Savannas in Trinidad

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Distribution, Size and Macrotopography

The natural savannas of Trinidad were more extensive in the recent past than they are today. In the north, svannas like those at Aripo were also well developed at Piarco, Mausica and O'Meara. Now, most of the savanna at Piarco has been replaced by an airport while those at Mausica and O'Meara have succumbed to industrial and housing development. Beard (1946) mentions two savannas in south Trinidad, one at Erin which is well known and still exists, and the other, St. John, which he briefly mentions but fails to pinpoint. Beard's report also includes photographs of savanna around Longdenville in central Trinidad. As to the whereabouts of St. John Savanna, Graf (1961) states that this savanna is located near Buenos Ayres and is the largest of the Erin Savannas.

The only other natural savanna in Trinidad is the St. Joseph which occurs on the mountain flanks just west of Mount St. Benedict. I believe these slopes were once forested but since early colonial times have been disturbed so frequently by fire and cutting that the forest has never been allowed to recover. Nature doesn't like a vacuum, thus the downgraded drier environment saw the proliferation of savanna-like vegetation.

The savannas which I will focus on in this article, therefore, are Aripo which has recently been designated part of a scientific reserve, St. Joseph which is slowly being replaced by pine tree plantation, and that portion of Erin in which no pine trees have been planted. The savannas described are treeless but dominated by sedges and grasses growing on mineral soil with an absence of organic matter. Rainfall would normally be sufficient to support a tree cover. However, modified soil conditions enable edaphic factors to override climate in determining the vegetation type. Sharp ecotones between forest and savanna are characteristic of Aripo and Erin. All the savannas have high surface evaporation rates owing to intense insolation, on average as much as six to seven hours daily.

The savannas at Aripo, which are basically flat, cover approximately 267 hectares and consist of ten separate areas designated by Roman numerals. (Anon. 1980) The five largest ones range in size from 56.6 ha (Savanna I) to 21 ha (Savanna II). The savannas form a mosaic with palm stands and marsh forest which together constitute the Long Stretch Reserve. Rainfall here ranges betweeen 250 and 280 cm per annum which is about the same amount that falls at St. Joseph. Erin Savanna is dry by comparison receiving approximately 160 cm per annum. Both Erin and St. Joseph occur on hilly topography and are roughly the size of Savanna II at Aripo.

Geology and Soils

Two of the three savannas form distinct watersheds, the exception being St. Joseph which straddles a south-oriented flank of the Northern Range. The Long Stretch Reserve containing the Aripo Savannas rises to 45 m above sea level forming the central watershed of the Caroni Plains with drainage east via rivers like the Guaico and west via the Aripo River. Geologically, the area constitutes a marine terrace elevated above sea level near the end of the Pleistocene geological period that began two million years ago. Erin Savanna occurring within the Erin Reserve is approximately 115 m above sea level and forms part of a watershed that drains northward towards the Gulf of Paria and south into the Columbus Channel. Here sandstone is the bedrock from which soils develop. St. Joseph Savanna ranges between 150 and 200 m above sea level and is underlain by quartzite, a metamorphic rock which weathers very slowly.

The soils at the Aripo Savannas consist of fine sand over sand or silty-clay, the sand and silt being almost pure quartz. The clay is high in kaolinite which has a 1:1 crystal lattice, tight chemical bonds and low cation exchange potential. The pH ranges between 4.8 and 5.5 (Richardson 1963). Intense leaching removes iron and aluminum from the upper horizons. Particles of quartz sand provide the nuclei around which iron oxide precipitation occurs. Poor lateral drainage with a fluctuating water-table results in oxidation-reduction processes. The water level fluctuations may also be influenced by drainage ditches dug by the Americans during the 1940s which persist to this day. The reversal of moisture conditions, the almost complete absence of humus and maximum sun exposure cause cementation with iron oxides producing a plinthite material that changes irreversibly to hardpan (Schwab 1988). Intense mottling (red blotches) owing to iron and aluminum oxides, occurs beneath the upper horizons but above the hardpan.

The impeded drainage so characteristic of Aripo is not seen at St. Joseph Savanna. Here the abnormally high percentage of quartzite in the parent rock produces a soil which consists of a shallow layer of quartz grit and pebble over impermeable bedrock (Beard 1946). Similar conditions also occur in Venezuela where savannas are found on the slopes of the Cordillera del Interior (Walter 1979).

At Erin Savanna the soils derived from sandstone have a high iron content which upon oxidation produces iron incrustations both on and beneath the surface thus making root penetration difficult.

Microtopography

Biotic factors play a significant role in shaping the microtopography of the savanna's surface. Although at a casual glance the savanna's surface looks smooth, and in the case of Aripo, flat, closer inspection reveals a varied topography consisting of hummocks and hollows as well as smooth areas. At Aripo, hummocky microtopography is more frequent near forest and island margins while flat areas predominate in the central portion of each savanna producing the most severe habitat conditions. The hummock-hollow complex was described as hog-wallows by early researchers possibly because this terrain resembled the frozen tracks left by pigs in a muddy European farmyard in winter and presented as much difficulty in maintaining balance while trying to traverse such areas on foot. With respect to the plants growing in this type of terrain, the hummocks provide better habitat conditions than the depressions. Termites and earthworms contribute to hummock formation and play a role in soil development, altering both texture and structure. Termites help to produce fine-textured upper soil layers free of stones. They also play an important ecological role in breaking down dead plant tissues and releasing nutrients to the environment. The common termite at Aripo is *Nasutitermes ephratae*, a ground dweller. Its nests have outer walls of soil and inner walls of carton, which is a plaster of fecal material containing undigested plant fibres. Ground termite mounds have been observed at Erin Savanna as well.

The earthworms at Aripo produce numerous piles of worm casts made up of soil material that has passed through their digestive tract. These worms are not very large, on average about 10 cm in length, but are responsible for the majority of the

Table I: The Common plants at Aripo Savannas

Family	Species (Total : 35)
SHRUBS:	
Malpighiaceae	++ *Byrsonima crassifolia* (savanna serrette)
Rosaceae	*Chrysobalanus icaco* var. *pellocarpa* (fat pork)
HERBS (growth can exceed 35 cm in height) :	
Cyperaceae	*Becquerelia tuberculata*
	Lagenocarpus rigidus subsp. *tremulus*
	Rhynchospora globosa
	Rhynchospora holoschoenoides
	+ *Rhynchospora longibracteata*
Orchidaceae	*Epistephium parviflorum*
HERBS (growth usually less than 30 cm in height):	
Burmanniaceae	*Burmannia capitata*
Cyperaceae	+ *Rhynchospora barbata*
	Rhynchospora podosperma
Gramineae	*Andropogon leucostachyus*
	Panicum cyanescens
	Panicum parvifolium
	Panicum stenodes
	+ *Paspalum pulchellum*
	Thrasya paspaloides
Lentibulariaceae	*Utricularia amethystina*
	Utricularia hispida
	Utricularia subulata
Melastomataceae	*Acisanthera bivalvis*
	Comolia veronicaefolia
Ochnaceae	*Sauvagesia sprengelii*
Orchidaceae	+ *Habenaria leprieurii*
Polygalaceae	*Polygala appressa*
	Polygala timoutou
Rubiaceae	*Perama hirsuta*
Xyridaceae	*Xyris caroliniana*
HERBS (growth usually less than 5 cm in height):	
Cyperaceae	*Rhynchospora curvula*
Droseraceae	*Drosera capillaris*
Gramineae	*Raddiella esenbeckii*
Lauraceae	*Cassytha filiformis*
Lycopodiaceae	*Lycopodium carolinianum* var. *meridionale*
Xyridaceae	*Abolboda americana*
	Xyris grisebachii

*Surveys based on Savannas I, II, III, V and VIII
+ Occurs on Erin
++ Occurs on St. Joseph and Erin

Table II: The best represented families at Aripo Savannas*

Cyperaceae (Sedge)	31 species	(14 *Rhynchospora*)
Gramineae (Grass)	24 species	(9 *Panicum*)
Lentibulariaceae (Bladderwort)	13 species	(12 *Utricularia*)
Orchidaceae (Orchid)	8 species	(all ground orchids)
Melastomataceae (Melastome)	7 species	

* Sampling based on Savannas I, II, III, V, and VIII

Table III: Species recorded for St. Joseph and Erin and their affinity with Aripo.

Family	Species (Total : 45)	St. Joseph	Erin	Aripo
Compositae	*Elephantopus angustifolius*	x	x	
	**Eupatorium amygdalinum*		x	
	Eupatorium ivaefolium	x	x	
	Eupatroium laevigatum	x	x	
Cyperaceae	**Bulbostylis junciformis*	x	x	
	Rhynchospora barbata		x	x
	**Rhynchospora longibracteata*		x	x
	Rhynchospora nervosa	x		x
	Rhynchospora rugosa		x	x
	Scleria bracteata	x	x	x
Dilleniaceae	*Curatella americana*	x	x	
Gramineae	**Axonopus anceps*		x	
	**Leptocoryphium lanatum*		x	x
	* *Paspalum pulchellum*		x	x
	Pennisetum setosum	x		
	Setaria gracilis	x	x	
	Thrasya robusta	x		
Hypoxidaceae	**Curculigo scorzonerifolia*	x	x	x
Labiatae	*Hyptis lantanifolia*	x	x	x
	Hyptis mutabilis	x		
Leguminosae	*Aeschynomene brasiliana*	x	x	
	Cassia patellaria	x	x	x
	Clitoria rubiginosa	x	x	x
	Desmodium asperum	x		
	Desmodium barbatum	x	x	x
	**Eriosema crinitum*		x	
	**Eriosema simplicifolium*		x	
	**Eriosema violaceum*	x	x	
	Phaseolus linearis	x	x	
Malpighiaceae	*Byrsonima crassifolia*	x	x	x
Melastomataceae	*Clidemia rubra*	x	x	
Ochnaceae	*Sauvagesia erecta*		x	x
	Sauvagesia rubiginosa		x	
Orchidaceae	**Habenaria leprieurii*		x	x
	Pogonia grandiflora		x	
Polygalaceae	**Polygala angustifolia*	x	x	
	**Polygala longicaulis*	x	x	
Rubiaceae	*Borreria latifolia*		x	x
	Borreria ocymoides		x	x
	Borreria verticillata	x		x
Scrophulariaceae	**Buchnera lobelioides*		x	
	Buchnera longifolia		x	
	**Buchnera rosea*		x	
	**Buchnera weberbaneri*	x		
Verbenaceae	*Amasonia campestris*	x		x
		27	37	19

Aripo species in common with St. Joseph 10/27 = 37%
Aripo species in common with Erin 16/37 = 43%
Aripo species in common with both 7/45 = 16%
Erin species in common with St. Joseph 19
*Species confined to savanna in Trinidad

Table IV: Species confined to Aripo Savannas and not found elsewhere in Trinidad

Family	Species	Status
Aquifoliaceae	*Ilex martiniana*	
Cyperaceae	*Becquerelia tuberculata*	
	Eleocharis plicarhachis	
	Lagenocarpus rigidus subsp. *rigidus*	rare
	+Rhynchospora aripoensis	rare
	Rhynchospora curvula	common
	Rhynchospora emaciata	rare
	Scleria hirtella	rare
	Websteria confervoides	rare
Gramineae	*Raddiella esenbechii*	
Lentibulariaceae	*Genlisea pygmaea*	rare
	Utricularia adpressa	rare
	Utricularia benjaminiana	rare
	Utricularia cucullata	
	Utricularia guyanensis	
	Utricularia myriocista	
	Utricularia pusilla	
	Utricularia viscosa	
Lycopodiaceae	*Lycopodium carolinianum* var. *meridionale*	
Melastomataceae	*Acisanthera bivalvis*	
Orchidaceae	*Epistephium parviflorum*	
	Otostylis brachystalix	
	Pogonia tenuis	rare
Polygalaceae	*Polygala appressa*	
Schizaeaceae	*Schizaea pennula*	rare
Sphagnaceae	*Sphagnum perichaetiale*	rare
Xyridaceae	*Abolboda americana*	
	Xyris glabrata	

+Endemic to Trinidad

Table V: Species confined to the northern flat savannas in Trinidad*

Family	Species
Burmanniaceae	*Burmannia capitata*
Cyperaceae	*Lagenocarpus rigidus* subsp. *tremulus*
	Rhynchospora globosa
Gramineae	*Andropogon virgatus*
	Panicum cyanescens
	Panicum stenodes
	Paspalum pumilum
	Paspalum serpentinum
	Thrasya trinitensis
Lentibulariaceae	*Utricularia amethystina*
	Utricularia subulata
Ochnaceae	*Sauvagesia sprengelii*
Orchidaceae	*Habenaria leprieurii* var. *heptadactyla*
	Spiranthes grisebachii
Polygalaceae	*Polygala adenophora*
	+Polygala exserta
Rubiaceae	*Perama hirsuta*
Turneraceae	*Turnera guianensis*
Xyridaceae	*Xyris fallax*
	Xyris grisebachii

* Includes Aripo, O'Meara, Mausica, Piarco
+Endemic to Trinidad

hummocks found on the savannas. The species have yet to be properly identified. There are a few areas at Aripo where soil creep seems to be responsible for the hummock-hollow complex. In a marginal area on Savanna V the hummocks and hollows are clearly aligned in broadly curving parallel rows. The slightest degree of slope would allow these waterlogged soils to creep slowly in the wet season and become thrust into a series of waves.

Vegetation

As regards the vegetation found on the savannas, more data are available for Aripo than for the others. Detailed studies at Aripo have been carried out by Beard (1946), Richardson (1963), and Schwab (1988). Surveys on the five largest savannas at Aripo have so far revealed about 150 species of plants. Of these 35 can be regarded as common (Table I). The best represented families are shown in Table II.

Only limited plant surveys have been carried out at Erin and St. Joseph but they already indicate that Aripo has a closer affinity with Erin than with St. Joseph; 43% of the species at Erin occur at Aripo compared with 37% at St. Joseph (Table II). The majority of plants on all the savannas in Trinidad display xeromorphic characters.

Mauritia flexuosa (moriche) is the dominant palm in ecotonal areas at Aripo, while *Acrocomia aculeata* (gru-gru) replaces it at Erin and St. Joseph. Only one living specimen of moriche was observed at Erin and none at St. Joseph. This difference probably reflects the drier environmental conditions that prevail on these hilly savannas.

Of important families found on the savannas, the Cyperaceae is best represented at Aripo and Erin while the Compositae and Leguminosae are among the most conspicuous families at St. Joseph and Erin; the latter savanna also has the best showing of the Gramineae and Scrophulariaceae. Also to be noted is the large number of species known only from the savannas in Trinidad, a total of 64, of which Aripo has the highest proportion, 28 (44 percent) while Erin and St. Joseph have far fewer, six and one respectively (Tables III, IV and V). These vegetation profiles are based on limited data and may change whenever more survey work is completed.

We also need to look at some of the unique plants found on the savannas, like *Cassytha, Drosera* (sundew) and *Utricularia* (bladderwort), all of which have evolved special means for survival, the former being parasitic, the latter two insectivorous. In addition, we find orchids that are terrestrial rather than epiphytic, and a moss, *Sphagnum*, that belongs to a family normally associated with peat bogs. *Cassytha* has an artificial appearance of orange nylon twine strung out over other savanna plants; it belongs to the same family (Lauraceae) as the avocado. The sundews develop a deep red pigmentation when exposed to direct sunlight; when growing in shade they have a pale green appearance. Being very small plants, less than five centimetres in height, they trap correspondingly small insects. *Drosera capillaris* has club-shaped leaves covered with tiny glandular hairs which secrete sticky droplets that contain the enzymes necessary for digestion and absorption once the hairs have folded around the insect prey. The folding movement is actually brought about by the hairs growing rapidly, adding cells to increase their length once the insect has become trapped. The increased leaf's surface in contact with the prey speeds up the rate of digestion (Johnson 1985).

The bladderworts are also interesting as insectivorous plants. There are 12 different species of *Utricularia* just at the Aripo Savannas. Tiny bladders, the size of a pinhead, are attached to an

elaborate root system. The wall of each bladder is thin, usually only two cells thick. The bladders function on the basis of a pressure differential. Once the valve opening into the bladder is sealed, water within is absorbed by hairs lining the interior wall. This creates a negative pressure inside the bladder. Four sensory hairs located on the valve's exterior when touched cause contraction of valve tissues thus opening the valve. Owing to the negative internal pressure there is a sudden influx of water which carries the prey with it. Chemical secretions within the bladder then aid in digestion (Withycombe 1924).

Fire

Evidence based on surveys over a 40 year period, especially at Aripo, points to changes in the savanna vegetation. Fire may be an important abiotic factor here. Lately, fires have occurred on all the savnnas every dry season. These fires are not caused by spontaneous combustion, nor are they due to lightning as no thunderstorms occur in the dry season, January to April (Schwab 1988). These fires are caused by carelessness or are deliberately set. On the open savannas, the burnings are not intense owing to limited ground cover, hence perennating organs are usually not damaged. The blackened soil, however, causes more heat absorption which increases moisture loss and produces drier conditions; this in turn favors xerophytes.

Fire also alters the species composition of the savannas by allowing plants that can survive repeated burnings to thrive. Grasses that are cespitose or tufted provide protection for the meristems during fire. Burning appears to induce flowering in grasses such as *Paspalum pulchellum, Leptocoryphium lanatum, Panicum stenodes and Andropogon virgatus*. Some 'trackside' (disturbed area) species such as *Hyptis lantanifolia* and *Coutoubea spicata* can now be found on open savanna. Other plants like *Ryhnchospora barbata, Drosera capillaris* and *Sauvagesia sprengelii* show reduced flowering after fire (Schwab 1988).

If burning continues on a regular basis, plants like these, and others such as the *Lycopodium* species and *Selaginella cruegeri* which are sensitive to fire may eventually disappear from the savannas thus reducing species variety and the unique qualities which make the savannas worth preserving.

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