SAVANNA EXPANSION IN TRINIDAD, W.I.

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Introduction

Neotropical savannas have received considerable attention over the years because of their ecology, specially adapted plants and unusual soil conditions (Myers 1933, Beard 1953, Blydenstein 1967, Ahmad and Jones 1969a, 1969b, Eiten 1972, Sarmiento and Monasterio 1975, Medina 1982, Sarmiento 1984). In Trinidad, most of the published work on this unique ecosystem (Beard 1946, 1953, Richardson 1963, Quesnel 1979) has concentrated on the vegetation dynamics of the open savannas with recent studies focusing on the role fire plays in altering species composition (Schwab 1988, Comeau 1990). As a result, little attention has been directed towards the marginal or ecotonal areas (Leotaud 1992) except to point out the sharp boundaries that exist between forest and savanna (Marshall 1934, Beard 1946, 1953). The frequent burning of savanna margins is mentioned by Richardson (1963) but no evidence is presented to indicate that savanna plants are colonizing these damaged areas. Recent field work by the authors at the Aripo Savannas has shown that few sharp ecotonal boundaries remain, that a lot of the marginal area has been damaged by fire and that evidence exists which supports savanna expansion.

Background

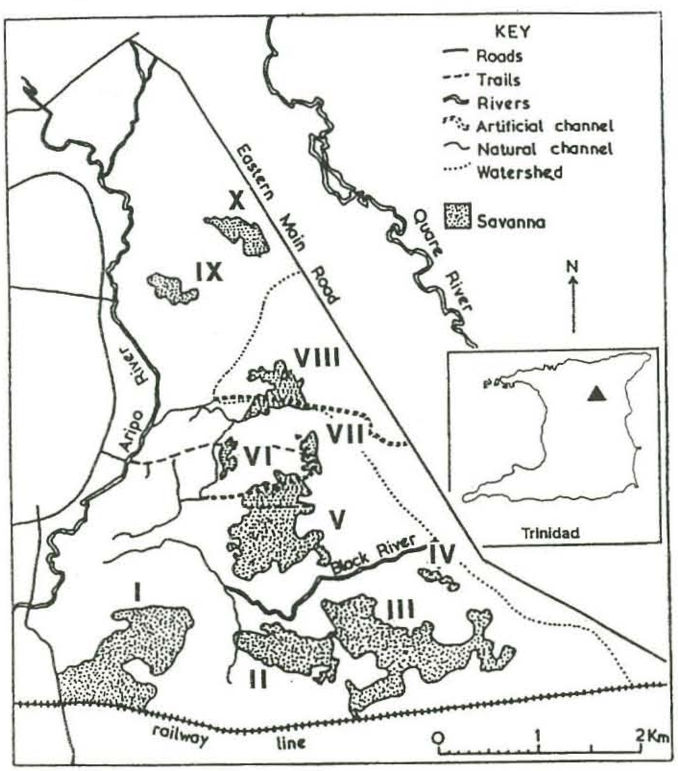

Figure 1: The ten savanas at the Long Stretch Forest Reserve Map Adapted from Schwab (1988)

The ten savannas at Aripo, covering 267 ha, are situated in the Northern Basin or Caroni Syncline of Trinidad. They are located within the Long Stretch Forest Reserve (Fig. 1), elevation 38 m, which contains the *Manicaria-Jessenia-Euterpe* association, *Calophyllum* faciation (Galba-Palm) of Marsh Forest (Beard 1946) or the *Calophyllum-Palmae* (Galba-Palm) type (Marshall 1934). The savannas include palm islands and open treeless expanses covered by sedges, grasses and other herbaceous plants. The surrounding forest, dominated by palms in the understory, together with the savannas form a vegetation mosaic that occurs on flat topography with rainfall ranging between 250 to 280 cm per annum. The savanna soil belongs to the Order: Ultisol, Suborder: Aquults, Great Group: Plinthaquults (Ahmad and Jones 1969b) which has a fragipan i.e., ironpan, restricting drainage.

Methods

Surveys were carried out along the marginal areas of the largest savannas at Aripo (I, II, III, V, VIII) as well as Savannas VI and VII. The sampling was done over a seven year period (1986-1993) during the months of November, December and January - end of wet to beginning of dry season; April, May, and June - end of dry to beginning of wet season; plus July and August - middle of wet season. All species growing around the perimeter of these savannas were recorded and notations made on abundance, habit, morphology, phenology and habitat. Those plants that could not be identified *in situ* were later keyed out using the Flora (Williams et al.1928-) and reference collection of the National Herbarium. Occasional forays were made into the forest during the marginal survey to determine the extent of the ecotone whenever it became diffuse.

Six 10 x 10 metre square plots were established to obtain quantitative data (Fig. 2). Three of these plots were controls located in stable communities, one from the open savanna of V, designated OS5, and two from sharp forest/savanna ecotones on the east and west sides of Savanna VI, namely FS6E and FS6W. These two plots were then divided into CFP6 for the combined forest phases and CSP6 for the combined savanna phases. The remaining three plots were located in diffuse unstable transition zones between savanna and forest, one in Savanna VI, designated TS6, and two in Savanna V, one located in the south-east section and the other in the north-west section of that savanna, designated TS5S and TS5N respectively. All species inside the plots were noted and visual estimates were made on occurrence, whether abundant, common or rare, as well as life-form, i.e. tree, shrub, herb, epiphyte, or climber.

Observations on marginal variability

A wide variety of marginal conditions occur with respect to species composition and habitat features. Amidst this variation,

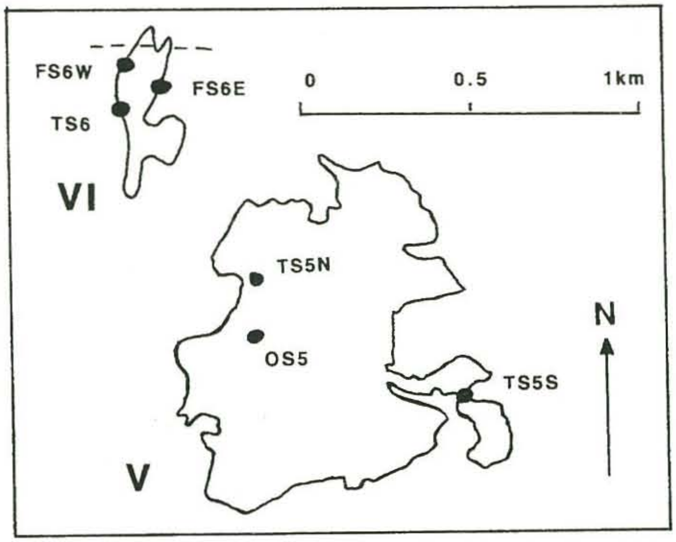

Figure 2: The positions of the sampling plots in Savannas V and VI at the Long Stretch Forest Reserve
Legend:
FS6W= Forest/Savanna 6 west
FS6E=Forest/Savanna 6 east
TS6=Transition Savana 6
TS5N=Transition Savanna 5 north-west
OS5=Open Savanna 5
TS5S=Transition Savanna 5 south-east

repeated patterns were observed and these formed the basis for establishing three succession hypotheses and comparing them with the stable communities which served as control sites. To understand the dynamics of savanna expansion and/or contraction it is necessary to first clearly define what are the more stable communities in the savanna/forest complex.

The most stable communities encountered during the survey were the marginal areas where the sharpest ecotones occur between forest and savanna, and the open savanna away from marginal disturbance. Sharp ecotones are not a common feature around any of the Aripo savannas reflecting the high degree of fire disturbance that occurs on a periodic basis (Schwab 1988). Some of the best sharp-boundary examples are found in Savanna VI (Plate 1) where two plots were set up. In the absence of disturbance, eg. fire and cutting, common mature forest trees near savanna margins include *Ilex arimensis* (Biscuitwood), *Isertia parviflora* (Wild ixora) and *Parinari campestris* (Bois bandé) together with all the dominant palms listed by Beard (1946) for Marsh Forest except *Attalea maripa* (Cocorite palm) which may be absent because edaphic conditions are too wet in ecotonal areas. Mature trees of the marsh forest reach an average height of 15m, the tallest being *Mauritia flexuosa* (Moriche palm), *Symphonia globulifera* (Yellow mangue), *Terminalia amazonia* (White olivier) and *Parinari.* Along some forest margins *Chrysobalanus icaco* (Fat pork) is the dominant tree. As these trees mature they lean toward the light, become top heavy and topple over which could explain their absence in some areas.

Plate 1: The sharp ecotonal boundary between mature marsh and savanna on the western side of Savanna VI

In the open treeless savanna (Plate 2), which represents the other stable community, the ground cover is dominated by the sedges *Rhynchospora curvula* and *R. barbata*, the grass *Paspalum puchellum* and the insectivorous *Drosera capillaris* (Sundew). Although these species are the most abundant, the vegetation does not form a continuous cover but is patchy with up to 40% of the ground surface being devoid of plants, except for algae, attesting to competition for limited nutrients and moisture extremes. The only shrubs present in open savanna are *Chrysobalanus icaco* (Fat pork) and *Byrsonima crassifolia* (Savanna serrette).

Plate 2: Treeless open expanse of Savanna V with stable ground cover dominated by grasses and sedges

The next step was to compare these communities with the unstable assemblages along savanna margins in order to gauge deviation away from or progression towards stability. In the transition plot in Savanna VI which appears to be reverting back to forest, the most abundant plants are the composite *Wedelia caracasana*, the sedge *Scleria bracteata*, the melastome *Miconia ciliata*, and *Heliconia psittacorum*. The former two are agressive competitors taking advantage of increased light when the margin gets opened up by fire

Plate 3: A diffuse margin on the western side of Savanna VI where relict Moriche palms are the only marsh forest trees to have survived the fire damaged habitat. Shrubs beneath the palms, such as *Ilex arimensis* (Biscuitwood) and *Isertia parviflora* (Wild ixora) are good indicators of the re-establishment of forest.

disturbance while the *Heliconia* is an invasive weed. *Mauritia flexuosa* (Moriche palm) was the only mature tree (Plate 3) indicating its ability to withstand fire as there was evidence of burning in and around the plot. Once the canopy is opened up by fire, the increased light produces a dense mid-story herbaceous layer made up mainly of sedges (*Diplacrum longifolium, Lagenocarpus guianensis* and *Scleria*) that allow little light penetration to the ground. In well-shaded areas, beneath shrubs and immature trees, forest species such as the woody vine *Rourea surinamensis*, and *Maprounea guianensis* (Petite-feuille) gain a foothold.

The two transition plots in Savanna V are composed of plants that show strong affinity with savanna vegetation. In the plot in the south-east sector, the most abundant plants are the marginal melastome *Comolia veronicaefolia*, the grass *Paspalum pulchellum* and the sedge *Rhynchospora filiformis*, the latter two being open savanna species. The melastome appears to be in decline being replaced by the grass and sedge. The microtopography, in this and other marginal areas, is hummocky due to worm and termite activity and possibly soil creep (Cômeau 1990). Relicts of the forest persist with species such as *Tabebuia stenocalyx* (Wild calabash), *Chrysobalanus icaco* (Fat pork) and *Mauritia flexuosa* (Moriche palm), the latter producing pneumatophores i.e., spike-like aerial roots at ground level, within the plot.

The other transition plot in Savanna V, which is located in the north-west sector, has two abundant plants, *Paspalum pulchellum* and *Rhynchospora globosa* both of which are true savanna species. In addition to *Paspalum*, several tall grasses form a dominant herbaceous cover, *Panicum cyanescens, P. parvifolium, Andropogon virgatus* and *A. leucostachyus*, which seems to have slowed succession towards savanna. Hummocky microtopography characteristic of marginal areas, combined with high water tables, creates wet hollows where algae flourishes. The relict forest tree *Mauritia flexuosa* (Moriche palm) adapts to this wetness by producing pneumatophores.

Plate 4: The north-west corner of Savanna V where expansion is taking place

Plate 5: The gap between the Moriche palms in the foreground once contained trees which were destroyed by repeated fires. Grasses and sedges such as *Paspalum pulchellum, Rhynchospora barbarta* and *Lagenocarpus rigidus*, once established, favour the development of savanna.

Both the transition plots in Savanna V occur in areas where forest once extended in a narrow band across the landscape isolating smaller pockets of savanna from larger ones. Recurring fires eliminated the forest trees and opened a permanent gap, allowing the isolated pockets of savanna to coalesce with the main savanna (Plates 4 and 5).

Marginal stability versus savanna expansion

Repeated observations along marginal areas at the Aripo Savannas showed a great variety of successional or retrogressional stages that deviated from the sharply defined ecotone that characterizes a stable climax for the forest/savanna complex (Plate 1). These deviations are a result of fire disturbance (Schwab 1988, Comeau 1990). From this variety, three general patterns emerged. First, transition areas that are reverting back to forest (Plate 3); second, transition areas that are becoming more savanna-like (Plates 4 and 5); and third, transition areas that are leaning in the direction of savanna but have become arrested in their development by species dominance and pronounced micro-relief (Plate 6).

To test this pattern hypothesis, the plots set up in the

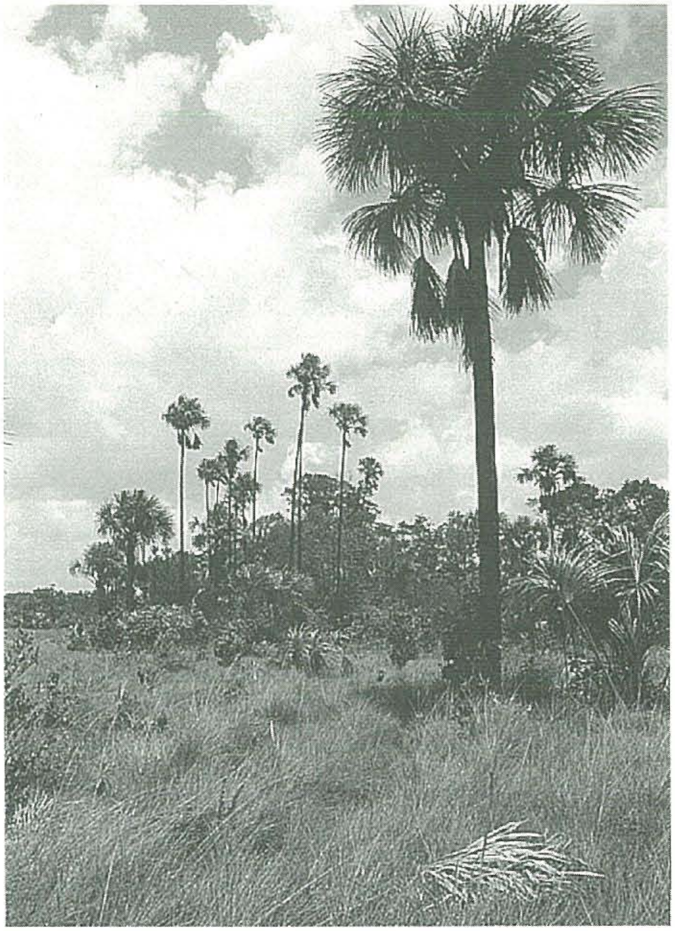

Plate 6: Savanna expansion has been slowed by the dominance of the tall grasses in the foreground, such as *Panicum cyanescens, P. parviforum, Andropogon virgatus* and *A. leucostachyus.*

transition zones were compared with the control plots (see Table I). The transition plot in Savanna VI (TS6) which represents re-establishment of forest has 41% forest species and only 4.5% savanna species while the transition plot in the SE section of Savanna V (TS5S) which represents establishment of savanna has 9.5% forest species and 40.5% savanna species, a reversal of the trend in TS6. The transition plot in the NW section of Savanna V (TS5N) which represents arrested development of savanna has 14% forest species and 42% savanna species, percentages which show similarities to those for TS5S. The trends are what would be expected from the observed general patterns. The three transition plots (TS6, TS5S, TS5N) also have the highest percentages of marginal and disturbance species compared with the control plots, namely FS6E, FS6W and OS5 (see Table I). In fact, the two forest/savanna control plots of VI have no disturbance species while the open savanna plot of V has no marginal species. This reinforces the validity of the controls.

If we look at the Sørensen similarity matrix (Sørensen 1948) for the various plots (seeTable II), the least similarity (index 2) occurs between the combined forest phase of the control plots in Savanna VI (CFP6) and the open savanna control plot in V (OS5). This result is expected as these plots represent the extreme opposites of stable vegetation and are,

Table 1 - Total species numbers and species percentages within the plots; duplicate species are excluded.

Species Plots	FS6E	FS6W	TS6	TS5S	TS5N	OS5
Total	63	67	44	42	36	22
Total F	35	36	18	4	5	1
Total F+S	9	10	8	10	6	2
Total M	8	8	9	8	6	0
Total S	11	13	2	17	15	18
Total D	0	0	7	3	4	1
% F	55.6	53.7	40.9	9.5	13.9	4.5
% F+S	14.3	14.9	18.2	23.8	16.7	9.1
% M	12.7	11.9	20.5	19.0	16.7	0.0
%S	17.5	19.4	4.5	40.5	41.7	81.8
% D	0.0	0.0	15.9	7.1	11.1	4.5

Legend: Species category
F = forest species
S = savanna species
M = marginal species
F+S = forest and savanna species
D = disturbance species

Plot designation
FS6E = Forest/savanna 6 east
FS6W = Forest/savanna 6 west
TS6 = Transition Savanna 6
TS5S = Transition Savanna 5 south-east
TS5N = Transition Savanna 5 north-west
OS5 = Open Savanna 5

therefore, the least similar in species composition. Conversely, OS5 has the greatest similarity (index 41) with the combined savanna phase of the control plots in VI (CSP6), again what would be expected. What is significant is the wide discrepancy, i.e., difference, between the low similarity (index 6) of OS5 and the transition plot in Savanna VI (TS6), and the higher similarities (31 and 34) between OS5 and the transition plots in the SE and NW sections of Savanna V, TS5S and TS5N respectively. This substantiates the contention that TS6 is reverting back to forest and that TS5S and TS5N and becoming more savanna-like in their species composition. To further reinforce this contention, a similar discrepancy exists between the low similarity (index 11) of CSP6 and TS6, and the much higher similarities (46 and 43) between CSP6 and TS5S and TS5N respectively.

Table II - Sørensen Similarity Matrix

Plots	CFP6	TS6	TS5S	TS5N	CSP6	OS5
CFP6						
TS6	47					
TS5S	24	35				
TS5N	19	32	52			
CSP6	28	11	46	43		
OS5	2	6	31	34	41	

Legend:
CFP6 = Combined Forest Phase 6
TS6 = Transition Savanna 6
TS5S = Transition Savanna 5 south-east
TS5N = Transition Savanna 5 north-west
CSP6 = Combined Savanna Phase 6
OS5 = Open Savanna 5

Key species in the transition process

There are several good indicator species that once well established in ecotonal areas affect the direction in which succession will proceed. These include *Ilex arimensis* (Biscuitwood) and *Isertia parviflora* (Wild ixora) which favour the re-establishment of forest while the grass *Paspalum pulchellum*, and the sedges *Rhynchospora barbarta* and *Lagenocarpus rigidus* would influence succession to proceed toward savanna-like conditions.

Conclusions

Strong floristic evidence exists for savanna expansion following repeated disturbance in marginal communities at the Aripo Savannas. The frequency of fire seems to be one of the determining factors that control the direction succession will take. Time-lapse aerial photography would provide additional support for this evidence.

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