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Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years

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Abstract

Changes were assessed in population density and species composition of the vegetation in a 3 ha permanent plot of a *Trachypogon* savanna protected against fire and grazing for 25 years (1961-1986). The regional vegetation is a bush island savanna with coexistent isolated trees and small patches of semi-deciduous forest. After 9 years of protection, the savanna physiognomy was similar to that of burned savannas but after 16 years, stem density increased exponentially. After 25 years of protection, stem density in the herbaceous layer and the groves increased 131 and 20 fold, respectively. As woody cover increased, coverage proportion of the herbaceous layer decreased. The floristic composition and structure of the herbaceous layer has been changing from a *Trachypogon plumosus* dominated herbaceous layer to one dominated by *Axonopus canescens*. After 1977, the invasion of *Hyparrhenia rufa*, an African grass, caused changes in the vertical structure from domination by short grasses to domination by tall grasses. Therefore, after 25 years of protection, the savanna is gradually changing from an open to a closed bush savanna with a taller grass layer. Up to now, vegetation colonization has been highly dependent on grove dynamics and the establishment of *H. rufa*. Groves may provide corridors for migration of species from the gallery forest. However, in places, ironstone outcrops limit vegetation changes associated with savanna protection.

Keywords: temporal changes, density, species composition, protected *Trachypogon* savanna.

Résumé

Une évaluation des changements de densité de population et de composition des espèces végétales a été réalisée sur une période de 25 ans (1961-1986) pour une parcelle permanente de 3 hectares d'une savane à *Trachypogon* protégée contre le feu et le pâturage. La végétation de la région est une savane arbusive coexistant avec des arbres isolés et de petites parcelles de forêt semi-décidue. Après 9 ans de protection, la physionomie de la savane est semblable à celle des savanes brûlées mais, après 16 ans, la densité croît de manière exponentielle. Après 25 ans de protection, le nombre d'individus de la couche herbacée et des bosquets est respectivement multiplié par 131 et 20. Au fur et à mesure que le couvert boisé croît, la proportion du couvert de la couche herbacée décroit. La composition floristique et la structure de la couche herbacée diffèrent d'un stade à l'autre, passant d'une dominance à *Trachypogon plumosus* à une dominance à *Axonopus canescens*. Après 1977, l'invasion d'une herbe africaine : l'*Hyparrhenia rufa* a induit des changements dans la structure verticale; on passe de la domination par des herbes courtes à une domination par les herbes hautes. Ainsi, après 25 ans de protection, la savane change graduellement : la savane arbustive ouverte devient savane arbustive fermée à couche herbacée haute. Jusqu'à présent, la colonisation par la végétation dépend fortement de la dynamique des bosquets et de l'établissement d'*Hyparrhenia rufa*. Ces bosquets peuvent constituer des couloirs de migration des espèces à partir de la forêt-galerie. Mais, par endroits, des affleurements de minerai de fer limitent les changements associés à la protection de la savane.

INTRODUCTION

The ecological role of fire on the origin and maintenance of savanna is a matter of controversy. Fire can cause vegetation to become savanna-like more and savanna vegetation has evolved in response to fire (Budowski, 1956; Vareschi, 1962, 1969; Blydenstein, 1967). Furthermore, savannas protected from fire move toward woody vegetation (Vuattoux, 1970, 1976; Menaut, 1977; Couthino, 1982; Huntley, 1982; Lacey *et al.*, 1982; Menaut & Cesar, 1982; San José & Fariñas, 1983; Walker, 1985) on all continents; with some exceptions (Blydenstein, 1967). Some evidence suggest (Blydenstein, 1967; Bourlière & Hadley, 1970; Sarmiento & Monasterio, 1975; Couthino, 1982; Gillon, 1983; Sarmiento, 1983, 1984) that savannas are relatively old ecosystems, even prior to the presence of man in South America.

Trachypogon savannas, major ecosystems in Northern South America (San José *et al.*, 1985), present a wide range of floristic and physiognomic types, which have been influenced to different degrees by human disturbances. These savannas have been considered as a secondary ecosystem of anthropogenic origin (Lasser, 1955; Vareschi, 1960; Tamayo, 1964; Aristeguieta, 1966). Establishment of a protected *Trachypogon* savanna plot (Blydenstein, 1962) and reported observations (San José & Fariñas, 1971, 1983) indicated that this savanna has been gradually changing into a denser arboreal community.

The aim of the present work is to analyze the temporal changes on density and species composition in the herbaceous and arboreal layers of a *Trachypogon* savanna following 25 years of fire and grazing suppression.

MATERIAL AND METHODS

A three hectare permanent plot was established by Blydenstein (1963) in 1962 on the permanent grid of contiguous quadrants (A7A8 D7D8) in the Biological Station of the Llanos (8°56'N; 67°25'W), Calabozo, Venezuela. The area has been protected from fire and cattle grazing since 1961. The Biological Station is located on a "conserved mesa" covered by a closed bush island savanna (Hill, 1969), where coexist isolated trees and small patches of semideciduous forests. The woody layer covers more than 40 percent of the total area and includes a well developed synusia of shrubs. Taxonomic nomenclature of the present work is based on Aristeguieta (1966).

Herbaceous species populations were analyzed by sampling the vegetation in 1962 (Blydenstein, 1963), 1969 (San José & Fariñas, 1971), 1977, 1983 and 1986 (data of present work) using the point-centered quarter method (Cottan & Curtis, 1956) as modified by Dix (1961). In each sample, 67 points were chosen at random according to Blydenstein (1963). Thus the data for the starting time and successive samples were uniformerly treated. However, due to the tendency for the quarter method to underestimate the density of aggregated populations (Greig-Smith, 1965; Risser & Zedler, 1968), only relative density was calculated. This index is really the apparition probability for each species and therefore it allows statistical inferences.

Herbaceous vegetation diversity was estimated using the complement of Simpson Index (c) (PIELOU, 1977) as based on the relative density of the species.

Density of tree species was assessed in 1962 (BLYDENSTEIN, 1963), 1969 (SAN JOSÉ & FARIÑAS, 1971), 1977 (SAN JOSÉ & FARIÑAS, 1983), 1983 and 1986 by counting all individuals in the three hectare plot. Since it was impossible to determine whether new individuals were the result of new seed establishment or vegetative propagation of existing trees, we will refer to them as "tree stems" or "stems".

Two groups were recognized: "isolated stems" and "grove tree stems". The first class consists of scattered tree stems on a continuous grass stratum dominated by *Trachypogon* and *Axonopus* sp; the

TABLE I. — *Presence data of the species in the herbaceous layer of a protected plot* (3 *ha*) *at the Biological Station* (*Calabozo*), *for the available samples.*

Species	Presence				
	1962*	1969	1977	1983	1986
Trachypogon plumosus (Humb. & Bonpl.) Ness.	154	132	65	37	59
Axonopus canescens (Nees & Trin.) Pilger	44	68	119	88	101
Bulbostylis capillaris (L.) Clarke	22	1	0	2	0
Andropogon brevifolius Swartz	13	6	4	5	6
Borreria suaveolens Mey.	2	1	3	3	2
Euphorbia thymifolia L.	6	1	0	0	0
Borreria ocimoides (Burm.) DC.	14	0	0	0	5
Cassia hispidula Vahl.	1	0	0	0	0
Cuphea micrantha HBK	2	0	0	0	0
Dichromena ciliata Vahl.	1	0	0	0	0
Pectis carthusianorum Less	9	0	0	0	0
Eragrostis maypurensis (HBK) Steud.	0	8	1	0	0
Paspalum multicaule Poir.	0	4	4	3	0
Andropogon angustatus (Presl.) Steud.	0	5	0	1	0
Hyptis suaveolens (L) Poit.	0	3	5	8	0
Sebastiania corniculata (Vahl.) Mull. Arg.	0	1	2	2	2
Desmodium barbatum (L) Benth. & Oerst.	0	2	1	2	0
Diodia teres Walth.	0	1	2	5	0
Bulbostylis conifera Kunth	0	6	3	3	0
Sida rhombifolia L.	0	3	0	0	2
Rhynchospora spp.	0	2	0	0	0
Axonopus purpusii (Mez.) Chose	0	7	0	0	0
Hachelochloa granularis (L) Kuntze	0	1	0	0	0
Indigofera asperifolia HKB	0	1	1	0	0
Sida linifolia Cav.	0	4	6	0	0
Galactia jussienana Kunth	0	1	1	0	0
Cassia bauhiniaefolia Kunth	0	1	1	0	0
Cordia curassavica (Jacq.) R. & S.	0	0	2	0	0
Hyparrhenia rufa (Ness) Stapf	0	0	20	63	81
Andropogon hirtiflorus (Nees) Kunth	0	0	28	24	1
Ageratum conyzoides L.	0	0	0	9	0
Borreria aff. latifolia (Aubl.) Schum.	0	0	0	7	2
Amazonia campestris (Aubl.) MLDKE	0	0	0	1	0
Calopogonium mucunoides Desv.	0	0	0	1	0
Evolvulus sericeus SW.	0	0	0	0	1
Andropogon semiberbis (Nees) Kunth.	0	0	0	0	3
Unknown seedling	0	0	0	0	2

* After BLYDENSTEIN (1963).

TABLE II. — *Mean basal diameter (mm) of the species with the highest importance value and of all species in the herbaceous layer of a protected plot (3 ha) at the Biological Station (Calabozo), for the available samples.*

Species	1962*	1969	1977	1983	1986
Trachypogon plumosus (Humb. & Bonpl.) Ness.	17,0	35,1	21,3	24,4	26,9
Axonopus canescens (Nees & Trin.) Pilger	14,3	31,7	30,7	39,5	34,6
Hyparrhenia rufa (Ness) Staff.	–	–	13,5	12,8	21,6
All species	13,1	32,4	21,7	21,1	26,0

* After BLYDENSTEIN (1963).

second class is composed of discontinuous patches with one or more tree stems, and the typical understorey layer of herbs and shrubs growing around the boundaries. Description of this vegetation type is given by ARISTEGUIETA (1966) and SAN JOSÉ *et al.* (1985).

Tree species diversity of the 3 ha plot was calculated using the Brillouin function (PIELOU, 1977) as based on the density of the species.

The rate of changes in the floristic composition of the vegetation was evaluated by using the Similarity Index (SI) (SORENSEN, 1948) as proposed by BORNKAMM (1981).

The depth of the indurated ironstone horizon was measured in each corner on a grid ($10 \times 10\ m^2$) established in the 3 ha plot. Thus, holes were bored with a bore (50 cm wide by 150 cm long) attached to a tractor.

RESULTS

1. Changes in the herbaceous vegetation

Trachypogon plumosus, *Axonopus canescens*, *Bulbostilis capilaris*, and *Andropogon hirtiflorus* evidenced major changes in the species presences (SP) (tab. I). The value of SP for *T. plumosus* was the highest in the 1962 and 1969 sampling, and thereafter it decreased in number to reach 59 in the 1986 sampling; whereas the SP of *A. canescens* increased and after 1977 was the species with the highest SP. At each one of the samples (1969-1986), the SP of *T. plumosus*, as a proportion of the sample size, was significantly different as compared to the SP for *A. canescens* (G test, SOKAL & ROHLF, 1981) and these differences become more apparent over time. The species *Bulbostilis capillaris* and *Andropogon brevifolius* became a relatively rare species in 1983 and 1986. The SP of *Hyparrhenia rufa*, an African grass that invaded the plot after 1977, rapidly increased. By 1986, *Hyparrhenia rufa* was the second most abundant species after *A. canescens*.

The mean basal diameter (MBD) of *T. plumosus* and *A. canescens* (tab. II) increased from 1962 to 1969. After applying the multiple comparisons test procedure (SOKAL & RHOLF, 1981) for the samples from 1969 to 1986, the mean values were not significantly different. In relation to the MBD of all species, a similar increasing trend was observed from 1962 to 1969; and the multiple comparisons test procedure for the samples from 1969 to 1986 indicated that the differences among samples were significant; except between 1969 and 1986 samples and between 1977 and 1986 samples.

The Index of Similarity (IS) (SORENSEN, 1948) related to the first sampling (1962) (fig. 1) decreased until the 1977 sampling. Thereafter, the rate of changes based on the preceding year increased from 0.34 (1977) to 0.55 (1986). Grass layer diversity (tab. III) increased from 0.632 in 1961 to 0.809 in 1983, and decreased to 0.717 in 1986.

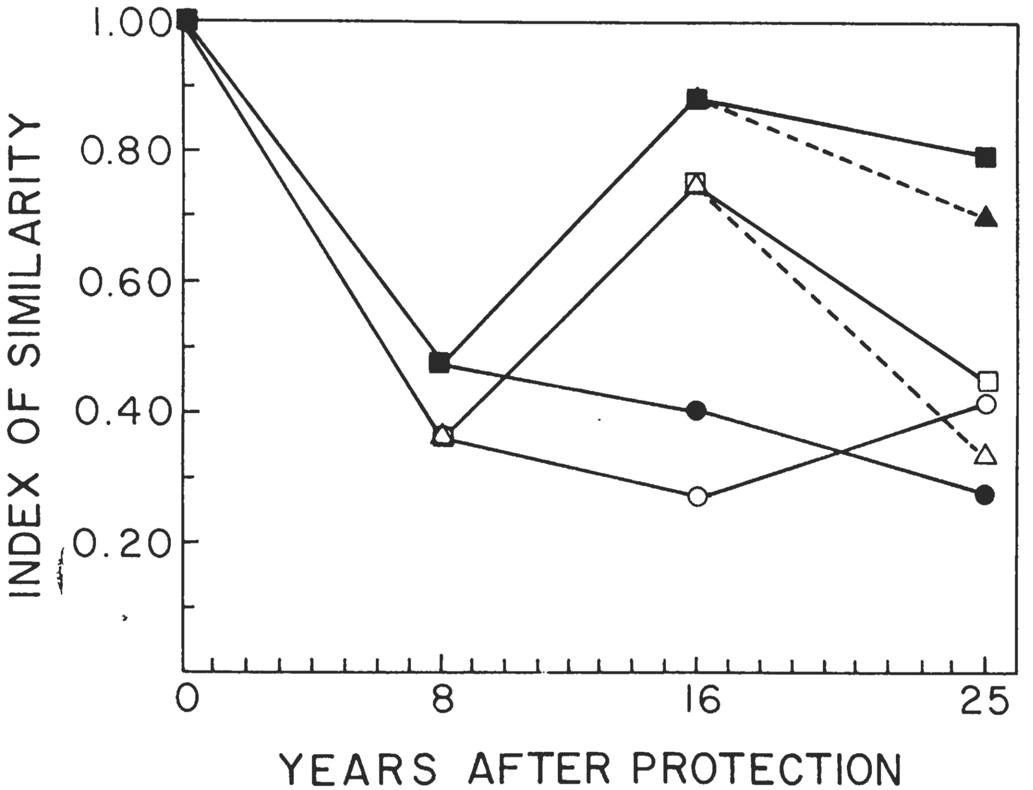

FIG. 1. — Temporal changes of the similarity index (SI) in a *Trachypogon* savanna protected for 25 years. SI of the herbaceous (○) and woody vegetation (●) as compared with the reference year (1962); SI of the herbaceous (□) and woody vegetation (■) as compared with the preceding year; secondary reference line of the herbaceous (△) and woody vegetation (▲).

TABLE III. — *Changes in the complement of the Simpson Index (1-C) of the herbaceous layer and Brillouin Index (H bits) of the arboreal vegetation in a protected plot (3 ha) at the Biological Station (Calabozo) for the available samples and census, respectively.*

	Herbaceous vegetation		Arboreal Vegetation	
Sampling	Number of Species	1-C	Number of Species	H
1962*	11	0.63	4	1.54
1969	22	0.69	14	2.61
1977	19	0.73	16	2.83
1983	20	0.80	24	3.16
1986	14	0.71	24	3.19

* After BLYDENSTEIN (1963).

The effect of soil heterogeneity on the results was evidenced after the relative presence of *T. plumosus*, *A. canescens* and *H. rufa* were calculated for each of three 1 ha subplots (tab. IV). Comparisons among these subsamples indicated that changes in the vegetation were only evident in the subplots, with the deeper ironstone.

TABLE IV. – *Mean depth of indurated ironstone (MDII, m), relative presences (%) of species in the herbaceous layer, and mean point to plant distance (MPPD, m) in 3 subplots of the protected plot (3 ha) at the Biological Station for the 1986 samples.*

Subplot (1 ha)	MPPD	*Trachypogon plumosus*	Relative Presence		MDII
			Axonopus canescens	*Hyparrhenia rufa*	
1	0.09	8	33	42	0.59
2	0.15	18	24	48	0.60
3	0.13	32	46	2	0.12

2. Changes in the arboreal vegetation

During the 25 years of protection from fire and grazing, the woody vegetation became floristically more complex (tab. V) and the rate of changes related to the first census (1962) increased linearly from 1969 (0.53) to 1986 (0.72) (fig. 1). However the rate based on the preceding year decreased (0.11-0.20) after 16 years of protection. In the 1986 census, the species with the highest density were *C. americana*, *C. vitifolium*, *G. macrocarpa* and *Allophyllus occidentalis*. The remaining species were present in smaller proportions but represented an important compositional change (72 percent) compared to 1961, where the proportions of *B. crassifolia* (44%), *C. americana* (34%) and *B. virgilioides* (21%) made up 99% of the total.

The number of isolated stems (fig. 2) increased from 50 in 1962 to 6 542 in 1986; and in the groves, the number increased from 231 in 1962 to 5 380 in 1986.

After eight years of protection (1961-1969), the number of isolated stems increased 6 fold (50 to 304 individuals) and the stems growing in groves 2 fold (231 to 492 individuals). This increase was mainly due to *B. crassifolia* and *C. americana* (tab. V). One exception was *C. vitifolium*, a fire sensitive species. Thus, vegetation structure in the enclosure was similar to the structure of burned savanna.

The number of individuals per species (fig. 2) increased rapidly just beyond 16 years of protection, and community density increased from 1592 individuals in 1977 to 9 577 in 1986. The trend followed by the increase in the number of individuals (N) as a function of protection time (t) was fitted by an exponential curve, leading to the equation $N = 248.08\ e^{0.14t}$ ($r^2 = 0.966^{**}$); where, the value of N at the beginning of the protection period was 248 individuals and the relative growth rate 0.14 yr^{-1}.

Density of isolated stems in the herbaceous layer rapidly increased over time and their proportion in relation to the total number of individuals was 17, 38, 46, 55 and 56 per cent for the 1962, 1970, 1977, 1983 and 1986 samples, respectively. The last two samples (1983 and 1986) were very peculiar since the herbaceous

TABLE V. – *Number of stems of all tree species in a protected plot (3 ha) at the Biological Station, Calabozo, for the available censuses. New species recorded after 1961 were present in the groves of the nearby savanna but happened to be absent from this particular plot.*

Species	Number of isolated stems					Number of stems in groves				
	1962*	1969	1977	1983	1986	1962*	1969	1977	1983	1986
Curatella americana L.	13	117	254	1 448	2 071	82	114	160	421	577
Byrsonima crassifolia H.K.B.	23	95	181	336	340	111	135	142	204	210
Bowdichia virgilioides H.B.K.	23	20	18	84	85	35	40	55	52	54
Cassia moschata H.B.K.	–	–	–	5	6	3	4	5	9	10
Cochlospermum vitifolium (Willd.) Spreng	–	72	247	1 163	1 236	–	33	64	447	541
Godmania macrocarpa Hemsley.	–	–	6	588	651	–	14	24	198	251
Casearia hirsuta Sw.	–	–	1	7	10	–	–	23	23	25
Platymiscium pinnatum (Jacq.) Dugand	–	–	3	1	2	–	5	2	9	14
Genipa caruto H.B.K.	–	–	1	15	15	–	24	20	71	75
Guettarda elliptica Sw.	–	–	–	10	17	–	20	69	116	258
Cordia cf. C. hirta I.M. Johnston	–	–	21	435	433	–	64	202	531	529
Connarus venezuelensis Baill.	–	–	0	1	10	–	1	2	7	36
Capaifera officinalis H.K.B.	–	–	0	7	12	–	0	3	20	33
Machaerium pseudoacutifolium Pitt. (?)	–	–	0	107	188	–	0	3	20	33
Casearia decandra Jacq.	–	–	1	129	136	–	37	82	358	408
Bactris sp.	–	–	0	–	–	–	1	2	2	2
Allophylus occidentalis Radlk	–	–	–	115	118	–	–	–	807	817
Tabebuia blakeana Pittier.	–	–	–	1	1	–	–	–	–	–
Jacaranda obtusifolia H.K.B.	–	–	–	34	41	–	–	–	8	14
Vochysia venezuelana Staflen	–	–	–	9	9	–	–	–	1	1
Pterocarpus podocarpus Blake	–	–	–	1	1	–	–	–	40	43
Fagara caribea (Lam.) Mart.	–	–	–	–	–	–	–	–	9	9
Xylopia aromatica (Lam.) Mart.	–	–	–	–	–	–	–	–	1	22
Xylosma pallidifolium Sleumer	–	–	–	2	2	–	–	–	7	7
Total	50	304	733	4 496	5 380	231	492	859	3 534	4 197

* After BLYDENSTEIN (1963).

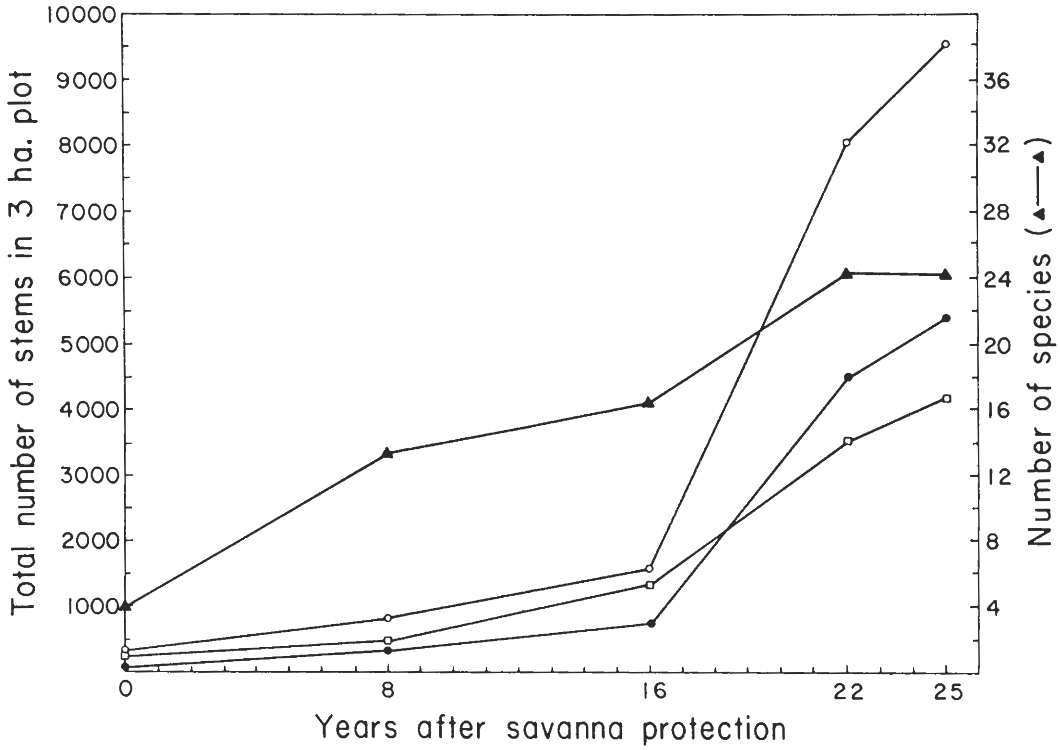

FIG. 2. — Temporal changes in the number of isolated stems (●), stems in groves (□), and total stems (○), in a *Trachypogon* savanna protected for 25 years.

matrix was colonized by species that in burned savannas are only growing in the groves.

DISCUSSION

After protection of the *Trachypogon* savanna from fire and grazing, the vegetation changed in species composition and dominance. Temporal changes in the relative presence of the herbaceous species depended upon soil heterogeneity as expressed by the depth of the ironstone hardpan. These results could be also related to changes in the nutritional status of the soil such as has been observed in fertilized (NPK) plots (HERNANDEZ *et al.*, 1982). Differential reproductive strategies of species would also aid to explain the observed results. Thus, vegetative propagation mainly occurs in *T. plumosus;* while sexual reproduction, and high probability of seedling survival in the absence of fires, is characteristic of *A. canescens* (SILVA & ATAROFF, 1985).

Changes in the spatial structure of the herbaceous layer were mainly due to the invasion of the tall African grass, *H. rufa* and the increasing abundance of the tall local savanna species, *A. hirtifolius*. Thus, the short grass-layer was replaced by a tall grass-layer.

Areas of the Biological Station have been completely covered by *H. rufa*. In one ha plot, set up in 1969 for vegetational studies and re-evaluated in 1977, species richness changed from 10 to 5, the complement of the Simpson index varied from 0.55 to 0.05, and the relative density of *H. rufa* from 0 to 97.8 percent. The high potential of *H. rufa* for savanna invasion might be associated to its reproductive pattern, dispersal mechanisms (SILVA & ATAROFF, 1985) and annual distribution of the assimilatory leaf area (RINCON, 1977). Invasion of savannas and displacement of local grasses by African grasses has been documented for protected plots in the Cerrado vegetation of Paraopeba (Minas Gerais) and Ema (Pirasununga) in Brasil (COUTHINO, 1982). In Emas, a protected Cerrado changed to a woody savanna, and the local grasses were displaced by *Melinis minutiflora.*

Before 16 years of protection, the trends of the Similarity Indexes for the herbaceous and woody vegetation were similar. The rate of changes in composition was relatively rapid (47-53 percent) during 1962-1969 and thereafter decreased toward stability. However, in the herbaceous layer, the index increased (0.40) and the year to year rate increased from 0.25 to 0.55 (1986) as the plot was invaded by *H. rufa* and the number of species decreased. Thus, the composition of the 1986 sample was more similar to the original samples than to previous samples.

The high initial rate of change in species composition was probably associated with the presence of groves as nuclei for tree dispersion as well as the corridors for migration of species from the gallery forest. A different situation was observed in a protected plot in the Ivory Coast (MENAUT, 1977) where the low rate of change in vegetation composition was due to the growth of savanna species mainly from root stocks, and of pioneer forest species, from the deciduous rain forest which lies at the contact with the savanna zone. Tree colonization in the protected *Trachypogon* savanna plot was by local species. After 20 years of protection, *Byrsonima verbasifolia*, a typical species of *Trachypogon* savanna and one individual of *Olyra longifolia* H.B.K., a bamboo occurring in the gallery forest of the Orinoco Llanos, were observed at the Biological Station.

The described changes in richness over time were not correlated to climatic variations. Comparisons between the data from a contemporary burned savanna occurring side by side in the Calabozo area with the changes occurring in the same habitat did not reveal a climatic trend. Furthermore, the secondary reference line of the similarity index graphics did not cross (BORNKAMM, 1981).

After protection, the original open bush island savanna has been gradually changing to a closed bush island savanna with a taller herbaceous layer. The increase in woody vegetation reduced the herbaceous layer and affected its vertical structure. Changes in protected savannas toward woodlands have been documented for different latitudes including the Lamto savannas of the Ivory Coast (VUATTOUX, 1970, 1976; MENAUT, 1977; MENAUT & CESAR, 1982) and savannas of northeast Ghana (BROOKMAN-AMISSAH *et al.*, 1980). However, the present *Trachypogon* savanna does not cover the entire protected area. Thus, in the *Trachypogon* savanna where indurated ironstone is close to the soil surface and it is not faulted with cracks, tree growth is impeded, and the area is covered by a grassfield (open savannas). A similar situation was reported (SCHNELL, 1976) for savannas of west Africa.

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