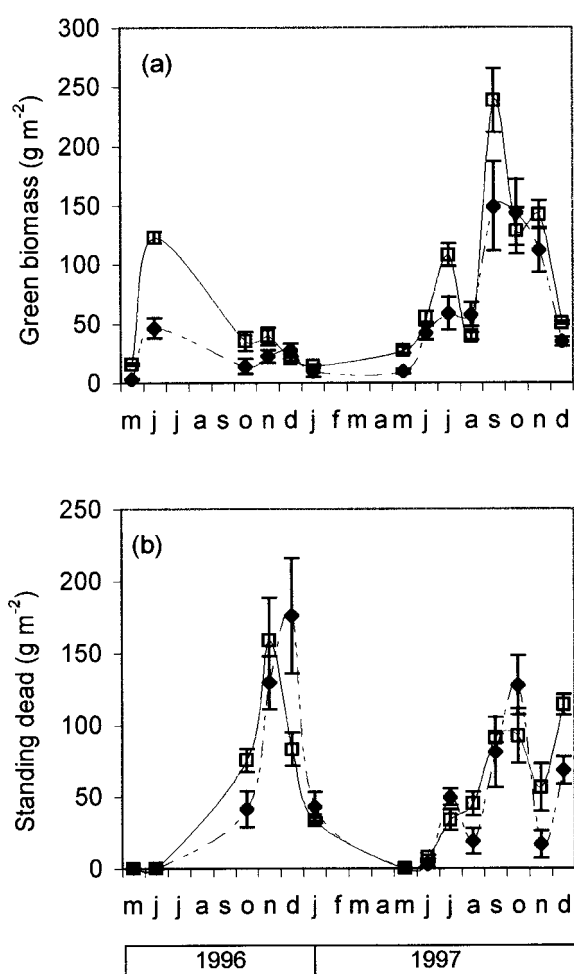


Figure 4. (a) Green above-ground biomass and (b) standing dead, in grazed (◆) and protected (□) plots, during the two growth cycles.

Differences among blocks were not statistically significant, except for the whole grassland ANPP ($P = 0.0004$) and for *Paspalum chaffanjonii* ($P = 0.015$). ANPP was calculated as (*) the sum of the positive increments in the above-10-cm biomass for each species; (**) by adding to

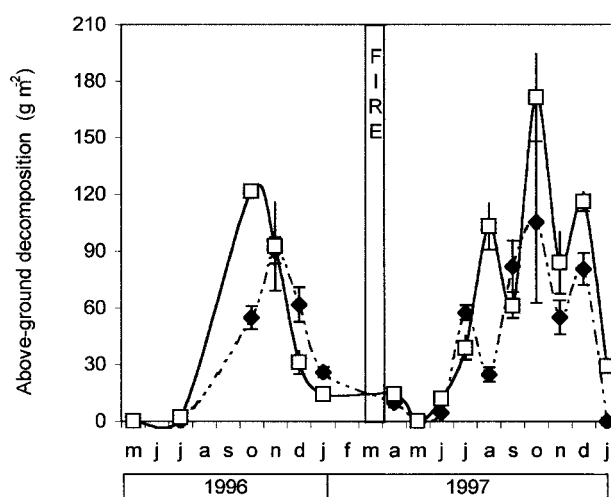


Figure 5. Annual pattern of above-ground decomposition in grazed (◆) and protected (□) plots, during the two growth cycles.

Table 5. Primary production ($\text{g m}^{-2} \text{y}^{-1}$) in grazed and protected plots, calculated as the sum of the positive increments in biomass for each species (*), including values of 0–10-cm above-ground production (**), and taking also into account cattle intake (***)

	1996		1997	
	Grazed	Ungrazed	Grazed	Ungrazed
Total ANPP (*)	236 ± 36	265 ± 38	428 ± 71	601 ± 58
Total ANPP (**)	352 ± 45	418 ± 43	601 ± 82	659 ± 68
Total ANPP (***)	460 ± 45	418 ± 43	731 ± 82	659 ± 68

these values the annual increase in the 0–10-cm biomass, (***) also adding to these last values cattle intake in the grazed plots (Table 5). In any case ANPP did not differ between treatments but differences between years were highly significant (Table 6). *Paspalum chaffanjonii* was the leading species in both treatments in 1996 but, according to the t-test, *Panicum laxum* reached a similar biomass in both treatments the following year, and other species

Table 6. Probabilities (P) from the ANPP ANOVA. When $P \leq 0.05$ for year and/or treatment and $P > 0.05$ for interaction, differences are significant ($n = 16$). See Table 5 for explanation of the different ANPP estimates.

	Year	Treatment	Interaction
ANPP *	0.001	0.109	0.241
ANPP **	0.002	0.335	0.955
ANPP ***	0.001	0.375	0.820

became equally important in the ungrazed treatment in 1997 (Table 7). ANPP of *Paspalum chaffanjonii* did not show differences between years and treatments (Table 8). The other three grasses, as well as the remaining species, did show significant differences between years. Other species were the only group responding to treatments while the results for *Axonopus purpusii* are inconclusive due to the significant interaction between treatment and year effects ($P \leq 0.05$). Notice, however, that the t-test indicated significant differences between treatments, for this species, in 1997 (Table 7).

DISCUSSION

Soils and soil water content

The data on RWC in the topsoil, together with the PWP, FC and saturation figures, allow a more precise delimitation of the dry and wet periods as they affect the natural vegetation. As can be seen in Figure 2, RWC rapidly decreases as the dry season progresses, reaching in January values well below the PWP. Certainly the deeper soil layers may maintain higher RWC values for some more days, but finally the entire profile will dry out completely. The 1996–97 dry period lasted for 4 mo. After the onset of the rainy season in May, RWC increased to stand between the PWP and the FC, but immediately afterwards the soil became water saturated (above FC) to stay so for 7 consecutive mo, 3 of them with a surface water sheet in 1996, and 1 mo in 1997. Obviously, a perched water table has been formed above the clay-

Table 8. Probabilities (P) from the ANOVAs for species above-ground production. When $P \leq 0.05$ for year and/or treatment and $P > 0.05$ for interaction, differences are significant ($n = 16$).

	Year	Treatment	Interaction
<i>Paspalum chaffanjonii</i>	0.798	0.580	0.704
<i>Leersia hexandra</i>	0.028	0.785	0.918
<i>Axonopus purpusii</i>	0.003	0.003	0.011
<i>Panicum laxum</i>	0.001	0.582	0.487
Other species	0.024	0.008	0.087

pan leading to this flood. As we already mentioned, the 1996 3-mo flood period was due to the breakdown of the dyke upstream from the study area caused by the nearly 500 mm of rain that fell in May and June. In 1997, a normal year as concerns rainfall, the soil remained water saturated for 6 mo, but it only was waterlogged in August.

Consequently, the topsoil in these savannas remains physiologically dry for about 4 mo each year, and certainly the entire profile at rooting depths dries out completely during this time. The behaviour of grasses during the dry season reflects these facts since the daily minimum leaf water potential in *P. laxum*, *P. chaffanjonii* and *L. hexandra* reaches values as low as -2.8 to -3.7 MPa (unpubl. data), surely a hard enough stress to, first, restrict leaf area to a minimum, and then transform the above-ground biomass to dry straw. Quite the opposite situation prevails during the rainy season, when RWC is continually above FC for 7 mo, and when the terrain may remain waterlogged for several weeks. Then, with a 4-mo dry season, and a 7-mo period of soil water excess, this savanna only has two normal half-months, when the soil is neither dry nor water-saturated. These two quite short periods of favourable soil water conditions result from the abrupt start and end of the rainy season, the high rainfall during these months, the negligible general slope of these plains, and the generalized presence of a nearly impermeable clay-pan close to the ground. All these factors combine together to produce the sharp seasonal contrast that characterizes hyperseasonal savannas, an ecosystem that could be considered a wetland if visited during the rainy season, or a quite dry grassland when

Table 7. Primary production ($\text{g m}^{-2} \text{y}^{-1}$) of the main grasses and all other species in grazed and protected plots. According to t-test, values sharing the same superscript letter are not significantly different ($P \geq 0.05$).

Species	1996		1997	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Paspalum chaffanjonii</i>	205 ± 30 ^{ab}	197 ± 50 ^{ab}	211 ± 39 ^a	168 ± 30 ^{ab}
<i>Leersia hexandra</i>	4 ± 2 ^c	13 ± 3 ^{bc}	67 ± 40 ^{bc}	71 ± 18 ^b
<i>Axonopus purpusii</i>	0 ± 0 ^c	8 ± 7 ^c	9 ± 2 ^c	89 ± 20 ^{ab}
<i>Panicum laxum</i>	17 ± 5 ^{bc}	13 ± 10 ^c	119 ± 10 ^{ab}	157 ± 50 ^{ab}
Other species	9 ± 1 ^c	34 ± 18 ^{bc}	23 ± 2 ^{bc}	115 ± 18 ^{ab}

seen towards the end of the dry season, just before the normal occurrence of fire.

Richness, diversity and dominant species

By its total number of species (122), mean number per site (22.4 ± 4.2), and the Shannon Diversity Index H' (2.83), this flooded savanna may be considered as a relatively rich tropical ecosystem, at least at this spatial scale of analysis, despite the fact that just a few species of grasses attain importance by their cover and frequency. In fact, 122 species in 220 m^2 is well above the richness of non-flooded savannas in the same region (Sarmiento 1996). We may see too (Table 3), how the species number in the experimental plots decreased in 1996, probably due to the exceptional flood, but the pre-flood values were already recovered the following year. Our data also suggest that richness may increase under grazing exclusion. Two contrasting processes seem to be at work, on the one hand, exceptional but not at all infrequent floods seem to reduce the number of species other than grasses, that is of species that might be considered as weeds. In this sense, floods clean the rangelands controlling undesirable species. On the other hand, even moderate grazing pressures lead to a reduction in richness and diversity.

It is well known that grazing affects the floristic composition of rangelands, decreasing the species grazed preferentially and promoting the growth of the neglected species. But the precise response of a given grassland community to different grazing modalities and pressures are far more complex than that. Thus, in a long-term experiment in a species-poor grassland in the UK submitted to various grazing treatments (Bullock *et al.* 2001), most species responded to grazing in some way, some of which, like the two dominant grasses, declined drastically, while most other species became more abundant. After 12 y, some new species appeared, while species richness either increased or decreased according to treatment. Still less is known about the effect of soil water on the composition of a sward. In the shortgrass steppe, in the US, irrigation led to sharp shifts in composition in a relatively short period of time (Lauenroth *et al.* 1978), and in an experimental study in the much more humid tallgrass prairie (Knapp *et al.* 2001), the plant community also changed with increasing water availability. In our case the floristic changes were due, first to the stress caused by an exceptionally severe flooding, and second by grazing exclusion.

Biomass, forage on offer and primary production

Although ANPP is limited to the period with available soil water, the adverse effect of soil water excess was also evident (Figure 6). The overall effects of herbivory

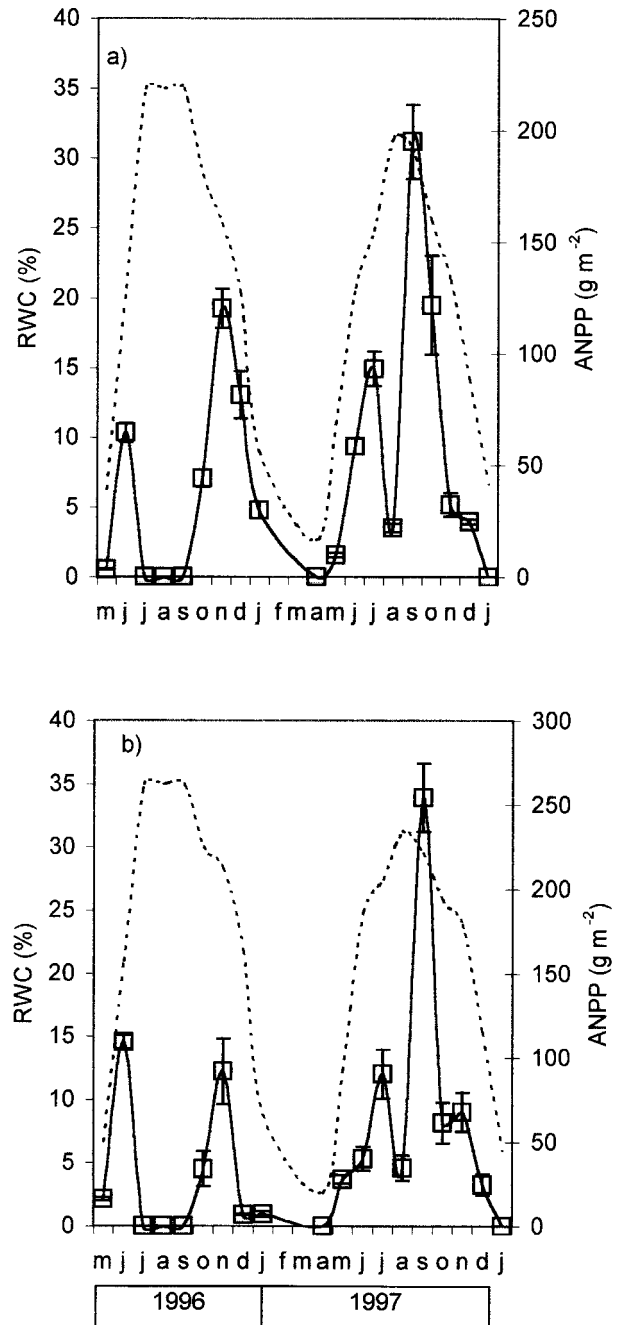


Figure 6. ANPP (\square) (above 10 cm), and soil relative water content (—) (0–10 cm), in the (a) grazed and (b) protected plots.

on grass growth and primary production of grasslands are still controversial, with some authors claiming co-evolutionary adjustments of the grazed plant to grazing by large, generalist herbivores, while others deny this possibility (Belsky 1986, 1987; McNaughton 1979, 1984, 1986; Milchunas & Lauenroth 1993, Milchunas *et al.* 1988, Westoby 1986). Some grasses may exhibit compensatory or overcompensatory growth when defoliated, but this functional behaviour has not yet

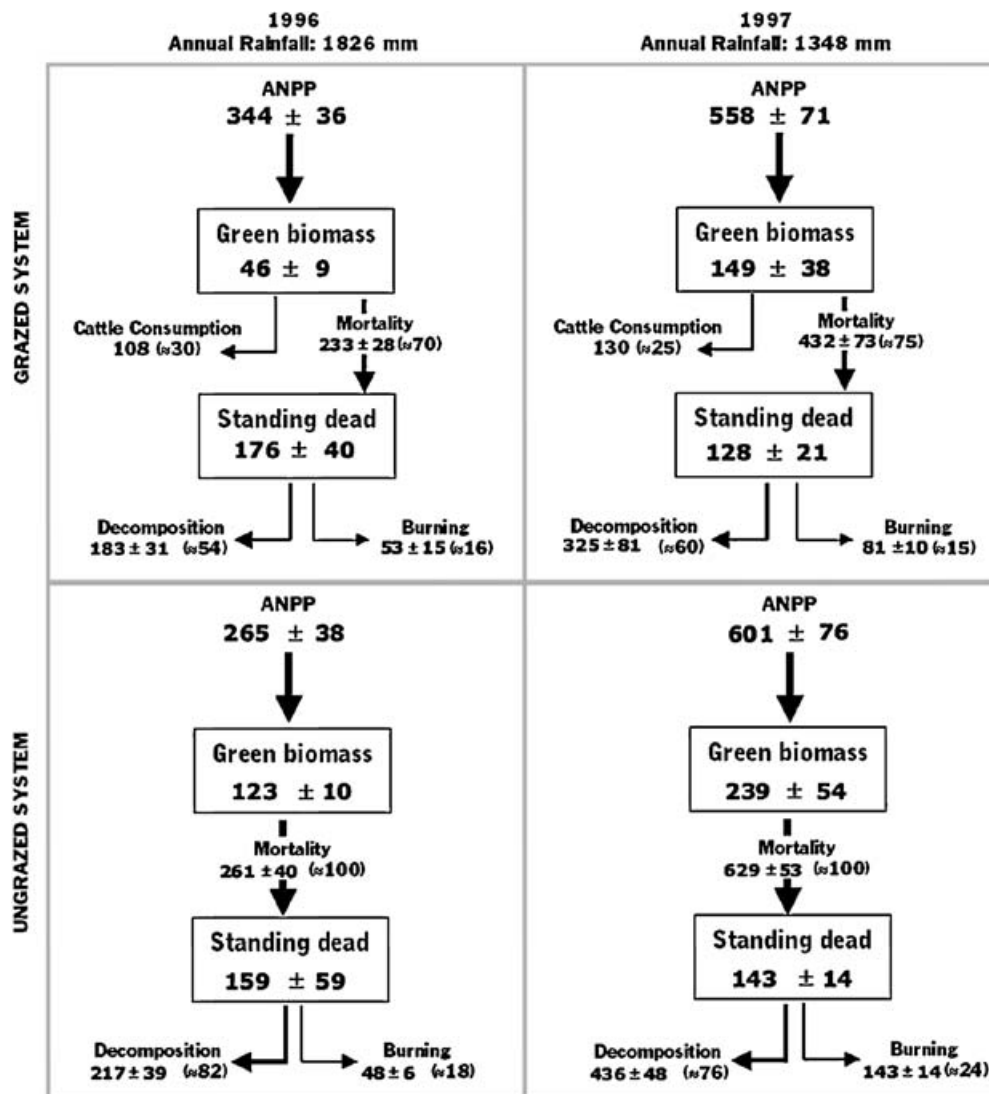


Figure 7. Stocks (g m^{-2}) and fluxes of above-ground organic matter (forage on offer, $\text{g m}^{-2} \text{y}^{-1}$), in the two systems, during the 2 years. The figures in parentheses are the respective rough per cent of the ANPP.

been reported in tropical American species. Probably, as tropical American savanna grasses did not evolve under significant grazing pressures by large, wild herbivores as the African grasses did, functional mechanisms to compensate losses by herbivory are absent. The relative importance of key functional processes in the response to grazing in a West African humid grassland was quantified through a modelling approach (Leriche *et al.* 2001). It emerged that the response of NPP to grazing intensity results from both positive and negative, direct and indirect effects on biomass removal, on light absorption efficiency, soil water availability, grass nitrogen content and productivity, and root/shoot allocation pattern.

It seems clear that in the case of the hyperseasonal savanna three independent factors: soil water excess, drought and grazing, act upon primary production,

and that the response of each species to each of these factors is different. Besides, fire and nutrient stress surely influence production processes in this system, but as they were common to both grazed and ungrazed plots, their action could not be disentangled from the three aforementioned external constraints. Further research is needed, but we want to emphasize that the composition of the savanna plant communities, the total richness and diversity, as well as its primary production, are noticeably influenced by the interannual variability in soil water conditions, while grazing or exclusion had less important effects, at least in the short-term.

Our estimation of total ANPP of the grazed savanna is basically coincident with the few available data, obtained through sequential cropping, on similar inundated

ecosystems in the Venezuelan Llanos (Bulla *et al.* 1980, González Jiménez 1979, Sarmiento & Vera 1979). In the *Loudetia simplex* savanna grassland at Lamto, Ivory Coast (Lamotte 1982), with 1200 mm annual rainfall, the peak of total above-ground biomass attained $700 \text{ g m}^{-2} \text{ y}^{-1}$, that is within the same order as our results. The close dependence of ANPP in grasslands on rainfall conditions is well known. Particularly in the North American prairies the adjustment between the predicted ANPP on the basis of annual rainfall and the real values are quite close (Knapp *et al.* 2001, Paruelo *et al.* 1999). It is interesting that using the equation provided by these last authors ($\text{ANPP} = 154.5 + 0.405 \text{ mean annual precipitation}$), the predicted ANPP under the rainfall conditions of the El Frio savannas reaches $748 \text{ g m}^{-2} \text{ y}^{-1}$, a figure entirely within the range of our values. This agreement suggests that all grasslands, either temperate or tropical, share some basic functional behaviour derived from similar vegetation structure and plant forms. Knapp *et al.* (2001) also found that 40% of the interannual variation in ANPP in the tallgrass prairie could be attributed to annual rainfall oscillations, pointing out the decisive weight of this natural variation on annual plant production, as seems to be the case in the Apure flooded savanna. Our data show that differences in primary production between both years, that is differences due to soil water excess, are the most important variation factor, while grazing is not important for the whole system and for most of the species under consideration. Two exceptions were *A. purpusii* in 1997 and other species in both years. The behaviour of *A. purpusii* may be easily explained on account of its high palatability, while the increase in other species in the protected plot may be explained either by absence of cattle trampling or by more mesic conditions derived from the larger biomass of the ungrazed savanna (Figure 4).

A further point we want to stress is the influence of spatial heterogeneity on primary production. The ANOVA indicates that differences among blocks introduce an important source of variation in the case of *Paspalum chaffanjonii* and, therefore, in the whole grassland ANPP. More experimental plots would be necessary for a more precise evaluation of this issue.

The stocks and annual fluxes of organic matter in the grazed and protected savannas in both years show that cattle intake accounts for 25–33% of the above-ground production (Figure 7), while the remaining biomass decomposes during the same growth cycle or is finally consumed by fire. In the ungrazed system above-ground decomposition is more important than burning, reaching 76–82% of the ANPP. The decomposition of the above-ground biomass seems to be much more important in this system than in non-flooded savannas where combustion by fire consumes the undecomposed standing dead plant material (Gillon 1983).

CONCLUSIONS

We have first to emphasize how in an ecosystem regularly switching from waterlogging to drought, soil water content appears as the key factor regulating plant composition, richness and primary production. With just 2 y of data, any generalization about the community changes that may be induced by interannual variation in rainfall, and therefore in the intensity or length of flooding, would be premature. However, it can be said that the aperiodic pulses of flooding are responsible for dramatic floristic changes and may therefore contribute to maintain species diversity.

Besides the key role played by soil water, grazing under the actual grazing pressure does not seem to influence forage production. In our case, the accumulation of standing dead material in the ungrazed savanna after the peak of growth probably hinders carbon assimilation, decreasing primary production to the level of the grazed system. This fact further ratifies the generalization that most grasslands, either tropical or temperate, having a strong dominance of below-ground biomass and productivity, seem to be minimally influenced by moderate grazing pressures from cattle or other large herbivores, since they represent relatively small changes in their carbon and nutrient cycling (Burke *et al.* 1996, 1999). However, we suggest that any possible effect of grazing on these hyperseasonal savannas, through the limitation of nutrient and carbohydrate translocation from the above-ground to the below-ground plant parts, would be more noticeable over a wider time frame.

The importance of each of the four codominant grasses relies heavily on the particular combination of soil water regime and grazing in any particular period. The balance among these perennial grasses shifted rapidly from one year to the next, maintaining the grassland community in a state of permanent non-equilibrium through the continuous oscillation around a hypothetical steady state.

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