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COMPARATIVE ANALYSIS OF EIGHT NEOTROPICAL SAVANNA ECOSYSTEMS: PRODUCTION-DECOMPOSITION INDEXES

ABSTRACT: Comparative studies of the functioning of eight neotropical savannas were conducted in Venezuela and Panąma. Savannas were classified in the following 4 types of increasing productivity: *Trachypogon* savanna, "Bajio" savanna, *Paspalum* savanna and *Hyparrhenia* savanna. Each savanna type was reprezented by sites ungrazed or grazed by cows. All stands, except for the flooded "Bajio" were burnt at the end of the rainy season. The rates of two ecosystem processes were measured: productivity (NPP) and decomposition. The index of productivity was the maximum biomass of ABVG (above ground biomass) and BLG (below ground mass of roots); this was measured at the end of the rainy season just before the fire. Decomposition rate was evaluated using litterbags with local litter or filter paper exposed in different layers of savannas.

ABVG production of biomass is highest in non-grazed *Hyparrhenia* savanna, where it reaches 19–20 g d.w.m^{-2} daily and 2850–2950 g d.w.m^{-2} in the rainy season. This is a very high figure rarely noted in grasslands. The lowest productivity –544 g d.w.m^{-2} ABVG in the rainy season – was noted in *Trachypogon* savannas. Roots constitute a small part of savanna biomass: 14–25% in *Hyparrhenia* savanna, and 6–45% in Venezuelan savannas. The biomass of roots is concentrated in the 0–10cm layer: 86–90% in *Hyparrhenia*, 40–72% in Venezuelan savannas.

The decomposition of litter evaluated for 6 Venezuelan savannas and calculated for the wet season ranges from 180 to 1126 g d.w.$^{-2}$. Higher decomposition occur in stands with higher productivity.

To the new findings can be assigned the results of comparative measures of decomposition on four levels (from soil to 40 cm above the ground surface). In the *Hyparrhenia* stand as much as 52% of decomposition takes place in the standing plants.

The OM budget calculations suggest that all 8 stands are characterized by an accumulation of organic matter; however, decomposition rate is underestimated as the fraction of OM decomposed in standing plants is not considered.

KEY WORDS: neotropical savannas, grass production/decomposition, decomposition of standing plants

1. INTRODUCTION

The aim of the investigations described here is an attempt to compare the functioning of different savanna ecosystems by an evaluation of production and decomposition of organic matter. The maximum standing crop of grass was treated as an index of production of the system, and the disappearance of litter and cellulose as an index of decomposition. It was assumed that the grasses achieve the maximum standing crop at the end of the rainy season; the rate of decomposition was estimated at the same time.

The four types of grass ecosystems called here savannas were examined by the author in Panama and Venezuela. The term "savanna" is used without analysing its different meanings, in accordance with Bourliere and Hadley (1970): "The term savanna is used in its broad sense to refer to tropical formation where the grass stratum is continuous and important but occasionally interrupted by trees and shrubs; the stratum is burnt from time to time and the main growth patterns are closely associated with alternating wet and dry seasons". Nix (1981) after analysis of rainfall measurements from 4000 climatic stations in savanna areas concludes that for savannas "seasonality of rainfall pattern (effective rainfall during the growing season and the duration and severity of the dry season or seasons) are of greater importance". Author suggests that greatest development of tropical savanna ecosystems occurs in zones with between 1000 and 1500 mm of annual rainfall. Similarly Cola (1986) and Walker (1987) stresses importance of strong seasonality of climate. Tropical savannas are ecosystems characterized by continuous herbaceous cover of mostly C4 grasses and sedges and discontinuous cover of trees and shrubs. Sarmiento and Monasterio (1975) describing American tropical savannas state, that extensive areas in Cuba, Colombian-Venezuelan llanos, the Bolivian llanos and the interior Brasilian plateau have a plant cover with a predominance of savannas.

2. STUDY REGIONS AND STANDS

All examined stands are located below 100m above sea level. Their position with coordinates measured at the nearest climatic stations are included in Fig. 1 description.

Climadiagrams (in accordance with Walter and Medina 1971) for the 4 regions are shown in Fig. 2. All locations meet the requirement of clear seasonality emphasized by Nix (1981). The dry and wet seasons follow each other without any transitory period (Fig. 3). Venezuelan stands are located in a visible humidity gradient which does not however exceed the limits of 1000–1500 mm set by Nix (1981). Panamanian stands are characterized by a slightly heavier rainfall reaching 1973 mm per year. It seems probable that, as Lamotte and Bourliere (1983) suggest, the savanna of the Panamanian Isthmus is a secondary ecosystem, introduced by man on the site of a forest. However, the savanna complies with the description by Bourliere and Hadley (1970) quoted above. It has been established that the territory of today's Panama was covered mainly by different types of permanent grazing land ecosystems. According to the UNESCO/UNEP/FAO Report (1979), the extent of tropical grazing land ecosystems in Panama is 1 140 000 ha (crops 430 000 ha, other 80 000 ha); in Venezuela, permanent

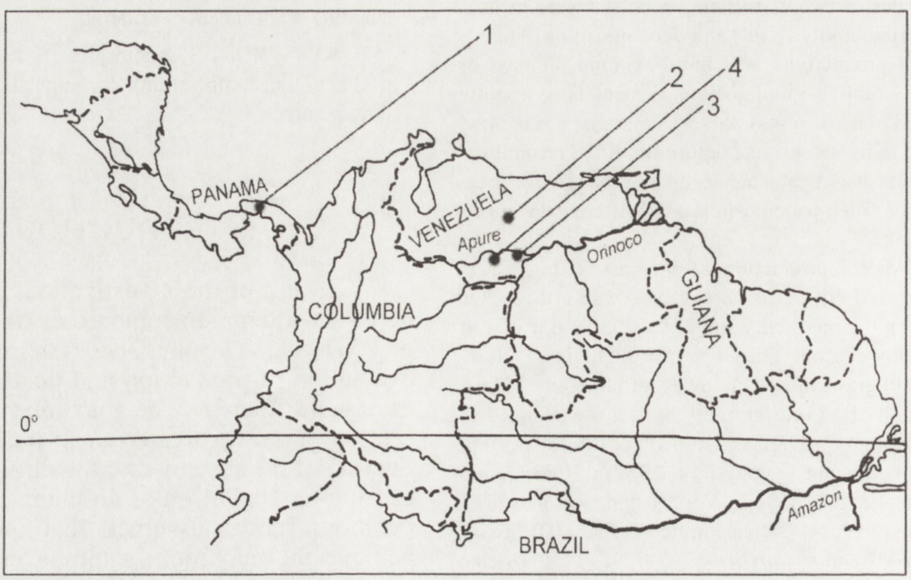

Fig. 1. Localization of 4 studied areas marked on the map. Geographic coordinates and names of the nearest climatic station are following: 1. *Hyparrhenia* savanna – 9°05'N 79°23'W, Tocumen Airport, Panama; 2. *Trachypogon* savanna – 8°56'N 67°23'W, Calabozo Scientific Station, Venezuela; 3. *Paspalum* savanna – 7°54'N 67°30'W, San Fernando City, Venezuela; 4. Bajio savanna – 7°33'N 69°10'W, Mantecal City, Venezuela.

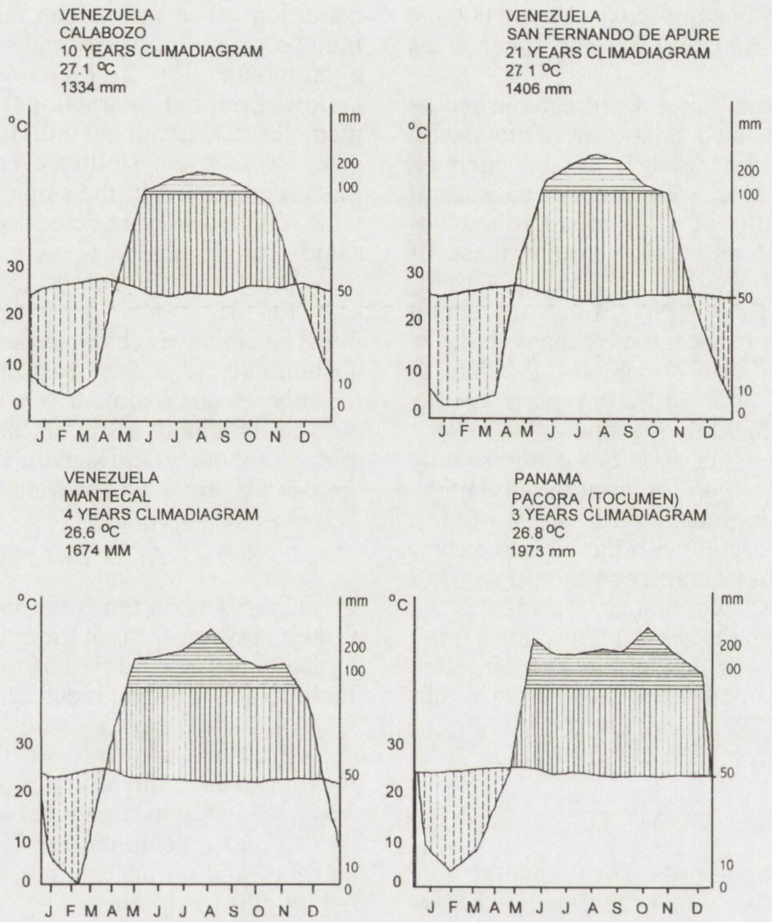

Fig. 2. Climadiagrams for 4 studied areas. Sources: Ramia 1974, Ramia and Montes 1975, Walter and Medina 1971. Annual average values for stands are indicated for the temperatures and the sums of precipitation. The deficits and surpluses of water are visible. Data from nearest climatic stations.

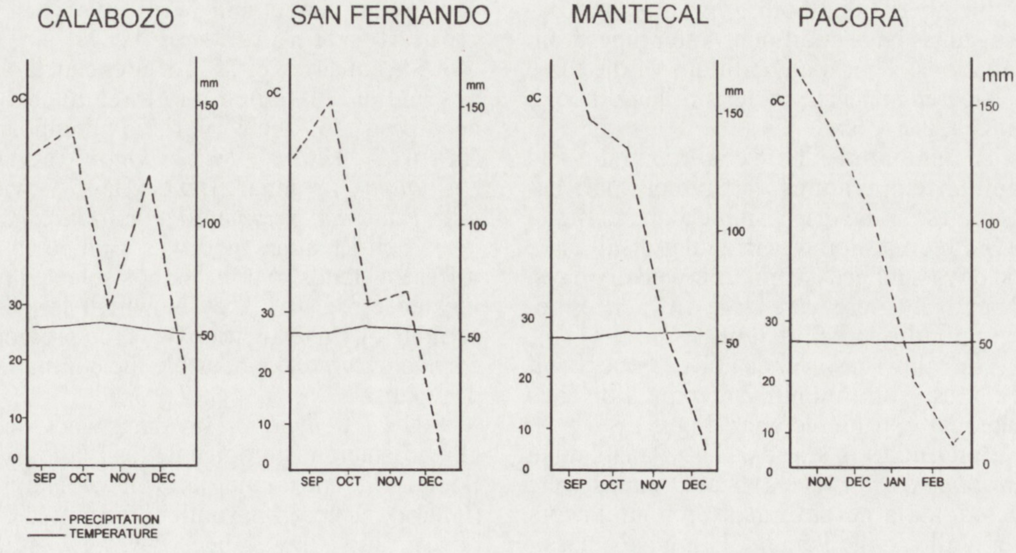

Fig. 3. Monthly sums of precipitation and means of temperature in the period of transition from rainy to dry season at four savanna areas (September–December). Long term data.

grasslands and pastures cover 13 900 000 ha, arable land 4 600 000 ha, and other areas 24 000 ha.

Eight studied sites were established in four areas. In each area paired plots with similar vegetation and different management were selected. Each plot was visited several times and samples of grass aboveground biomass (ABVG) and belowground mass of roots (BLG) were collected. Evaluation of savanna productivity (Pn) from maximum grass biomass is accepted by many authors. Piedade *et al* (1992) compare the data of some authors from different parts of the world using "maximum biomass" index for tropical herbaceous species. Authors state that *Echinochloa polystachya* (Kunth) Hitchc achieves very high annual Pn of 99.3 t ha^{-1}, what "is comparable with the highest values ever recorded for natural communities". The value 88 t ha^{-1} was noted (Beadle *et al.* 1985) for elephant grass (*Pennisetum purpureum* Schumach.) under management. It is worth to remained here that Lieth and Whittaker (1975) estimated the Pn of tropical rain forest to be around 25 t ha^{-1} y^{-1}.

2.1. CLIMATE

Venezuelan stands. The climadiagrams (Fig. 2) show the long term climatic characteristics of the study sites. Calabozo (*Trachypogon* savanna) is the driest area with 1334 mm of yearly precipitation, San Fernando (*Paspalum* savanna) has 1406 mm and Mantecal (Bajio savanna) 1674 mm. It should be remembered that both, *Paspalum* and Bajio savannas have additional water input from inundations. Thermic conditions of the three investigated areas are rather similar although Mantecal is cooler.

The amplitudes between maximum and minimum temperatures were rather small, being greatest in the driest site, Calabozo (up to 17°C). Precipitation was irregular on all three sites: days with heavy rain followed dry days, and similarly there were large differences between monthly precipitation.

The rainy season ends in December in all three sites. Total monthly precipitation falls dramatically from October (Fig. 3).

Panamanian stands. The Panamanian *Hyparrhenia rufa* (Nees) Stapf. stands were selected in large savannas area in Pacora River Valley. The Panama Isthmus is classified within the humid tropics and is characterized by seasonal changes in climatic conditions. The dry season lasts about four months (January–April) and the wet season eight months (Fig. 2). Meteorological observations from the international airport Tocumen, located about 30 km from the study plots, were used. Both the airport and the plots are situated in the same large lowland with rounded hills covered by grass, at the same altitude (Phot. 1). A rapid transition from the dry to wet season is typical of this area (Fig. 3).

The climate is characterized by very high air humidity. The drier part of the day lasts for only 8 hours (from 10 a.m. to 6 p.m), during the remaining 16 hours the relative humidity is about 80–90% in the dry season and up to 100% in the wet season.

2.2. SOILS AND PLANT COVER

The Venezuelan savannas cover approximately one third of the country; they are gradually being modified by intensifying agriculture and growing industry.

All studied stands were located in the area of "Llanos" which covers the central part of Venezuela with altitudes of 50–500 m above sea level, mean annual temperature of 27.5°C, mean precipitation of 800–1200 mm per year, and an accentuated dry season of 6–8 months (Velasques 1965). The "Llanos" are delimited by the Andes (north and west), the Cordillera de la Costa (north), the delta of the Orinoco (east) and the Orinoco River (south). All savannas in this area have been well defined and described as tropical savannas (Sarmiento and Monasterio 1975; Gonzales Jimenez *et al.* 1981).

Savannas cover 75% of Venezuelan Llanos and are classified into three main types according to their floristic composition (Ramia 1967): *Trachypogon* savanna, *Paspalum* savanna, Banco-Bajio savanna with *Panicum laxum* and *Leersia haxandra.*

Each savanna type was studied in two different stands. All the stands selected were located close to places in which long-term ecological investigations were previously carried out to make possible the comparisons of results.

The *Trachypogon* savannas were located at the Estacion Biologica de los Llanos of the Sociedad Venezolana de Ciencias Naturales (Guarico State, 8 km south of the city of Calabozo) and have been widely studied (McNeil 1964; Eden 1967; San Jose 1980). Two ungrazed and unburned stands

Phot. 1. Panamanian not grazed *Hyparrhenia* stand in dry season (Panama, Pacora River Valley).

Phot. 2. Sampling in *Hyparrhenia* not grazed stand at the end of rainy season when according to our assumptions the grass reach maximum biomass (Panama, Pacora River Valley).

Phot. 3. Overgrazed *Hyparrhenia* pasture in dry season; bare spots are visible. The pasture was located in a distance of few meters from not grazed *Hyparrhenia* stands.

Phot. 4. *Paspalum* savanna in La Guanota farm (Venezuela, San Fernando region).

were selected: *Trachypogon* 1 on red lateritic soil and *Trachypogon* 2 on gray sandy soil. Table 1 gives the main characteristics of these soils. Lopez *et al.* (1981) have described this lateritic soil (known as "arrecife" or "ripio") in detail. They found granules and ferritic concretions which had formed from silicated particles cemented by iron and other metals; chemical analysis found large amounts of SiO_2, Al_2O_3 and Fe_2O_3. San Jose and Me- dina (1977) showed that lateritic soil limits soil water movement and growth of plants. Smith *et al.* (1977) consider the superficial ferruginous horizon as a lithoplintic one. Low levels of exchangeable ions and permeability indicate the low fertility of these soils (San Jose and Garcia Miragaya 1979).

The plant cover of' these savannas was composed of few grass species. At the *Trachypogon* 1 stand, plant biomass was represented by *Trachypogon plumosus* Nees (60%) and *Axonopus pulcher* Kuhlm. (20%). On the stand *Trachypogon* 2, three species covered 100% of the area as genus *Trachypogon* appeared here with two species, *T. plumosus* Nees and *T. vestitus* Andersson, Velasques (1965) and Monasterio and Sarmiento (1968) give a detailed description of the phenology of these grass species. Both *Trachypogon* stands belong to bunchgrass savannas with grass heights of 30–50 cm at *Trachypogon* 1 and 60–70 cm at *Trachypogon* 2 stand.

The *Paspalum* savanna stands were located at the south bank of the Apure river, near to the city San Fernando de Apure , in a large farm called "Hato la Guanota". In 1961 the fields of La Guanota were closed by dams to accumulate the rain water and reduce dry season desiccation. *Paspalum* 1 stand was moderately grazed by cattle, *Paspalum* 2 was not grazed and was located on the gentle dam slope.

The dominant species at both stands was *Paspalum fasciculatum* Willd. ex Fluegge (90% on non-grazed and 60% on the grazed stand). The main associated species were *Teramnus volubilis* Sw. (20% on grazed stand), *Malachra* sp. Borraja (P) and *Setaria geniculta* (Lam.) Beauv. *P. fasciculatum* grew up to 1.8 m at the non-grazed stand and 1.4 at the grazed one. This grass is green during the dry season, but it is not very palatable for cattle when mature because of its strong, woody stems (Escobar 1977). For this reason *Paspalum* savanna is commonly burned in Venezuela at the beginning of the dry season. Ramia (1978) gives a phenological description of this species.

The soils are fertile alluvial clay loams (Ramia 1967). Table 1 shows a relatively high content of organic matter in the grazed plot; the lower amount in *Paspalum* 2 stand 1 is probably caused by erosion of upper soil particles by water during the rainy season due to it's location on the dam slope. Escobar (1977) reports 2–3% of organic matter in the upper layers of these soils.

The Bajio stands were located in the "Modulo Experimental de Mantecal" (Apure state). The "bajio" savanna was described by Ramia (1967) as a flooded savanna located between depressions ("esteros") and small hills ("bancos"). A large area of these savannas (up to 1 million hectares) was closed by dams in the last 10 years in order to control inundation and increase grass and cattle production. Those dams form a net of cells called

Table 1. Selected soil characteristics of studied savannas plots

Stand		Organic matter	pH	Nitrogen (%) dw	Phosphorus (ppm)	Humic acids (%)
TRA	1	1.40±0.08	5.59±0.32	0.070±0.018	4.5±0.6	62.9
	2	1.97±0.25	5.2±0.0.37	0.036±0.027	13.6±0.9	69.5
BAJ	1	2.01±0.37	5.15±0.25	0.054±0.020	14.4±1.7	74.7
	2	1.32±0.49	5.55±0.44	0.030±0.002	22.5±6.2	76.2
PAS	1	2.09±1.36	5.38±0.40	0.074±0.011	7.75±1.6	62.7
	2	0.91±0.27	5.70±0.29	0.045±0.010	10.8±2.8	n.d.
HYP	1	3.3	4.20	n.d.	n.d.	n.d.
	2	3.2	4.15			

TRA – *Trachypogon* savanna (1 – lateritic, 2 – sandy); PAS – *Paspalum* savanna (1 – grazed, 2 – not grazed); BAJ – Bajio flooded savanna (1 – grazed, 2 – flooded); HYP – *Hyparrhenia* savanna (1 – ungrazed, 2 – grazed); n.d. – not determined.

"modulos" of about 3200 hectares each. Modulos have been studied and described by Alio Ming *et al.* (1968); Corrales and Gonzales (1973); Perez *et al.* (1974); and Gil Beroes (1976). Bajio 1 stand being out of the influence of the dams, was naturally flooded with 30–40 cm of rain water for about 6 months. The Bajio 2 stand, directly under the influence of impoundment, was flooded with 1.4 m of water in deepest points. Depending on the management of the sluice gates, the water can cover the savanna all the year.

Bajio savannas are covered by a mixture of two dominant grasses, *Panicum laxum* Swartz and *Leersia haxandra* Swartz. Other important species are *Eragostris cutiflora*, *Paspalum chaffanjonii, P. orbiculatum* Poir, *Sporobolus indicus* (L.) R. Br., *Eloacharis minima, Trichospira verticillata* (L.) S.F. Blake and *Cynodon dactylon* (L.) Pers. (Ramia 1972, 1974; Entrena 1976; Gomez 1976). Some of these grasses are very palatable for cattle, having high nutritive value (Bartoli 1976; Gonzales 1977).

The area has been described as a recent alluvial plain or interior delta, with deep soils mainly composed of heavy clay silts (Schargel and Gonzales 1973). The main nutrients (N, P, Ca, K) appear in medium or low content (Lopez-Hernandez and Manzo Lares 1981). Organic matter content ranges around 2% (Table l). High content of humic acids is characteristic for flooding areas.

Savanna in the Panama Isthmus is located within the humid tropical jungle zone. For many reasons about 40% of this area is now deforested, including 12% used as pastures. A spontaneous tendency to cut down forests resulted either in a rapid erosion of lighter soils or in hardening of lateritic soils. Heavy rains and exposure to strong sunlight after clearing caused the destruction of soils. However, not all deforested areas have recently been created. Archeological investigations indicate that long before the development of contemporary agriculture the Panama Isthmus was managed by the Indians. According to the opinions of staff of the local university and the FAO Station the study area has been deforested since those days.

The study plots were located about 50 km north-east of Panama city, in the Pacora River basin. This part of Panama consists of low rolling hills sparsely covered with single trees or clumps of shrubs. The number of shrubs increases with declining altitude towards the river, and they form a dense bush along the Pacora bank. The plots were situated on a gentle slope exposed to the west, on both sides of a path. The area on one side of the path was grazed by cow, and the other side was not grazed but burnt off when the seeds had been produced. Such "seed reservations" are preserved in this region every several years to enrich heavily grazed pastures with seeds. Our "seed reservation" was ungrazed for two years.

A 0.5 ha plot on either side of the path was fenced after the first sampling. These were almost homogenous stands of *Hyparrhenia rufa* (Ness) Stapf. In Panama this grass is called "faragua", in other countries of Latin America "jaragua". It was introduced to Panama in 1914 (Bennett 1968). Its nutritive value is not very high but it is commonly cultivated as it is well adapted to Panamanian conditions and preserves some green leaves over the dry season. According to Bennett (1968) and McCorkle (1968) it is one of the most common grasses in Panama.

The soils of the *Hyparrhenia* plots were formed as an old alluvial terrace. Clay and sandy clay loam textures are generally observed in the soil profile (more detailed characteristics can be found in Breymeyer (1978). Fertility of these soils is low. The content of phosphorus is particularly low; also the content of potassium is rather low throughout the profile. The surface horizon, generally of small thickness, contains 2.7–3.6% organic matter (Table1). Low contents of K and high contents of iron and aluminium oxides were noted. This is an effect of weathering under very humid climatic conditions where such elements as Ca, K and Mg are rapidly released from the soil, while Al and Fe enrich the dispersed phase of the soil (Breymeyer 1978).

3.METHODS

Venezuelan savannas. All samples were collected at the end of rainy season, during the last week of November and the first days of December 1978. The decomposition experiments were carried out over period of about 50 days, from October to December 1978, at the end of the wet season.

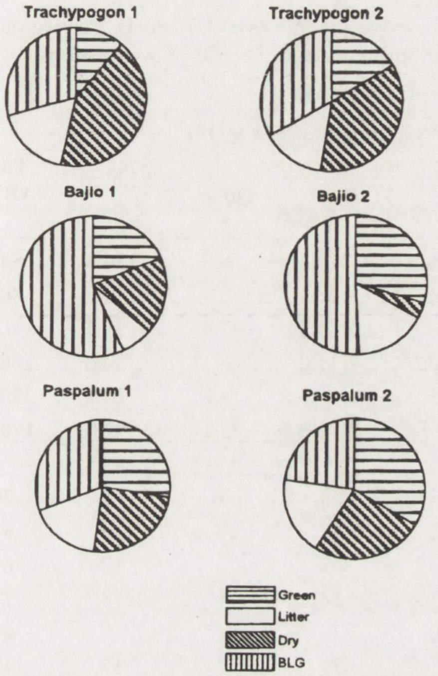

Fig. 4. Percentage contribution of four fractions of plant material in total biomass at six Venezuelan savanna stands. BLG – belowground parts of plants

Soil samples (7–10) were taken from each stand using corers of 100 cm^2 and 10 cm^2 (the smaller one for sampling in lateritic and stony soils). The depth of samples was 15 cm, they were stored in plastic bags, carried to laboratory, frozen and analyzed.

Plant samples: Aboveground plant biomass was estimated in 15–20 circular samples of 0.25 m^2 using a randomly-placed metal ring. The grass inside the ring was cut and the surface litter was collected. Grass was separated into live and dead fractions. The same procedure was applied in the case of litter from the *Paspalum* stands where a tight mixture of live and dead stems covered the surface of the soil. Additionally, 5 samples of grass from each stand were separated into stems and leaves.

The roots were sampled using 10–20 cores (l00 cm^2). Each soil core was divided into three depths: 0–10 cm, 10–20 cm, 20–30 cm. The roots were separated, dried and weighed. Fine roots were not separated and considered as a mixed organic fraction.

All fractions of plant material were dried for 3 days at 90° C and weighed.

The decomposition rate was studied using the litter bag method (Wiegert and McGinnis 1975). Two kinds of material were exposed for decay in each stand: 20 bags with grass litter and 60 bags with cellulose filter paper. In each stand 40 samples of 10 g fresh litter were weighed in the field; 20 samples were closed in nylon mesh (5 × 5 mm) and exposed for 50 days at the soil surface. The other 20 samples were stored in paper bags, dried and weighed in laboratory to obtain the ratio fresh/dry weight. Cellulose filter papers were dried and weighed in a laboratory earlier. Each piece was labeled and placed in a nylon net bag. The set of 60 filter papers were exposed in each stand at three different levels: 20 were laid on the soil surface, 20 were hung between the grass at 10 cm height and 20 were buried at 10 cm depth. In this way several levels of decomposition in the savanna were sampled. After the same exposure time, the litter and filter paper bags were collected, cleaned, dried, weighed, burned and again weighed to obtain the dry weight and ash content. The loss of weight during the exposure time was treated as an index of decomposition rate at the site.

Panamanian savannas. Plant biomass was estimated using 10 circular samples of 700 cm^2 each, selected at random, in which the vegetation was clipped at the ground surface (Phot. 2). From the clipped area soil cores were taken to a depth of 20 cm. They were divided into two 10-cm layers and washed over mesh screens to extract roots. The grass was dried at 60–80°C and weighed.

The rate of cellulose decomposition was measured in 3 layers: upper soil layer, the soil surface and grass layer by exposure of filter papers.

The described set of samples was taken twice: in March, during last weeks of the dry season (expected minimum biomass) and in August–September in the middle of the wet season (expected maximum biomass). After the first sampling an area of about 0.5 ha was fenced in each plot and left untouched for five months, until the second sampling of highest plant mass.

4. RESULTS

4.1. PLANT PRODUCTION

Venezuelan savannas. Total biomass measurements for all 6 stands show the highest production values for *Paspalum* savannas (2204–4196 g d.w. m^{-2}) and the lowest for *Trachypogon* (768–1195 g d.w.m^{-2}) (Table 2).

Table 2. Composition of fractions of plant biomass A. above ground (ABVG) and B. belowground (BLG) in 6 Venezuelan savannas (peak of vegetation biomass at the end of wet season)

A. Above ground biomass fraction (ABVG)

Stand		Aboveground biomass fractions (ABVG) grams d.w. per 1m^2							
		Grass fractions					Others	Litter	**Total ABVG**
		Green grass	Dry grass	Leaves	Stems	Grass total			
TRA	1	85.0	325.4	271.4	139.0	410.4	-	134.4	**544.8**
	2	196.8	429.0	489.1	136.7	625.8	3.8	170.7	**800.3**
BAJ	1	251.1	233.7	339.9	144.9	484.8	47.5	93.4	**625.7**
	2	635.0	76.0	243.0	393.0	711.0	-	350.0	**1061.0**
PAS	1	1152.6	1015.7	874.4	1293.9	2168.3	14.8	722.1	**2905.2**
	2	726.8	563.4	475.1	815.1	1290.2	23.1	392.0	**1705.3**
		Percentage							
TRA	1	21	79	66	34	53	-	17	**70**
	2	31	69	78	22	52	-	14	**67**
BAJ	1	53	47	70	30	52	-	17	**69**
	2	89	11	37	63	58	1	18	**77**
PAS	1	52	48	40	60	36	4	7	**47**
	2	56	44	37	63	31	2	17	**47**

B. Belowground biomass fractions (BLG) and total biomass

Stand		Belowground biomass fractions (BLG) grams d.w. per 1m^2						
		Depth (cm)			Total roots	SOM	**Total BLG**	**Total ABVG + BLG biomass**
		0-10	10-20	20-30	0-30			
TRA	1	52.8	54.3	36.6	143.7	79.9	**223.6**	**768.4**
	2	112.0	107.9	45.4	265.3	129.8	**395.1**	**1195.4**
BAJ	1	436.1	75.8	84.6	596.5	108.4	**764.9**	**1130.6**
	2	381.4	116.5	29.7	527.6	564.0	**1091.6**	**2152.6**
PAS	1	108.6	94.2	52.3	255.1	1035.9	**1291.0**	**4196.2**
	2	172.1	40.8	42.1	255.0	243.7	**498.7**	**2204.0**
		Percentage						
TRA	1	7	7	5	19	10	**30**	**100.0**
	2	9	9	4	22	11	**33**	**100.0**
BAJ	1	3	2	1	6	25	**31**	**100.0**
	2	8	2	2	12	11	**33**	**100.0**
PAS	1	33	6	6	45	8	**53**	**100.0**
	2	18	6	1	25	27	**53**	**100.0**

TRA, BAJ, PAS – see Table 1.

The two *Trachypogon* sites show similar proportions between biomass fractions although lateritic *Trachypogon* 1 had lower absolute green grass biomass and belowground parts biomass. Similar results were obtained by San Jose and Medina (1977) and San Jose and Garcia Miragaya (1979). There are some differences in the proportion of fractions of plant biomass (Table 3; Fig. 4), the roots show tendency of deeper penetration in the lateritic soil of *Trachypogon* 1 stand (Fig. 5).

The main differences between two "Bajio" stands are much larger amount of biomass in flooded "Bajio" especially in the fractions of "green grass", "litter", and "belowground biomass"; dead biomass is larger in nonflooded Bajio 1 (Fig. 4). The plant total biomass of "Bajio" 2 (flooded) is almost 50% higher than Bajio 1. Several papers refer to

Table 3. Allocation of biomass fractions in three types of Venezuelan savanna. Indexes counted as ratios of aboveground (ABVG) and belowground (BLG) biomass registered at the end of rainy season

Stand		ABVG/BLG	Green Grass/Dry Grass	Grass/Litter	Leaves/Grass total
TRA	1	2.44	0.26	3.05	0.66
	2	2.03	0.46	3.67	0.78
BAJ	1	0.89	1.07	5.19	0.34
	2	0.97	8.36	2.03	0.34
PAS	1	2.25	1.13	3.00	0.40
	2	3.42	1.29	3.29	0.37

For explanations compare Table 1.

low biomass of plants in natural Bajio areas (Entrena 1976; Gil Beroes 1976; Gonzales Jimenez and Escobar 1976a, b; Gomez 1976; Gonzales Jimenez *et al.* 1981) in contrast with high values found in areas under the effect of dams (Ojasti 1978; Bulla *et al.* 1980, 1990). According to the root distribution, both Bajio stands show distinct concentration of roots in the upper 0–10 cm layer (70–80%) (Fig. 5).

Both *Paspalum* stands show high biomass values similar to those reported by Gonzales Jimenez and Escobar (1976a, b), Escobar and Medina (1977), and Gonzales Jimenez *et al.* (1981). A comparison of *Paspalum* 1 (flooded and grazed) to *Paspalum* 2 (not grazed, located on the slope of a dam) indicates much higer productivity in *Paspalum* 1. The proportions of all plant matter fractions are almost identical in both stands (Fig. 4). Not flooded *Paspalum* 2 stores almost 70% of root biomass in 0–10 cm soil; flooded *Paspalum* 1 – only 45%. Simple indexes characterizing the biomass allocation in three types of savanna were calculated (Table 3). The two wetter stands (Bajio and *Paspalum*) have higher proportion of green/dry plant parts biomass. Bajio is characterized by reasonably large amounts of BLG biomass. All three studied types of savannas maintain more biomass in stems than in leaves.

In all 3 types of Venezuelan savannas, root biomass decreases rapidly below 10 cm

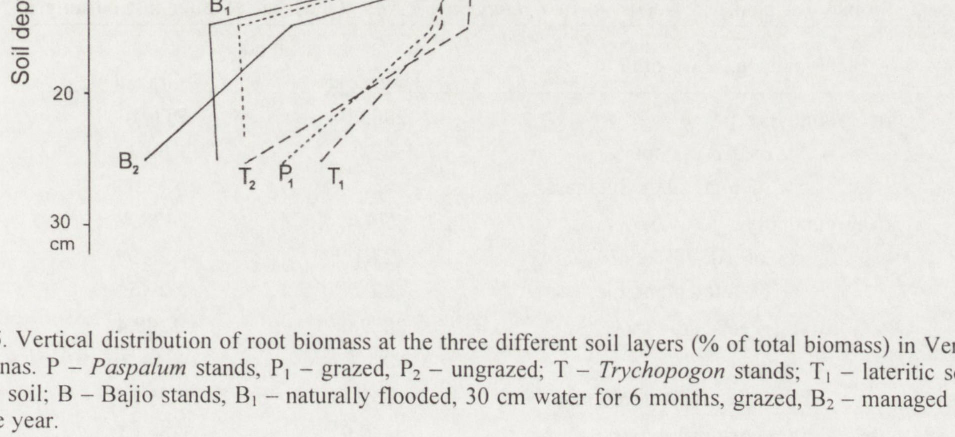

Fig. 5. Vertical distribution of root biomass at the three different soil layers (% of total biomass) in Venezuelan savannas. P – *Paspalum* stands, P_1 – grazed, P_2 – ungrazed; T – *Trychopogon* stands; T_1 – lateritic soil, T_2 – sandy soil; B – Bajio stands, B_1 – naturally flooded, 30 cm water for 6 months, grazed, B_2 – managed flooding all the year.

Table 4. Biomass of the plants from two Panamanian stands of *Hyparrhenia rufa* at the end of dry season (March)

Plant parts g. d.wt. m^{-2}	Stand	
	Ungrazed	Grazed
Aboveground green	445.0	165.2
% of ABVG total	13.1	36.8
Aboveground dry	2961.3	283.4
% of ABVG total	86.9	63.2
Total ABVG	3406.3	448.6

depth (Fig. 5). In response to flooding, plants show some characteristic tendencies such as an increase in biomass of stems and green plant parts. It can be well demonstrated on the Bajio stands where the influence of growing water level is very drastic: proportion green/dry biomass is as high as 8.36 in flooded stand and only 1.07 in non-flooded; the leaves/stems biomass reach 2.35 on flooded and only 0.62 on non-flooded.

Paspalum savannas do not react so sharply to flooding as these species are very well adapted to changes in water level. They are grasses characteristic of valleys of large, inundating rivers.

Panamanian savannas. *H. rufa* is a tall grass, it can reach 275 cm (McCorkle 1968). In the plots under study it only slightly exceeded 2 m. Like other high tropical grasses, it can be grazed only when it is low. Ungrazed grasses grow luxuriantly, lignify, and wither during the dry season; they become inedible and are burnt off. The phenological year lasts from April to April (burning usually takes place at the end of March or in early April).

As was already mentioned, the samples were taken twice a year, in two adjacent plots. The pasture was overgrazed throughout the previous year. The grass never exceeded 20 cm, and bare patches were visible among the tufts of the grass. The ungrazed "seed reservation" was kept for seeds from some months.

At the first sampling in March, there was 3406 g d.w.m^{-2} of aboveground plant material in the ungrazed plot and only 448 g d.w. m^{-2} in the grazed one (Tables 4, 5). The "seed reservation" had not been grazed since last September (about 150 days), so, the production rate in this ungrazed plot can be calculated as follows:

$$\frac{3406\,\mathrm{g}}{150\,\mathrm{days}} = 22.7\ \mathrm{g\ d.\ w.\ m^{-2}\ day^{-1}} \tag{1}$$

Thus, the average production rate of the ungrazed plot was above 20 g d.w. m^{-2}.day^{-1}.

The proportion of dead (dry) to live (green) grass biomass should be noted for March. In the ungrazed stand, dead biomass accounted for 86% of the total, and in the permanently grazed pasture – only for 63%. This was certainly a result of the dry season which lasts 3–4 months. After sampling in

Table 5. Biomass of plants in August in two *Hyparrhenia rufa* stands fenced after last burning in March

Plant parts g. d.wt m^{-2}	Stand	
	Ungrazed	Grazed
Aboveground green	2085.0	731.0
% of ABVG total	72.0	60.4
% of total plant biomass	62.3	45.0
Aboveground dry	774.6	478.4
% of ABVG total	27.1	39.6
% of total plant biomass	22.7	29.5
ABVG total (green +dry)	**2859.6**	**1209.4**
Roots 0-20 cm	481.3	413.7
% of total plant biomass	14.4	25.5
Roots + aboveground parts	**3340.9**	**1623.1**

Table 6. Biomass of roots at different depths in soil of two *Hyparrhenia* savannas

Depth		Ungrazed	Grazed
0–10 cm			
	g d. wt. m^{-2}	417.5	372.5
	% of total root biomass	87	89
10–20 cm			
	g d. wt. m^{-2}	63.8	41.2
	% of total root biomass	13	11
0–20 cm			
	g d. wt. m^{-2}	481.3	413.7

March 1971, the vegetation was burnt off and the two plots were fenced and left untouched till August, 1971 (about 150 days again). The results of the second sampling are shown in Table 5. There was a considerable change in the proportion of weight between dead and green biomass. Green biomass accounted for 60% of total weight in the pasture, and 72% in the ungrazed stand ("seed reservation"). Thus, the situation was reversed compared with the end of the dry season (March). The total plant ABVG biomass was 2859 g d.w.m^{-2} in the ungrazed plot and 1209 g d.w. m^{-2} in the pasture (production rate 19.0 and 8.1 g m^{-2} day^{-1}, respectively). Therefore, the rate of ABVG biomass production in the ungrazed plot was similar as during 150 days a half year ago; production in the overgrazed pasture was 50% lower, although grazing was excluded by fence.

The biomass of roots was small in relation to the total biomass, being 14% in the ungrazed plot and 25% in the pasture (Table 5). Root biomass (BLG) rapidly decreased below 10 cm (Table 6). In the lower soil layer (10–20 cm) there was only 10–14% of the total root biomass.

The contents of N, P and SiO_2 in the plant material are shown in Table 7. A shortage of the first two elements and large amounts of silica were expected, which was supported by the results of the analyses. In particular, phosphorus was deficient. The high content of silica was probably mainly responsible for the high content of ash found in plant mass – above 12% in ABVG biomass and up to 25% in BLG biomass.

Table 7. N, P and SiO_2 content in dry mass of grass in two *Hyparrhenia rufa* stands

Stand	Ungrazed			Grazed		
Nutrient	% N total	P mg g^{-1}	SiO_2 mg g^{-1}	% N total	P mg g^{-1}	SiO_2 mg g^{-1}
Roots 0–10 cm	0.615	0.3822	183.2	0.485	0.3292	104.9
Aboveground parts						
Green	0.584	0.3407	88.1	0.537	0.2429	80.2
Dry	0.214	0.1030	240.1	0.417	0.1562	124.6
Mean	0.405	0.2219	148.9	0.489	0.2082	102.4

4.2. DECOMPOSITION RATE

Venezuelan savannas. Dry weight of litter samples was evaluated twice: first in the moment of exposition of wet 10 g litter portions and second, after exposition time when the loss of litter mass was estimated. In both cases low standard deviations were found for the dry weights of litter samples measured before and after exposure in the field. The moisture content of the initial 10 g litter portions collected in the field was highest in the litter of Bajio 1 and lowest on both *Trachypogon* stands. These results are related to the retention of water in the soil and its presence on the soil surface (flooded stands).

The rate of litter decay expressed as percentage loss per day was lower on the two *Trachypogon* stands compared with the 3 more humid stands (Table 8). Even more drastic differences were found after computing the loss rates per mass of litter accumu-

Table 8. Mean values of decomposition of litter registered in litter bags and calculated for the whole litter biomass on the stands

Stand		Loss from litter bags		Litter layer biomass in stand	Rate of litter layer decay	Decay (g.d.w.m^{-2}) of litter in wet season
		g d.w. day^{-1}	% day^{-1}	g d.w. m^{-2}	g d.w.m^{-2} day^{-1}	
TRA	1	0.0546	0.63	134.4	0.85	153.0
	2	0.0380	0.41	170.7	0.70	126.0
PAS	1	0.0643	0.87	722.1	6.26	1126.8
	2	0.6840	0.94	392.0	3.68	1104.0
BAJ	1	0.0583	1.08	93.4	1.00	180.0

TRA, BAJ, PAS – see tab. 1

Attention: For calculation of annual litter decay the following duration of wet season was assumed: TRA stands – 6 months, PAS 1 stand – 6 months, PAS 2 stand – 10 months, BAJ 1 stand – 6 months.

lated on the stands. The two *Trachypogon* stands, characterized by slow decay rates had the lowest decomposition rate per sq. meter per wet season. The Bajio stand, with a high absolute value of decay rate (above 1% daily), had a small amount of litter (Table 8) and, as a result, litter loss per sq. meter per season was low (Bulla *et al.* 1979). The two humid *Paspalum* stands, with the largest litter layer and high absolute decay rates showed the highest litter decomposition – above 1000 g. d.w. m^{-2} wet season^{-1}.

The lowest rate of cellulose decomposition was recorded at the *Trachypogon* stands, it was much higher for more humid stands (Table 9). The highest decay of cellulose was found in the Bajio stands.

The highest rate of decomposition processes was found in the upper soil layer, medium rate on the surface of the soil, and the lowest in the grass layer. The only except was found in *Paspalum* high grass stand, where cellulose between the standing grass decays 1% per day.

Panamanian savannas. The decomposition rate of cellulose filters was used as an index of the intensity of organic matter decomposition in soil (Table 10). In the top (0–10 cm) horizon of the soil cellulose decomposition were 7.8 mg g^{-1} .day^{-1} in the ungrazed, and 5.7 mg g^{-1}.day^{-1} in the grazed stand. The decay rate registered every few days shows some pattern in time: in both stands it decreases during the course of experiment. In the case of the seed reservation a distinct effect of an initial increase of decomposition is observed. This pattern is known from decomposition of litter and it is interpreted as initial fast decay of carbohydrates followed by slower decay of cellulose and lignin. Of course in the case of samples of pure cellulose exposed for decomposition this interpretation does not fit.

Table 9. Mean values of decomposition rates of filter paper at three different levels (in % day^{-1}, ± SD). The means were calculated for 6 stands, 3 savanna types and 3 layers as well as the sums for stands and savanna types

Stand		Levels of cellulose exposition			Mean for 3 layers and stands	
		Grass layer	Soil surface	Upper soil layer		
TRA	1	0.06±0.03	0.28±0.02	1.66±0.34	0.52	TRA $\bar{x}$ = 0.48
	2	0.06±0.02	0.10±0.05	1.17±0.45	0.44	
PAS	1	1.06±0.03	1.11±0.32	1.69±0.03	0.95	PAS $\bar{x}$ = 0.79
	2	0.03±0.02	0.47±0.20	1.38±0.30	0.62	
BAJ	1	0.17±0.13	1.01±0.41	1.64±0.17	0.94	BAJ $\bar{x}$ = 0.93
	2	0.18±0.10	1.17±0.35	1.39±0.26	0.91	
MEAN		0.09	0.69	1.48		

TRA, PAS, BAJ – see Table 1.

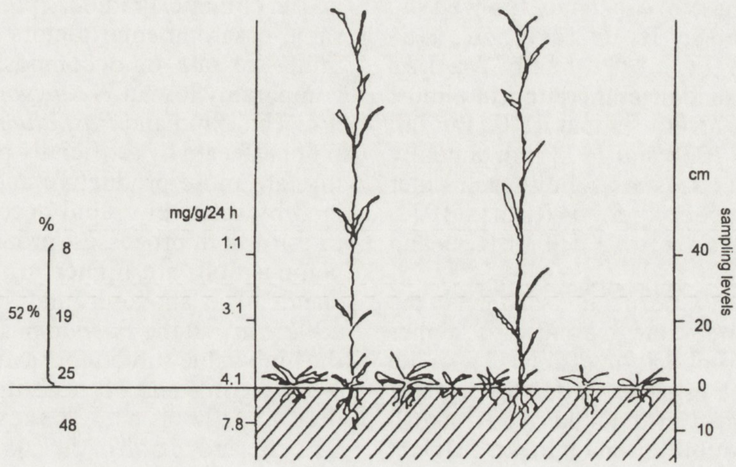

Fig. 6. Daily cellulose decomposition rate (mg g–1 and %) in different layers of ungrazed *Hypparrhenia* savanna (Panama).

Table 10. Decomposition rate of cellulose filters in *Hyparrhenia* savanna soil (at a depth of 10 cm, during 21 days of the wet season, mean values for 3-5 samples)

Exposition time	Ungrazed		Grazed	
	Mean loss of cellulose		Mean loss of cellulose	
	mg day^{-1}	mg g^{-1} day^{-1}	mg day^{-1}	mg g^{-1} day^{-1}
17–24 Aug. 1971	2.9186	5.9096	3.6993	8.0500
17–28 Aug. 1971	5.9775	12.4417	2.5315	5.2261
17 Aug.–2 Sept. 1971	4.5020	9.1765	2.3937	4.9699
17 Aug.–7 Sept. 1971	1.6395	3.8502	1.8661	3.8466
Mean	3.7594	7.8413 = 0.78%	2.6219	5.7315 = 0.57%

Interesting results were obtained for the experiment on the decomposition rate of cellulose placed among stems. The filter papers exposed in different layers copy the behaviour of surrounding plant material and can be treated as index of rate of plant decay. The filters suspended among the grasses were decomposed at a relatively high rate: more than 50% of it was decomposed above the ground (Fig. 6). Such a high decomposition rate of standing vegetation – much higher then those obtained for savannas in Venezuela probably results from high air humidity in Panama. This explains why such a small amount of organic matter was found on the ground as it has no time to fall being decomposed while still standing.

5.CONCLUSIONS

1. Organic matter productivity and decomposition were studied in eight neotropical savannas: *Hyparrhenia* savannas in Panama,*Trachypogon*, *Paspalum*, and Bajio type savannas in Venezuela. The Venezuelan savannas were studied in many programs and the results were published (Blydenstein 1963, Ramia 1967, Bartoli 1976, Escobar 1977, Ojasti 1978, Bulla *et al.* 1979, Gonzales Jimenez *et al.* 1981, Sarmiento 1984 and others); special attention was given to the *Trachypogon* savannas surrounding the Scientific Station in Calabozo region (Vareschi 1960a, b, Velazquez 1965, Eden 1967, Monasterio and Sarmiento 1968, Lopez *et al.* 1971, Medina *et al.* 1977, San Jose and Medina 1977, San Jose and Garcia Miragaya 1979) and to Modulo Experimental Program organized by state in Alto Apure (Perez *et al.* 1974, Ramia 1974, 1978, Entrena 1976, Gil Beroes 1976, Gonzales Jimenez and Escobar 1976a, 1976b, Bulla *et al.* 1980, 1990). Panamanian *Hyparrhenia* savannas are not known from so rich literature.

2. The climate of all stands fits well the pattern described by Bourliere and Hadley (1970), Nix (1981) and Walker (1987). Mean annual temperature is almost constant on the level of about 25°C; rainfall ranges between 1330 and 1973 mm annually and dry and wet seasons follow each other without any transitory period (Ramia 1974, Ramia and Montes 1975, Walter and Medina 1971).

3. In six Venezuelan savannas the ABVG production rate was always higher than that of decomposition (Table 11), so the accumulation of organic matter takes place on the soil surface in the study ecosystems. However, it should be remembered that decomposition processes occur in standing plants and are fastest in the upper soil layers (results obtained for decomposition of cellulose filters exposed at different levels). Our litter was only exposed on the soil surface, so the decomposition rate may have been underestimated.

and a climatic gradient (precipitation). The same environmental factors probably determine the rate of decomposition processes, comparably low in *Trachypogon* stands.

The Bajio and *Paspalum* savannas, even if not affected by artificially prolonged flooding, are more productive and are characterized by relatively rapid decomposition. The rates of both processes, productivity and decomposition, are higher in the two flooded stands. The above-ground standing crop of 2906 g m^{-2} in the *Paspalum* stands is close to the high values noted for savannas in Panama – 3406 g m^{-2} and of the *Eragrostis* type (India) – 3296 g m^{-2} (Breymeyer 1978; Singh and Joshi 1979). Escobar and Medina (1977) note lower above-ground productivity values for some Venezuelan *Paspalum* savannas, ranging from 1040 to 2540 g m^{-2}. According to this study, the productivity of *Paspalum* savanna can be 2–4 times higher as that of *Trachypogon* and Bajio savannas.

Table 11. Comparison of ABVG standing crop, the computed rates of ABVG production and litter decomposition in 6 Venezuelan savanna stands. The lower part of the table represents kind of budget of organic matter on 6 stands: daily production/decomposition of OM is calculated for each m^2

Stand	*TRACHYPOGON*			BAJIO			*PASPALUM*		
	laterit	$\overline{X}$	sandy	natural	$\overline{X}$	flooded	natural	$\overline{X}$	flooded
ABVG standing crop & litter g d.w. m^{-2}	544	**672**	800	625	**843**	1061	1705	**2305**	2905
ABVG prod. rate g d.w. m^{-2} day^{-1}	3.02	**672**	4.44	3.47	**3.81**	3.53	9.47	**9.60**	9.68
Litter decomp. rate g d.w. m^{-2} day^{-1}	0.85	**0.78**	0.70	1.00	**1.98**	2.96	3.68	**4.97**	6.26

NOTE: the production rate was computed assuming that the growing season lasts from 6 to 10 months similarly as it is described in Tab. 10. The decomposition rate was computed on the basis of a 50 day exposition of litter samples (in litterbags) during rainy season.

The low productivity of *Trachypogon* savanna's is discussed in several papers (Blydenstein 1962, 1963; Monasterio and Sarmiento 1968; Medina *et al.* 1977; San Jose and Medina 1977; Sarmiento and Vera 1979; San Jose and Garcia Miragaya 1979) and is explained by a combination of such unfavorable factors as low photosynthetic capacity, the poor sand and lateric soils and extreme seasonal drought. The comparative study of San Jose and Montes (1991) ordinates *Trachypogon* savannas along gradients of soil physics and chemistry (Mg concentration and bulk density)

The highest daily production rate (over 20 g d.w.m^{-2} wet $season^{-1}$) and maximum biomass (3406 g d.w.$^{-2}$ ABVG + 481 g BLG = 3887 g d.w.m^{-2}) was obtained in *Hyparrhenia* savanna. There are very high values for grasslands ecosystem; however already mentioned results of Piedade *et al* (1992) are even higher.

4. ABVG biomass produced in these savannas ranges from 544 g d.w.m^{-2} in *Trachypogon* on lateritic soil to 3406 g d.w.m^{-2} in *Hyparrhenia* kept ungrazed from 2 years (Table 12). Root biomass collected to a depth of 20 cm (Panama) or 30 cm (Venezuela) was

Table 12. ABVG maximum biomass of 8 studied savannas (g d.w. m^{-2})

Stand		Biomass (green & dry) for each stand	Biomass (green & dry) mean for savanna type
HYP	1 ungrazed	3406	1927
	2 grazed	448	
PAS	1 grazed	1705	2305
	2 flooded	2905	
TRA	1 laterit	544	672
	2 sandy	800	
BAJ	1 natural	625	843
	2 flooded	1061	

HYP, PAS, TRA, BAJ – see Table 1.

evaluated as: 14–25% of savanna biomass (ungrazed – grazed) in Panama and 6–44% in Venezuela. The flooded stands tend to develop smaller root mass. Biomass of roots decreases with soil depth.

5. Litter decomposition measured in litter bags ranges from 0.41% per day in lateritic *Trachypogon* to 1.08% per day in non-flooded Bajio (measures from litterbags in Venezuelan savannas). Decomposition of cellulose filter papers exposed between the grass at heights 0, 20, 40cm above the ground reaches 52% of the whole decomposition on stand, as compared with 48% from samples in the upper soil layer (soil depth 0–10 cm where the fastest decomposition usually takes place). This experiment was performed in the Panamanian *Hyparrhenia rufa* ungrazed seed reservation, where the height of the grass was above 200 cm and air humidity was high.

6. The literature already contains many measures of biomass and productivity for savannas; majority of these evaluations are on lower level, some are similar (Kinyamario and Imbamba 1992, Jones *et al* 1992, Scholes and Hall 1996). However, simultaneous evaluations of production and decay of organic material are very rare so our study is perhaps a pioneer in this field.

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6. SUMMARY

Eight neotropical savannas studied are distributed between 9 °05'N (in Panama) and 7°33'N (in Venezuela) – Table 1. The thermic regime is very similar at all sites and constant temperatures of 25–27 °C are characteristic for all locations (Table 2). Precipitation is more diversified: the wettest *Hyparrhenia* stands (Panama) receive 1973 mm of rain per year. The Venezuelan stands have 1334, 1406 and 1674 mm of rain annually, with the driest conditions in the Calabozo area where *Trachypogon* savannas occur (Figs 1, 2, 3). An attempt was made to calculate and compare the rates of OM productivity and decomposition of 6 Venezuelan and 2 Panamanian savannas (Table 12).

The above-ground production rate was always higher than that of decomposition (Table 11), so the accumulation of organic matter was occurring on the soil surface in the study ecosystems. However, it should be remembered that decomposition processes occur in standing plants and are fastest in the upper soil layers – Fig. 6, Tables 9, 10. Our litters was only exposed on the soil surface, so the decomposition rate may have been underestimated.

The low productivity of *Trachypogon* savannas is discussed in several papers and is explained by a combination of such unfavorable factors as low photosynthetic capacity, the poor sand and lateric soils and extreme seasonal drought. The same environmental factors probably determine the rate of decomposition processes, comparably low in *Trachypogon* stands (Table 8).The Bajio and *Paspalum* savannas, even if not affected by artificially prolonged flooding, are more productive and are characterized by relatively rapid decomposition. The rates of both processes, productivity and decomposition, are higher in the two flooded stands. The above-ground standing crop of 2906 g d.w. m^{-2} in the *Paspalum* stands (Table 2) is close to the high values noted for savannas in Panama – 3406 g d.w. m^{-2}. According to this study, the productivity of *Paspalum* savanna can be 2–4 times higher as that of *Trachypogon* and Bajio savannas.

The highest daily production rate (over 20 g d.w.m^{-2} wet $season^{-1}$) and maximum biomass (3406 g d.w.$^{-2}$ ABVG + 481 g BLG = 3887 g d.w.m^{-2}) was obtained in *Hyparrhenia* savanna. There are very high values for grasslands ecosystem. ABVG biomass produced in these savannas ranges from 544 g d.w. m^{-2} in *Trachypogon* on lateritic soil to 3406 g d.w. m^{-2} in *Hyparrhenia* kept ungrazed from 2 years (Tables 3, 12).

Root biomass (Tables 5, 6) collected to a depth of 20 cm (Panama – Table 6) or 30 cm (Venezuela – Table 5) was evaluated as: 14–25% of savanna biomass (ungrazed – grazed respectively) in Panama and 6–44% in Venezuela. The flooded stands tend to develop smaller root mass. Biomass of roots decreases with soil depth (Fig. 5).

Litter decomposition measured in litter bags ranges from 0.41% per day in lateritic *Trachypogon* to 1.08% per day in non-flooded Bajio (measures from litterbags in Venezuelan savannas – Table 8).

Decomposition of cellulose filter papers exposed between the grass at heights 0, 20, 40 cm above the ground (Fig. 6) reaches 52% of the whole decomposition on stand, as compared with 48% from samples in the upper soil layer (soil depth 0–10 cm where the fastest decomposition usually takes place).

The subject literature already contains many measures of biomass and productivity for savannas; majority of these evaluations are on lower, few on similar level. However, simultaneous evaluations of production and decay of organic material are very rare so our study is perhaps a pioneer in this field.

Similarly, this is probably the first attempt to evaluate so fast decomposition between standing savanna plants; something made possible by the extremely humid air on the Isthmus of Panama and the very dense high grass *Hyparrhenia rufa*.

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