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ASSESSMENT OF THE ECOLOGICAL EQUILIBRIUM IN A NEOTROPICAL SAVANNA EXCLUDED FROM FIRE AS A DRIVING FORCE

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SUMMARY

The effect of fire on the dynamic of the well drained savannas of the Orinoco Llanos was assessed in the same area by using censuses from a permanent plot protected during 25 years against fire and cattle grazing. The historical vegetational trend was evaluated from side by side comparisons between the protected savanna plot and the vegetation types. Data of tree density and species composition were analyzed by using a multivariate approach (Principal Component Analysis). Results of the ordination diagram indicate that the vegetation of the protected plot is changing toward a woodland vegetation, which is similar to the present forest groves. Under fire conditions, there is a dynamic spectrum which spans from equilibrium to non-equilibrium systems; whereas under fire suppression conditions, a semi-deciduous forest with gaps and herbaceous savanna patches in the shallow soil areas are integrating an unstable equilibrium system.

INTRODUCTION

Neotropical savannas encompass a wide range of physionomic types and floristic units, which are associated to a wide geographical scope, including diverse environment conditions and different levels of human disturbance.

To understand the ecological factors, which determine and maintain the complex matrix of savanna vegetations, we might use the ecological hypothesis on system equilibrium of stability (Holling 1973; Noy-Meyer 1975; Weins 1977; DeAngelis and Waterhouse 1987; Ellis and Swift 1988). It has been observed that savannas in stable equilibrium with fire disturbance are able to return to previous stage once that source (fire) is suppressed. Although, Vareschi (1962) and Tamayo (1964) pointed out that the original vegetation of the Orinoco savannas was a semi-deciduous or deciduous forest and following fire disturbance, the community organization was lost and oportunistic since fire resistance species invaded the vegetation, Weins (1984a,b) observed that the system dynamic ranges from stable equilibrium or stably interactive, and is influenced by biotic and feedback activities to non- equilibrium or weakly interactive, which is stochastically dominated. This hypothesis was further developed by DeAngelis and Waterhouse (1987) and Ellis and Swift (1988).

The paramount role of the effect of fire on the stability and persistence of the savanna vegetation has been scarcely evaluated. Few long term studies have been undertaken to analyze the fire effect as a driving force of the savanna ecosystems. Permanent protected plots were established in paleotropical and neotropical savannas (Blydenstein 1962; Vuattoux 1970; Eiten 1972; San Jose and Fariñas 1971, 1983, 1991). However, the protection time of these plots has not been long enough to predict the vegetational sequence from the pioneer to the persistent stage. Therefore, side by side comparisons of permanent plots, with other typical vegetation types occurring in the same region, could be an useful tool to elucidate the trend in vegetation and to evaluate the stability hypothesis.

The aim of this work is to analyze the stability and persistence of the Orinoco savannas by using both a permanent protected savanna as well as a side by side comparisons between the protected savanna plot and the vegetation types occurring in the well drained Orinoco Llanos.

MATERIAL AND METHODS

Studies in the same area. Protected savanna plot.

A three hectare permanent plot was established by Blydenstein (1963) in 1962 on the permanent grid of contiguous quadrants (A7A8D7D8) of the Biological Reserve (8° 56' N; 76° 25' W), Calabozo, Venezuela. The plot was protected from fire and cattle grazing since 1961.

Density of tree species was assessed in 1962 (Blydenstein 1963), 1969 (San Jose and Fariñas 1971), 1977 (San Jose and

Fariñas 1983) and 1986 (San Jose and Fariñas 1991) by counting all individuals in the three hectare plot. Thus, the vegetational trend of the protected savanna was judged from studies of same plot during 25 years of protection. However, due to length of time necesary to infer savannas changes, the data sequence of the protected plot was compared with savannas and woody communities occurring side by side on the same region.

Side by side comparisons

Savanna vegetation.

Density of tree species was assessed on the 190 ha permanent grid at the Biological Reserve (Calabozo, Venezuela) which was described previously. This census is the starting point (1969) for the vegetational comparison, when annual fire has not been completely excluded from the Biological Reserve (San Jose et al. 1978).

Woody vegetations. (original data of the present work)

In the Orinoco Llanos, the forest vegetation is represented by forest groves, intermingling the savanna grassfields and the gallery forests along the water courses. The largest forest grove (1.3 ha) at the Biological Reserve was selected as the research site (Fig 1).

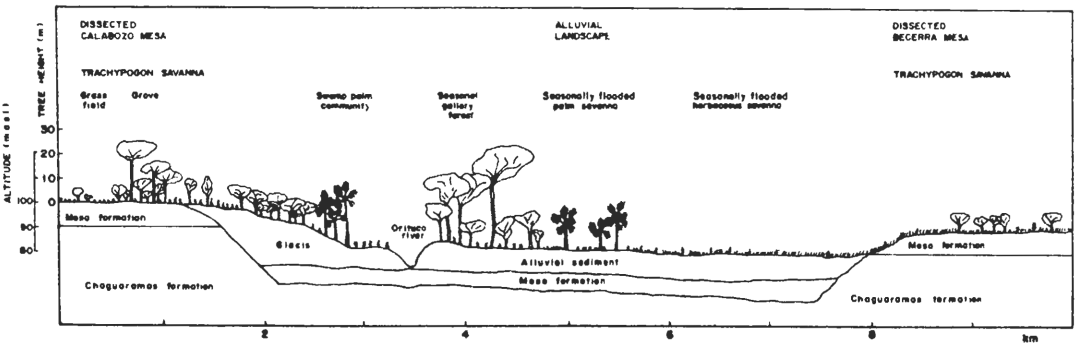

Fig 1. Sketch profile of the studied communities in the Orinoco Llanos.

The soil was classified as Haplustoxs with a ironstone cuirass at 0.5 m mean soil depth.

Two, well drained, gallery forests were selected in contrasting geomorphological positions of the Calabozo area. The first one corresponds to the seasonal gallery forest, located on the first terrace of the Orituco river at 6 Km from the south of the Biological Reserve. The soil, which is well drained, was classified as Haplustoxs according to U.S. Taxonomy (Soil Survey Staff 1975).

The second, well drained, gallery forest was selected on the glacis of a swamp palm community located 3 Km to the north of the Biological Reserve. The soil was classified as Psamments according to U.S. Soil Taxonomy (Soil Survey Staff 1975).

A three ha plot was selected at each gallery forest and density of the tree species was measured by counting all individuals above 5 cm height.

Data analysis

Structural data of the woody vegetations as expressed by the density of tree species was summarized in a 92 X 182 (species X plots) matrix. Because the length of the ordination axes were less than 2.5 standard deviations, most of the response curves (surface) was monotonic (Jongman et al. 1987). Therefore, the vegetation data matrix was individually ordinated using Principal Component Analysis (CANOCO: Ter Braak 1986, 1994).

RESULTS

The findings of the PCA indicated that eigenvalues for the first four PCA axes were 0.611, 0.199, 0.092 and 0.001, respectively. The first of the four axes of species data accounted for 61 percent of the variance.

The results of the PCA (Fig 2) were displayed in an ordination diagram with: a) the 190 ha plots of the Biological Reserve represented by points, b) the protected savanna and the woody vegetation plots by code and c) the species by lines.

The ordination diagram allowed the delineation of the following dominant pattern in the community composition indicating that when the fire was not totally excluded, the species composition was similar among the Biological Reserve plots and mainly distributed around the center of the diagram.

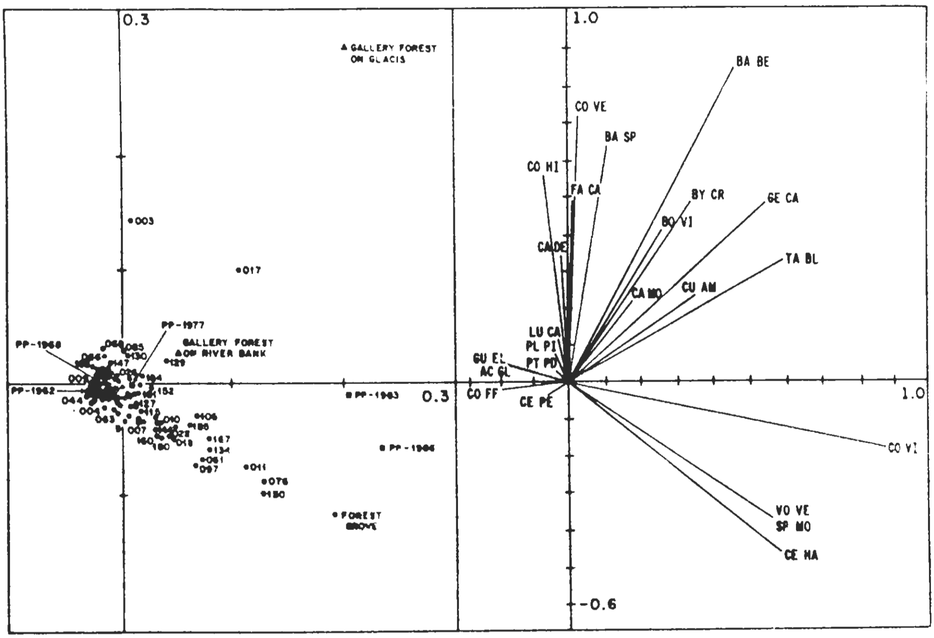

Fig 2. Ordination diagram of the floristic variables on the sites of the Orinoco Llanos in two dimensional PCAmodel. The letters refer to the species ACGL. Acacia glomerosa, BABE. Bauhinia benthamiana, BASP. Bactris minor, BOVI. Bowdichia virgilioides, BYCR. Byrsonima crassifolia, CADE. Casearia sylvestris, CAMD. Cassia moschata, CEHA. Cereus hexagonus, CEPE. Cecropia peltata, COFF. Copaifera pubiflora, COHI. Cordia hirta, COVE. Connarus venezuelensis, COVI. Cochlospermum vitifolium, CUAM. Curatella americana, FACA. Fagara caribea, GECA. Genipa caruto, GUEL. Guettarda elliptica, LUCA. Luehea candida, PLPI. Platymiscium pinnatum, PTPO. Pterocarpus podocarpus, SPMO. Spondias mombin, TABL.

Tabebuia blakeana, and VOVE. Vochysia venezuelana. Numbers of the dots and plot on the permanent grid of the contiguous quadrants at the Biological Reserve. PP= protected plot indicating the year from protectiòn.

The species corresponding to this central cluster of plots were Cecropia peltata, Copaifera pubiflora, Acacia glomerosa, Guettarda elliptica, Pterocarpus podocarpus, Luehea candida and Platymiscium pinnatum. These species are found growing exclusively in the forest groves. On the edges of all woody vegetations the pyro resistant species Curatella americana, Byrsonima crassifolia and Bowdichia virgilioides were found. Individuals of these species are found as isolated plants in the burned Orinoco savannas.

Censuses of the protected plot (PP) were located along the first axis of the ordination diagram, with the increasing number of species and tree density as a function of the protection time. The ordination display evidenced two separate groups of censuses from the protected plot (PP) along the first ordination axis. The first one indicates that after eight years of protection (PP 1962 - PP 1977), the vegetation structure and floristic composition were similar to the disturbed plots of the Biological Reserve savanna. The second group (PP 1983 - PP 1986) corresponding to 22 and 25 years after protection, respectively, were located at the end of the positive first axis. These censuses were characterized by a more rapid compositional change with a further increase in the species number and tree density. This last group was associated with the non-fire resistant Cochlospermum vitifolium, Vochysia venezuelana, Spondias mombin and Cereus hexagonus. In the case of C. vitifolium, a wind dispersed species, the number of individuals measured in 1986 increased 5.6 fold as compared to that in the 1977 census.

In the 1986 census, the abundance and species composition in the protected plot was similar to that in the largest forest grove of the Biological Reserve as indicated by their localizations in the ordination diagram. Thus non-fire resistant species from the larger forest groves were able to invade the herbaceous savannas as well as the smaller forest groves.

All forest vegetation plots were found in the first and fourth quadrants, respectively. The dominant pattern in the gallery forest on the glacis was delineated by the species Bauhinia benthamiana, Connarus venezuelensis, Fagara caribaea and Bactris minor. In contrast, the abundance of species in the gallery forest of the Orituco river bank was similar to that in the plots of the Biological Reserve with associated species such as Tabebuia blakeana, Genipa caruto and Cassia moschata. In the forest grove, the species Vochysia venezuelana, Spondias mombin and Cereus hexagonus reached their maximum abundance.

DISCUSSION

Results from the censuses based on the vegetations of the Orinoco Llanos indicate that in the unprotected savanna plots of the Biological Reserve there occurs a vegetational spectrum spanning pyro-resistant trees, scattered in the grass matrix, to forest grove which cover from a few square meters up to 2 x 10^3 m^2. Then, there is a dynamic mosaic created from the scattered trees, indicators of a non equilibrium system dominated by the stochastic effect of fire to the persistent groves, which are influenced by biotic interactions and feedback mechanisms, such as those reported by Wiens (1984a,b) for bird communities in arid and semi-arid environments of north American grasslands, and considered by DeAngelis and Waterhouse (1987) as a fundamental property of the fuctioning of the ecological systems.

Even though, under fire conditions, the woody vegetation has been reduced by the stochastic fire disturbance, a net sequential dispersion of pyro resistant species occurs from the grass layer to the grove edges forming an ecotonal belt, which prevents the forest grove from being wiped out by fire (Blydenstein 1962; San Jose et al. 1978).

In the edge groves, the pyro resistant species are persistent as seeds, seedlings and saplings until their growth is activated after fire sensitive species are removed and competition is reduced. In the ecotone, intraspecific competition and mortality is evidenced by comparing the mean density of the newly established plants with that of plants in the interior of the groves (San Jose et al. 1991).

In the forest groves homeostatic biotic interactions and feedback mechanisms, which dominate the systems occur, such as is evidenced by the structure of the populations (San Jose et al. 1991). Although, these forces have depleted the groves of some species, these groves can be invaded by species coming from other groves, which act as nuclei for late dispersion as well as corridors for the exchange of species from or to the gallery forest such as the Orituco River gallery forest. Thus forty six percent of the woody species were common between these vegetational sites (Montes and San Jose 1994a). This situation is corroborated by the high initial rate of exchange in species composition after the establishment of the protected plot (San Jose and Fariñas 1991).

After 25 years of protection, density and species composition of the protected plot was similar to that for the largest forest grove of the Biological Reserve as evidenced by the ordination diagram. Actually, the vegetation of the protected savanna is changing toward a woodland. Therefore, these groves could be the relics of the original semi-deciduous forest, which covered the whole area, except in places where shallow ironstone cuirass was covered by herbaceous savannas. These savanna patches were no doub, the core vegetation, where the expansion of the savannas began at expenses of the forest.

In summary, under fire supression conditions, the semi-deciduous forest might be considered as stable equilibrium system based on the available information, on the structure and functioning of the largest forest grove of the Biological Reserve. Previous consideration were related to spatial scale of the forested cover, whereas the forest in toto, includying the forest gaps, and the patches of herbaceous savannas on the outcrops of ironstone cuirasses, is integrating an unstable equilibrium system or unstably interactive community according the nomenclature of DeAngelis and Waterhouse (1987).

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