America *Tropical grazing land ecosystems of Venezuela*

I Ecophysiological studies in the *Trachypogon* savanna (central Llanos)

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The existence of a Biological Station at Calabozo, founded by the Sociedad Venezolana de Ciencias Naturales (see Fig. 1), has stimulated several studies on the ecology of savannas conducted in the central Llanos.

Climate

Table 1 shows the rainfall figures for localities within the savanna area. An east–west rainfall is apparent, but rainfall also increases towards the Andes and approaching the Guyana highlands. The eastern Llanos, in the States of Monagas, Anzoátegui and northern Bolivar, are the driest. El Tigre (1 006 mm/a) and Ciudad Bolivar (972 mm/a) may be taken as representative stations for a rainfall regime where precipitation scarcely surpasses 1 000 mm/a. The central Llanos are wetter; in the major part of the States of Guárico, Cojedes, Portuguesa and Barinas rainfall ranges between 1 200 and 1 500 mm/a. Calabozo (1 312 mm) and El Baúl (1 295 mm) may be taken as typical localities for this intermediate climate. Finally, the western and southernmost regions of the savanna area are the wettest.

TABLE 1. Rainfall data for localities in the savanna areas of Venezuela

Locality	State	Rainfall (mm/a)	Percentage of rainfall during the wet season
Maturin	Monagas	1 320	76
El Tigre	Anzoátegui	1 006	88
Calabozo	Guárico	1 312	87
Valle de la Pascua	Guárico	1 040	95
Ciudad Bolívar	Bolivar	972	84
Santa Elena de Guairén[1]	Bolivar	1 796	55
El Baúl	Cojedes	1 295	92
San Carlos	Cojedes	1 582	88
Guanare	Portuguesa	1 477	89
Bruzual	Barinas	1 493	92
Barinas	Barinas	1 418	91
San Fernando	Apure	1 415	94
El Amparo	Apure	1 755	89
Sabana Grande	Trujillo	1 333	75
Villa del Rosario	Zulia	1 110	85

1. Not in the savanna area, but the nearest rainfall station to the Gran Sabana.

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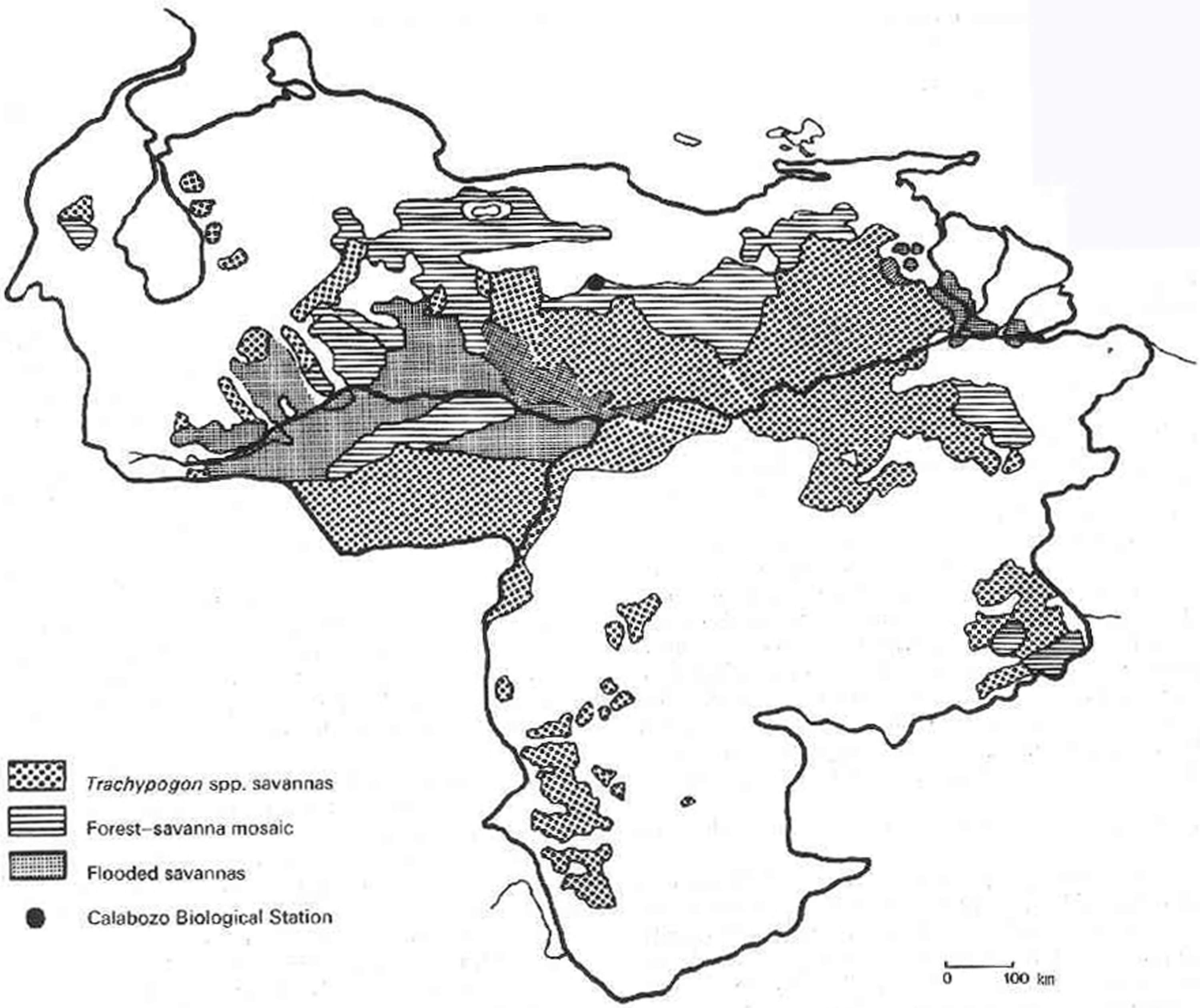

FIG. 1. The savanna types of the Venezuelan Llanos (from Ramia, 1967)

These include a major part of Apure State, the southern part of Bolivar and the areas of Cojedes, Portuguesa and Barinas near the Andean piedmont. El Amparo (1 755 mm/a) and Santa Elena de Guairén (1 796 mm/a) represent these wetter climates. Around the Maracaibo Lake, the savannas occur under intermediate rainfall values, and Sabana Grande (1 333 mm/a) and Villa del Rosario (1 110 mm/a) are representative of this situation.

The seasonal distribution of rainfall is characteristic. In the whole region (with the exception of southern Bolivar State) the rainfall is sharply concentrated in a 6–8-month wet season. Monasterio (1971) analysed a typical situation, Calabozo, in the central part of the Venezuelan Llanos. Eighty-seven per cent of the 1 312 mm/a rainfall falls in 6 months (May–October), 11 per cent in 2 transitional months (April and November) and just 2 per cent in the 4 dry months (December–March). The same pattern of rainfall seasonality is found in the entire area, with 4 rainless months everywhere, while the 2 transitional months could be rainless in the driest regions or included in the wet season in the more humid climates.

By any criterion, the savanna area of Venezuela has 4 exceptionally dry months (December–March). This constitutes the main environmental stress acting upon vegetation and conditioning the land use. In sharp contrast, the wet season shows an important water surplus.

Most rainfall is intensive. The number of rain days (rainfall > 0·1 mm) during the wet season in this region ranges from 60 to 120/a. Heavy storms of 30–40 mm/d are frequent, while rainfalls of ≥ 80 mm/d are not exceptional. Interannual pluvial variation is high, particularly in the driest areas where

TABLE 2. Rainfall (mm/a) in 4 localities of the Venezuelan central Llanos (Guárico State) during the dry period 1971–74

Locality	Long-term mean	1971	1972	1973	1974	Mean 1971–74	Deficit 1971–74 (%)
Calabozo	1 312	1 174	794	1 108	1 023	1 025	22
El Calvario	1 130	1 017	794	724	853	847	25
Valle de la Pascua	1 040	744	948	532	706	732	30
El Sombrero	1 215	752	673	1 039	777	810	33

it may approach the unreliability of semi-arid climates. In Calabozo for example, with mean rainfall of 1 312 mm/a, the extremes in 35 years of records are 581 mm and 1 998 mm; a coefficient of variation (standard deviation over mean) of 0·208. This high variability leads to catastrophic droughts, as that of 1971–74 which severely affected regional cattle-raising (Table 2). When two consecutive dry years occur, the rainless period may easily last 180 days (Monasterio, 1971).

Although there are no run-off data available for natural savanna ecosystems, field observations suggest that it is not an important ecological or geomorphogenetic factor. When savannas have not been disturbed or overgrazed, the soil surface horizons show good structure leading to efficient rain infiltration. The drainage system feeds more on ground water than on surface run-off. Only in restricted places of broken relief or in heavily overgrazed areas does sheet run-off become apparent and erosion occur.

Field data on seasonal variation of water-tables are scanty.

Two broadly opposite situations of fluctuations of water-tables can be considered. The case occurs in seasonal marshes and hyperseasonal savannas, where an *aquic* soil humidity regime prevails. As the wet season begins, soils rapidly become water-saturated because of the bad drainage and the lateral infiltration of run-off from higher positions. In a few weeks the soils reach saturation throughout the profile and remain constantly or intermittently waterlogged for the rest of the wet season. In bottomlands, such as the *esteros* of the Llanos, according to their relative position and the general configuration of relief, the level of waterlogging may range from a few centimetres, which disappear if the period between successive rains is long enough, to ⩾ 80 cm that drain slowly only when the dry season is already well advanced (Ramia, 1974). After the end of rains, soils begin to dry and water-tables fall sharply. In marshes, the maximum depth attained by the water-table remains within the rooting zone of the herbs. In hyperseasonal savannas, however, the water-tables become out of the reach of roots, at depths of 150–250 cm. Because of the universal occurrence of clay hard-pans near the surface in these hydromorphic soils, their below-ground biomass is almost completely restricted to the top 60 cm (Sarmiento and Vera, 1974).

A second water-table fluctuation occurs in seasonal savannas that occur in zonal well-drained soils. Here, at the end of the wet season, the water-table scarcely reaches 100–150 cm. Only in transitional situations, near the base of slopes, do the water-saturated zones reach 50–100 cm (Sarmiento and Vera, 1974). The existence of these seasonal water-tables in upland, well-drained savannas can be explained by the lateral infiltration from the neighbour bottomlands. As the dry season advances, the water-table quickly descends in such a way that, after a few weeks of dry season, it is out of reach of even the deep-rooted savanna trees. At the end of the dry season, the water-table may be at 3–8 m. Particularly in high topographic positions or in deeply dissected landscapes, such as the mesas of the eastern and central Llanos, the water-table practically disappears during the dry season.

Mean annual temperatures are high: 25°–28° C. Only in the plateau of the Gran Sabana, are mean temperatures lower, *c.* 21° C. The difference between means of warmest and coldest months does not exceed 2°–3° C. The highest mean, minimum and maximum temperatures occur towards the end of the dry season. The absolute minima are > 18° C and the absolute maxima are seldom > 40° C.

In Calabozo, daily thermal oscillations vary from an average of 14·3° C in April to 10·6° C in September (Monasterio, 1971). This annual thermoperiodism exists, with wider daily ranges in the dry season than during the wet season. He suggests that thermoperiodism may determine certain rhythms in savanna species. The development of new leaves before the beginning of the wet season or the distribution of flowering through the year indicate probable thermo- or photoperiodical effects. This has been clearly demonstrated in a common weed, *Hyptis suaveolens*, which behaves as a short-day plant and is sensitive to 15-minute differences in day-length (Wulff, personal communication). See also Monasterio and Sarmiento (1976).

Vareschi and Huber (1971) give some data on the micro-climate within a savanna at Calabozo. During 3 successive daily cycles in the dry season, the range of temperatures inside the grass layer (20 cm above the ground) was 16°–18° C, with minima of 23°–24° C and maxima of 40°–41° C; in 3 days of the wet season daily oscillations were 5°–12° C, minima 21°–22° C and maxima 27°–33° C. These

TABLE 3. Some radiation figures for the savannas of Calabozo (after Vareschi and Huber, 1971)

Radiation	Dry season		Wet season	
	cal/cm²/d	%	cal/cm²/d	%
Total possible radiation	512	100	512	100
Global radiation	473	92	459	89
Direct radiation	421	82	399	78
Diffuse radiation	52	10	60	11·5
Radiation reflected by vegetation	90	17·5	33	6·4
Radiation absorbed by vegetation	284	54	384	75
Radiation reaching the soil surface	99	19·5	78	15

data suggest that thermal conditions inside the grass layer reproduce the same trends shown by standard meteorological records.

Vareschi and Huber (1971) measured radiation in the Calabozo savanna during some days of the dry and wet season. Their figures for representative days are reproduced in Table 3.

The figures show that the components of incoming solar radiation (global, direct and diffuse radiation) are not very different in the two seasons, but the behaviour of plant cover differs greatly since during the dry season the yellowish grasses reflect about thrice as much radiation as the green grass of the wet season.

It does not seem possible to discern short-term climatic fluctuations, for most rainfall stations have records for only a few years; fewer than six have continuous records for fifty years.

However, there are periods of exceptional drought. In the central Llanos, particularly in Guárico State, one such period began in 1971 and has not yet finished. Mean annual rainfall as well as data for 1971–74 in four localities within the drought area are reproduced in Table 2. A large part of the savanna region had up to 33 per cent less rainfall. This caused a catastrophic drought and cattle mortality was exceptional.

Though there are not either palynological or other palaeoecological data for the Venezuelan Llanos, in adjacent areas of Colombia and Guyana (Wijmstra and Van der Hammen, 1966) with similar vegetation the pollen record shows that the present ecosystems have existed at least since the beginning of the Holocene. Furthermore, important vegetation changes (mainly related to the density of tree species, *Byrsonima* sp., within the savannas) are discernible in the fossil record. For several thousand years, more or less open savannas or grasslands were predominant, while in other equally long periods tree species became more widespread, giving rise to woodlands. According to these authors, these vegetation changes reflected significant changes between wetter and drier climatic phases that supposedly were related to glacial and interglacial changes in the Andes. It seems logical to suppose that the frequent alternation of climatic phases, already well documented in the American tropics, was responsible for concomitant changes in plant cover, with displacements from rain forests to savannas and changes in the composition and structure of these latter ecosystems.

Soils

Soils are very shallow around Calabozo and a hard-pan or lateritic cuirasse at variable soil depth is commonly found (Santamaria and Bonazzi, 1963; Bonazzi, 1967). This cuirasse is a relict of moister climates. Bonazzi states that it is a true hydromorphic precipitate, formed by concretion under water, and it is not a residual laterite. This statement is based on the finding of pollen grains, spores and other plant tissues in exfoliant structures of ferric oxide (Bonazzi, 1962). This cuirasse is widespread in the Venezuelan savannas and, because of its continuity and thickness, it has been considered the limiting factor for tree growth (Santamaría, 1965). Its low permeability and the shallow soil restricts the water retention and prevents forest (Santamaría and Bonazzi, 1964). Santamaría (1965) estimated 31 000 km² of lateritic cuirasse; 16 per cent of the area of Venezuelan savannas as calculated by Ramia (1967).

Foldats and Rutkis (1965) proposed that deep hard-pans enabled enough water to be accumulated for forest islands, typical of the Calabozo savannas, to develop. Nevertheless, in the vegetation map of the Calabozo Station of Santamaría and Bonazzi (1963), no clear correlation between forest islands and hard-pan depth was found. Later Monasterio and Sarmiento (1968) defined the geomorphological levels where forest islands are found.

Comparing soil and vegetation structure between Africa and northern South American savannas, Walter (1969) indicated that the hard-pan is not continuous. The distribution of the tree components reflects the broken hard-pan. Thus, isolated trees within the grassland obtain adequate water throughout the year.

The chemical composition of soils around Calabozo is variable within the grassland and forest

TABLE 4. Soil composition in Calabozo (from Medina, 1968; San José and Medina, 1975)

	Grassland	Forest island
Depth (cm)	0–70	0–30
pH	4·9–5·3	5·8
Organic matter (per cent)	1·2	2·7
N (per cent)	0·036	0·106
P (ppm)	4·1	5·8
K (ppm)	27	48
Ca (ppm)	344	520

islands. Table 4 shows soil analyses published by Medina (1968) and San José and Medina (1975). Analyses of profiles of the Calabozo Station have been reported by Monasterio and Sarmiento (1968). Values are similar in average, although they present higher values for phosphorus and nitrogen, and lower values for calcium and potassium.

Low nutrient content is characteristic of savanna soils and is somewhat higher in forest islands; acidity is correlated with deficiency in exchangeable bases, especially calcium.

Phytosociology (see Fig. 1)

Ramia (1967) grouped all savannas in the Venezuelan Llanos into three types.

Trachypogon savannas show predominance of one of the species of this grass genus. They are relatively dry, occurring on light-textured, acid, poor, well-drained soils. Trees may be present, and *chaparrales* is the term used, the *chaparro* (*Curatella americana*) being the principal tree species. Most of the eastern Llanos are covered by a treeless type of *Trachypogon* savanna, while the chaparrales occur in the central Llanos (western Anzoátegui and Guárico States) and in the Andean piedmont bordering the western Llanos.

The *banco*, *bajio* and *estero* savannas characterize the western Llanos and the northern part of the Apure State. They form a topographic series of communities. In the alluvial plains that form most of the western Llanos the pattern of savanna communities closely matches the land-form. The three main land-forms are the river-banks (bancos) with well-drained soils, the loamy flood-plains (bajios) with gleyed, ill-drained soils, and the alluvial bottoms (esteros) where the finest sediments are deposited in quiet waters during flooding and where soils never dry completely. Tables 5, 6 and 7 list the most important grasses in these savannas.

Finally, the *Paspalum fasciculatum* savannas are pure, up to 2 m tall grasslands on local areas of the Llanos which flood during the whole wet season. During the dry season the soil dries up, the grass cover declines, and at its end they are burnt.

Sarmiento and Monasterio (1969*b*) proposed a scheme for grouping Venezuelan Llanos savanna communities into four floristico-ecological types: *Trachypogon–Curatella* savannas, on well-drained soils, extending through the mesas of the eastern and central Llanos, the banks in the western Llanos and the dunes and high plains of southern Apure, including *Trachypogon* savannas and banco communities of Ramia's system; *Axonopus–Mesosetum* savannas, mostly pure grasslands that cover intermediate topographic positions on low alluvial banks and similar land-forms with soils gleyed only in depth; *Sorghastrum–Copernicia* savannas, grasslands or palm savannas occurring on heavy, ill-drained soils, roughly corresponding to Ramia's bajio communities; and *Paspalum fasciculatum* grasslands in flooded areas. Ramia's estero savannas were considered as marsh communities because the soil never completely dries in the root area.

TABLE 5. Most abundant grasses on the banco and dune savannas in Mantecal, Apure State (after Ramia, 1974)

Andropogon selloanus	*Imperata contracta*
Axonopus affinis	*Leptocoryphium lanatum*
A. anceps	*Paspalum chaffanjonii*
A. compressus	*P. plicatulum*
A. purpusii	*Sorghastrum parviflorum*
Cenchrus pilosus	*Sporobolus indicus*
Cynodon dactylon	

TABLE 6. Most abundant grasses on the bajío savannas in Mantecal, Apure State (after Ramia, 1974)

Andropogon bicornis	*P. laxum*
A. brevifolius	*P. versicolor*
Axonopus compressus	*Paratheria prostrata*
A. purpusii	*Paspalum chaffanjonii*
Cynodon dactylon	*P. convexum*
Eragrostis acutiflora	*P. millegrana*
Hymenachne amplexicaulis	*P. orbiculatum*
Imperata contracta	*P. plicatulum*
Leersia hexandra	*Sorghastrum parviflorum*
Panicum junceum	*Sporobolus indicus*

TABLE 7. Most abundant grasses on the estero communities in Mantecal, Apure State (after Ramia, 1974)

Hymenachne amplexicaulis	*P. laxum*
Leersia hexandra	*Paratheria prostrata*
Luziola spruceana	*Paspalum orbiculatum*
Panicum elephantipes	

A detailed vegetation analysis was produced by Sarmiento and Monasterio (1969*a*) using association analysis. This showed a fine-textured pattern of phytosociological variability. The floristic variation was related to edaphic factors derived from the occurrence of old lateritic cuirasses and to the pattern of the vegetation itself, in particular the distribution of forest patches.

Under regular fire, the forest/grassland boundary seems to be stable. Blydenstein (1963) made a thorough sampling of a 1 ha plot in the Biological Station of Calabozo. After seven years of protection from fire San José and Fariñas (1969) repeated the sampling and found that *Trachypogon montufari* and *Axonopus canescens* had a reduced density but increased diameter per bunch (*c*. 50 per cent). Some deciduous non-fire-resistant trees such as *Cochlospermum vitifolium* and *Godmania macrocarpa* had increased significantly. The number of isolated woody plants increased from 50 to 168, and from 231 to 289 in the tree groups. It seems that protection reduces seedling mortality of some tree species.

Nevertheless the vegetation remains the same physiognomically and does not change to forest.

Another study showed that protection from fire favoured the predominance of the main grass component (*Trachypogon plumosus*). Burning partially reverted this predominance and increased the above-ground biomass production of secondary components (San José and Medina, 1975).

Phenology

The cycles of rainfall and drought determine the general characteristic of vegetation. Above-ground biomass of grass cover dominated by perennial grasses dries out completely and only the buds remain alive near soil surface (Vareschi, 1962). Among trees, deciduous and evergreen species coexist (see life-forms after Vareschi in Aristeguieta, 1966). Monasterio (1968) reported on the phenological behaviour of *c.* 200 species while Ramia (1974) did so on 90 species from the banco-bajio-estero savannas in Apure State. Table 8 compares the two savannas. In both cases most species flower during the wet season but the flowering of grasses is limited to it. During the dry season, no more than 5 per cent of the herbaceous species flower and they are dicots. In the flooded savanna on the contrary, the facies not covered by water (bancos) always have *c.* 30 per cent of species (including grasses) flowering. In the properly flooded areas (esteros), flowering goes down to 9 per cent during May. Estero communities are less diverse (Ramia, 1974).

Water availability, regulating leaf duration, is most important for grassland productivity, which depends more on the length of the wet season than on the amount of rainfall.

Trees are more variable in their phenology, probably because many species depend on water from the water-table. Several trees flower after leaf-fall during the dry season; similarly several evergreen trees change canopy and flower almost simultaneously in the middle of the dry season. The evidences on leaf growth (Medina *et al.*, 1969), carbon balance (Medina, 1967), water balance (Vareschi, 1960; Medina, 1967), distribution (Foldats and Rutkis, 1965), flowering and leaf-fall (Monasterio, 1968; Medina, 1968), indicate that woody components in the *Trachypogon* savannas occupy well-differentiated ecological niches, not competing with grasses, and their distribution seems to be determined more by soil structure (Bonazzi, 1967; Walter, 1969) than by anthropogenic or competition effects. The evergreen trees growing isolated within the grassland, mainly *Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgilioides*, seem to be characteristic of poor shallow soils, and tolerate fire when adult.

Phenology of tree species in Calabozo is shown in Table 8 (Monasterio, 1968). There are two flowering peaks, the first mainly at the end of the dry season and the second mainly during the middle of the wet season. Litter-fall in the forest islands also follows a seasonal pattern; most occurs during the dry season (December–March) and the total is 8·2 t/ha. All this disappears at soil level during the first months of rain and no accumulation of organic matter in the soil was detected (Medina, 1968). See also Monasterio and Sarmiento (1976).

Productivity

First measurements of organic matter production of *Trachypogon* grasslands were reported by Blydenstein (1962, 1963). They referred only to above-ground production and were based on the comparison of the biomass at the beginning and at the end of the wet season on unburnt plots, and only total above-ground biomass at the end of the wet season in burnt plots. Significant underestimation is likely because decomposition of standing dead matter was not considered.

Blydenstein (1962, 1963) reported that biomass per unit area in these savannas is relatively low in comparison with figures of other latitudes (César and Menaut, 1974; Murphy, 1975). The maximum value of above-ground biomass measured by Blydenstein was 405 g/m^2 in a savanna plot burnt during the preceding dry season (see Table 9).

It was estimated that maximum root biomass was *c.* 28 per cent of above-ground biomass, and 80 per cent of below-ground biomass occurs in the

TABLE 8. Percentage of flowering species in the *Trachypogon* savanna of Calabozo (Guárico State) (Monasterio, 1968) and the flooded savannas in Mantecal (Apure State) (Ramia, 1974)

Community	Jan.	Feb.	March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Number of species
Banco	58	43	36	31	45	56	63	61	54	61	66	73	41
Bajio	43	28	18	18	39	46	71	68	75	71	64	64	28
Estero	18	14	9	14	27	36	59	50	54	68	63	45	22
Trachypogon savanna													
Herbaceous plants	1	1	5	2	2	10	22	31	16	8	2	1	101
Woody plants	7	5	7	17	2	8	16	18	6	4	3	2	97

TABLE 9. Production data[1] from *Trachypogon* savannas (in g/m²/a) (from Blydenstein, 1962, 1963)

Treatment	Year	Above-ground biomass	Below-ground biomass[2]	Total production
Not burnt	1961	241	96	337
	1962	309	124	433
Burnt	1961	351	140	491
December 1960	1962	308	123	431
January 1961	1961	175	70	245
	1962	252	101	353
March	1961	230	92	322
	1962	–	–	–
Cut				
November 1961	1962	293	117	410
Burnt				
November 1961	1962	405	162	567
March 1962	1962	294	118	412

1. Excluding organic matter decomposed during the growing season.
2. Estimated as 40 per cent.

upper 20 cm of soil. A shoot/root ratio of 2·5 seems remarkably high when it is compared with other savannas in Venezuela (Sarmiento and Vera, 1974) and Africa (César and Menaut, 1974) which have ratios < 1. The cause of this difference, in an environment which theoretically favours the translocation of assimilate towards the roots, is not clear.

A comparative study on the distribution of aerial and root biomass in several plant communities during August, when living biomass reaches its peak (San José and Medina, 1975; see Table 10), showed that the shoot/root ratio increased on relatively deep soils and decreased on seasonally flooded soils or where the lateritic cuirasse had been uncovered by erosion. In this study, root biomass was measured in the upper 20 cm of soil, which supposedly contain *c.* 80 per cent of root biomass. Maximal biomass accumulated in a humid savanna dominated by *Andropogon* sp. was 12·6 t/ha (above-ground + below-ground biomass). Leaf area index is higher in the humid savanna and in the *Trachypogon*

TABLE 10. Biomass per unit area (g/m²) of the *Trachypogon* savannas (from San José and Medina, 1976)

Community	Above-ground	Below-ground	Above-ground / Below-ground	Total dry weight	Leaf area index
Trachypogon spp. (deep soils)	570	227	2·5	797	5·7
Trachypogon spp. (shallow soils)	198	229	0·9	437	2·0
Andropogon spp. (flooded soils)	653	552	1·2	1 205	5·6
Hyptis suaveolens (weed)	436	143	3·0	579	2·9

grassland on relatively deep soils (5); the sparse grass cover on hard-pan outcrops scarcely reached 2.

Blydenstein's observations on the effects of fire during two consecutive years show that burning during the dry season increases aerial production compared with cut or unburnt plots. Increase in burnt plots compared with the unburnt was 32 per cent in 1961 (351 versus 241 g/m²) and 24 per cent in 1962 (405 versus 309 g/m²), while the increase in relation to cut plots was 28 per cent (405 versus 291 g/m²); this effect was partially explained by San José and Medina (1975) as due to water availability. Measurements of above-ground production in burnt *Trachypogon plumosus* grasslands in eastern Venezuela (Espinosa, 1969) result in similar values: *c.* 4 t/ha.

Blydenstein's measurements of aerial biomass accumulation seem to indicate that the maximum in *Trachypogon* grasslands in *c.* 10 t/ha; this value would be the steady state between organic matter production and decomposition. *Trachypogon* grasslands reach this level after approximately five years of protection from fire. This would mean that yearly above-ground biomass increase would be progressively reduced.

The effect of fire on organic matter production is partially caused by better water availability for new growth during the dry season (San José and Medina, 1975). The leaves of grasses do not dry out until the soil-water reserves are exhausted. Burning interrupts soil desiccation, maintaining water available in soil and allows a vigorous new growth. If the wet season begins before water reserves are exhausted, there is a substantial leaf area already present and production proceeds during the whole wet season. Nevertheless, fire has an additional effect which could be related to the nutritional balance of the new leaves.

Maximal above-ground biomass in burnt grassland plots studied by San José and Medina (1976, Table 11) is 7·5 t/ha, with a below-ground biomass (down to 30 cm) of 1·7 t/ha. The shoot/root ratio is high (2·5) and the leaf area index has a peak of 4·95 during August. Evaluation of the net above-ground biomass in the unburnt savannas is more difficult because of decomposition of accumulated dead biomass. While, in burnt grassland, living biomass reaches a maximum of 4·1 t/ha, the protected plot had a peak of 3·2 t/ha. Root biomass is significantly higher in the protected plot (2·7 t/ha) than in the burnt one (1·7 t/ha).

Using the criteria of measuring biomass increase between the beginning and the end of the wet season, it was found that above-ground biomass increases very little (9–10 t/ha). There is a considerable reduction of dead biomass during the first 3 months of the wet season and it increases progressively towards the end of the production period (San José and Medina, 1976). There are no measurements of decomposition rates of organic matter.

TABLE 11. Production ($g/m^2/a$) data in *Trachypogon* savannas (from San José and Medina, 1976)

Treatment	At the end of the growing season		Production including decomposition			Maximum leaf area index	Maximum growth ($g/m^2/d$)
	Above-ground biomass	Below-ground biomass	Above-ground	Below-ground	Total production		
Protected	1101	270	705	190	895	4·19	11
Burnt (December 1968)	731	170	909	120	1029	4·95	10·5

Very rough estimates based on soil respiration (Medina, unpublished) give a minimum value of *c.* 70 g of organic matter destroyed by soil respiration/m²/month during the wet season. This includes root turnover and decomposition of organic matter coming from above-ground biomass. César and Menaut (1974) give a value of 7·6 per cent per month for above-gound biomass decomposition of *Loudetia* grasslands in Ivory Coast and they consider that *c.* 70 per cent of the root biomass is turned over every year. Taking this value as a guide, above-ground biomass production in *Trachypogon* grasslands would be 9·1 t/ha/a in the burnt plot and 7 t/ha/a in the protected one. Corresponding root production would be 1·2 t/ha/a in the burnt plot and 1·9 t/ha/a in the protected one. Total production is then in the burnt plot 10·3 t/ha/a, in the unburnt plot 8·9 t/ha/a; so fire increases total productivity by 14 per cent.

The aerial production rate changes according to water availability. It reaches a maximum of 10·5 $g/m^2/d$ between 180 and 200 days after fire, while at the end of the wet season it is zero; thereafter it increases to 5 $g/m^2/d$ due to irregular rainfall. These measurements indicate that in tropical grasslands productivity depends more on the duration of the wet season than on the total rainfall. Experiments with irrigation (San José and Medina, 1976) showed that twice the amount of living aerial biomass can be maintained during the dry season in irrigated plots in contrast to plots drying naturally (220 g/m^2 against 100 g/m^2 between December and March).

Grassland productivity is correlated with water availability. Walter (1973) found in African grasslands that *c.* 100 $g/m^2/a$ of above-ground biomass corresponds to 100 mm rainfall. In *Trachypogon* savannas of Calabozo, this would mean an average of 13 t/ha/a, which is far above the reported data. The conclusion is that in *Trachypogon* grasslands water-use efficiency is low probably as a consequence of a poor soil-nutrient status. This is surprising as all savanna grasses at Calabozo are C_4 plants. The explanation is that P and N deficiencies strongly reduce protein synthesis including carboxylating enzymes. Correlation between carboxylating enzyme activity and photosynthesis has been demonstrated for C_3 and C_4 plants (Medina, 1971; Treharne *et al.*, 1971). While transpiration depends only on leaf surface development, photosynthesis depends on leaf area extension and activity of carboxylating enzymes. Therefore high transpiratory quotients (kg water transpired/kg organic matter produced) are to be expected under high temperatures and low nutrient availability.

Fire stimulates shoot production beyond the effect produced by the elimination of dead biomass accumulated. This stimulation might be related to an increase of mineral translocation from roots to shoots. Experiments of cutting and burning (Montes and Medina, 1977) showed an 8 to 10 fold increase in nitrogen and phosphorus in the regrowth of burnt plots as compared with cut plots. Towards the end of the growth period, differences in nutrient content disappear. When above-ground biomass dries out, a net retranslocation from shoots to roots of 44 per cent for nitrogen and 57 per cent for phosphorus is observed; up to 40 per cent of K is translocated. The average amount of nitrogen remaining in the dead leaf mass is 4·5 mg/g dry weight. Thus in savanna with a maximum of 700 g/m^2 at the end of the wet season, 31·5 kg nitrogen/ha could be volatilized by fire. This is less than 1 per cent of the total nitrogen present in the soil (4 t/ha considering an average soil bulk density of 1·6). Nevertheless, nitrogen might well not be available for the plants. Unfortunately, there are no data on nitrogen availability in soil of *Trachypogon* savannas. Data on amount of nitrogen brought by rain or by biological nitrogen fixation are necessary for a more precise evaluation of the impact of fire on nitrogen resources.