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CHANGES IN TREE DENSITY AND SPECIES COMPOSITION IN A PROTECTED *TRACHYPOGON* SAVANNA, VENEZUELA[1]

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Abstract. Changes were recorded in population and species density of a 3-ha permanent *Trachypogon* savanna plot, protected against fire and cattle grazing for 16 yr (1961–1977). This savanna is a grassland (mainly *Trachypogon* species), with scattered trees and groves. Under protection it is gradually changing into a denser arboreal community; trees in the grassland and in the groves increased 14.6- and 3.7-fold, respectively. In places, ironstone outcrops limit woody plant invasion and prevent the whole area from developing into a savanna woodland. Experimental explosions (using dynamite) in the ironstone outcrop led to the growth of trees in soil pockets formed in the artificial fissures.

Key words: fire; grazing; ironstone; savannas; Venezuelan Llanos.

Introduction

The *Trachypogon* savanna is an extensive ecosystem covering large areas of northern South America. This savanna includes a wide variety of physiognomic types and floristic units, but the grassland always dominates the landscape.

In the *Trachypogon* savanna of the high central plains (Llanos) of Venezuela, scattered trees and small patches of forest coexist under a pronounced seasonal rainfall of 1300 mm and a continuous dry season of 4 mo. It has been suggested that the savanna is a product of the burning and deforestation of the original deciduous forest (Vareschi 1962, Tamayo 1964, Aristeguieta 1966). Most of these interpretations are derived from studying contemporary communities of savanna and forests growing side by side, even though operational ecological factors may differ. Blydenstein (1962) established a permanent plot of 3 ha at the Biological Station of the Plains (8°56′N, 67°25′W) and protected it from fire and cattle grazing. In 1969, Blydenstein's permanent plot was reexamined by San José and Fariñas (1971), who found that its physiognomy was relatively unchanged after 8 yr of protection, although the number of trees had increased from 281 to 457 individuals, and the number of tree species had increased from 4 to 11.

Although fire affects plant biomass, structure, and shape of the vegetation in the *Trachypogon* savanna, interpretations of other ecological factors have given rise to many controversies concerning this ecosystem. Thus, the existence of these savannas could be attributed to extreme soil conditions rather than solely to the action of fire or the prevailing regional microclimate, as pointed out by Sarmiento (1968). The soil, which is acid and low in cation exchange capacity (San José and García-Miragaya 1979), presents an indurated ironstone horizon close to the surface. This horizon was classified as lithoplintic, belonging to the subgroup of Orthens (Smith et al. 1977).

According to Santamaría and Bonazzi (1963, 1964), the main operational factor in this savanna is the presence of an excessively dry soil and an indurated ironstone horizon close to the surface. The horizon mechanically prevents the penetration of tree roots, thereby setting a limit to the depth of the root systems. Santamaría and Bonazzi (1963) proposed to test this hypothesis by exploding the ironstone outcrops. Evidence for this hypothesis was presented by Foldats and Rutkis (1965, 1969).

The objective of the present paper is to assess tree density and species changes in the *Trachypogon* savanna when fire and cattle grazing are eliminated over a long period. It also includes data on the lithoplintic horizon depth and its effect on tree density.

Materials and Methods

Vegetation changes in a 3-ha permanent protected plot

From January 1961, Blydenstein (1962) fenced and protected against fire and cattle grazing a 3-ha plot located on the permanent grid of continuous quadrats (A7A8D7D8) in the Biological Station of the Plains (8°56′N, 67°25′W), Calabozo, Venezuela. The development of the tree species population was assessed in 1970 and again in 1977 by counting all individuals. Since

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TABLE 1. 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 in 1970 and 1977 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		
	1961*	1970	1977	1961*	1970	1977
Curatella americana L.	13	117	254	82	114	160
Byrsonima crassifolia H.B.K.	14	95	181	111	135	142
Bowdichia virgilioides H.B.K.	23	20	18	35	40	55
Cassia moschata H.B.K.				3	4	5
Cochlospermum vitifolium (Willd.) Spreng		72	247		33	64
Godmania macrocarpa Hemsley			6		14	24
Casearia hirsuta Sw.			1			23
Platmyscium pinnatum(Jacq.) Dugand			3		5	2
Genipa caruto H.B.K.			1		24	20
Guettarda elliptica Sw.					20	69
Cordia cf. *C. hirta* I.M. Johnston			21		64	202
Connarus venezuelensis Baill.					1	2
Capaifera officinalis H.B.K.						3
Machaerium pseudoacutifolium Pitt. (?)						4
Casearia decandra Jacq.			1		37	82
Bactris sp.					1	2
Total	50	304	733	231	492	859

* After Blydenstein (1962).

some new tree species have spread vegetatively, it was impossible to determine whether new individuals were the result of new seed establishment or vegetative propagation of existing trees. Therefore, we will refer to them as "tree stems" or "stems."

Two groups were recognized: isolated tree stems and grove tree stems. The first class consists of scattered tree stems on a continuous grass stratum dominated by *Trachypogon* and *Axonopus* spp.; the second class is composed of discontinuous patches with one or more tree stems and the typical understory layer of herbs and shrubs growing around the "island" margins. A thorough description of this type of vegetation is given by Aristeguieta (1966).

Groves occupy an area usually <12 m in diameter, although this may sometimes increase to 1 ha or more (San José et al. 1978). On the other hand, only the tree species *Curatella americana* L., *Bowdichia virgilioides* H.B.K., and *Byrsonima crassifolia* H.B.K. are found as isolated individuals in the burned savannas.

To compare the 1971 and 1977 species height distributions, stems between 5 cm and 4 m in height were measured with a measuring tape, and taller stems were measured with a Brunton pocket transit.

Enumeration of tree stems and measurement of ironstone depth

One hundred and ninety contiguous 1-ha plots (100 × 100 m) were selected in the savanna reserve of the Biological Station. All stems (≥5 cm tall) existing on these plots were numbered and counted. The depth at which the indurated ironstone horizon was first encountered was measured on each of the four plot corners by boring a hole with a bore (50 cm wide by 150 cm long) attached to a Massey Ferguson Model 35 tractor. Data of the number of individuals and hardpan depth of the plots were not normally distributed bivariates, as shown by the Kolmogorov-Smirnov test (Sokal and Rohlf 1969). The association between variables was tested by computing Kendall's rank correlation coefficient (Sokal and Rohlf 1969, Siegel 1976).

Vegetational changes after experimental modification of the indurated ironstone

In August 1971, two 1-ha plots were selected at the Biological Station. The soil contained ironstone outcrops of different degrees of hardness. The plots were covered by short grasses (*Trachypogon* spp. and *Axonopus* spp.), with some trees sparsely scattered on the edge of the cuirass. In one plot, the indurated ironstone consisted of rounded gravel with interconnected channels containing fine earth, which allowed grass root penetration. The cuirass of the other plot was of a rather less rounded gravel, apparently without channels. In spite of differences in hardness between these outcrops, the hardpan seemed to be an extremely firm and strongly cemented rock. A series of eight ironstone outcrops were selected on each plot, and a hole was drilled in the center of each to hold a commercial dynamite cartridge. The explosion produced cracks of different sizes in the ironstone, and tree invasion has been evaluted yearly by stem counting.

RESULTS

Changes in stem density in the 3-ha protected plot

Table 1 shows results of three censuses: 1961 (Blydenstein 1962), 1970, and 1977 (original data of the present paper). Isolated stems have increased from 50 to 733 individuals, in three species that were present

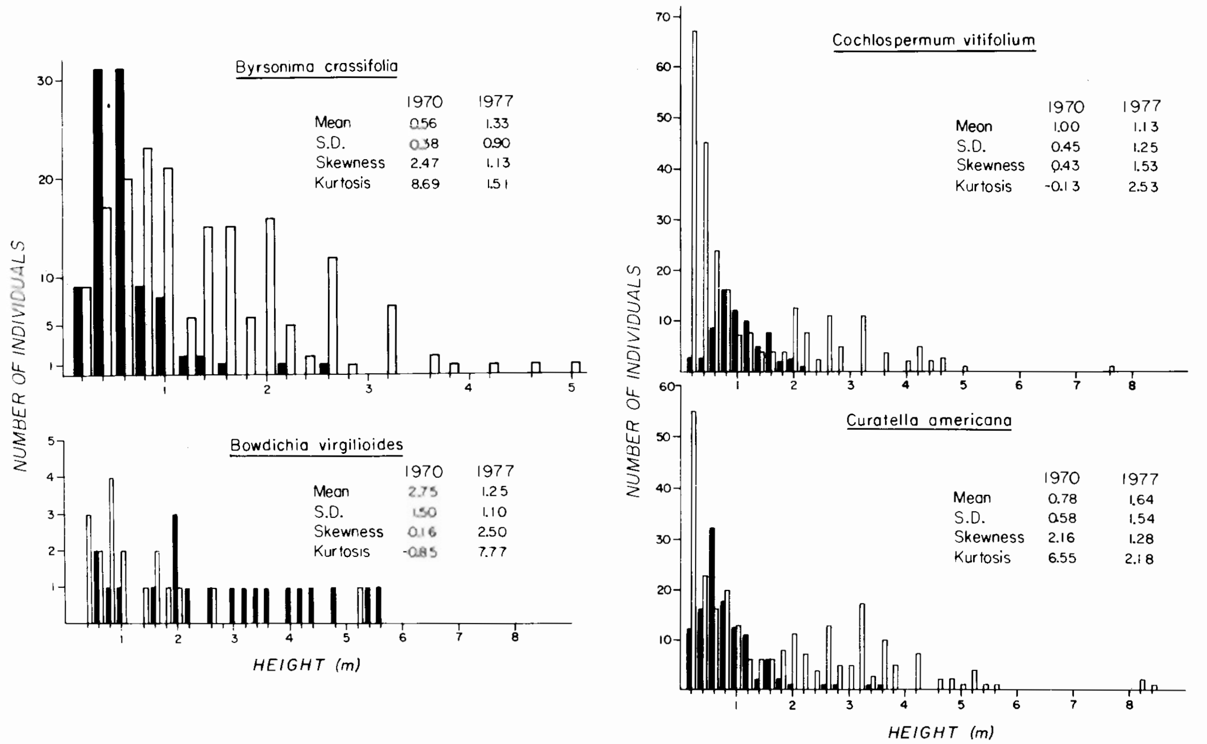

FIG. 1. Height distribution of isolated tree stems for the 1970 (■) and 1977 (□) censuses in a protected plot (3 ha) at the Biological Station of the Plains, Calabozo, Venezuela.

in the burned *Trachypogon* savanna and in seven new species that grew after the savanna became protected in 1961. Particularly remarkable was the increase in the population density of *Cochlospermum vitifolium,* a seemingly fire-sensitive species absent in 1961.

The grove stem increase was proportionately lower (3.7-fold) than that of the isolated stems (14.6-fold). However, groves became floristically more "complex." (Species number increased from 4 to 16 during the 16 yr of protection.)

In 1977, the dominant species (highest number of individuals) was *Curatella americana* (26%), followed by *Byrsonima crassifolia* (20%), *Cochlospermum vitifolium* (19.5%), and *Cordia hirta* (14%). The remaining species (20.5%) were present in smaller proportions but represented an important compositional change as compared to 1961, when the proportions of *Byrsonima crassifolia* (44%), *Curatella americana* (34%), and *Bowdichia virgilioides* (21%) made up 99% of the total.

Changes of tree height-class structure in the 3-ha protected plot

The height distribution of all isolated individuals changed significantly between 1970 and 1977 (Mann-Whitney *U* test, Siegel 1976). The number of isolated individuals in the 1977 small classes (stems <1 m in height; Fig. 1) was greater than in the 1970 ones, indicating that population expanded, reproduction increased, and/or extinction of small individuals decreased. An exception to this trend was *Byrsonima crassifolia.*

On the other hand, by applying the Mann-Whitney *U* test (Siegel 1976) to the 1970 and 1977 censuses, we noted that the height of grove individuals did not differ statistically. These results are evidence of a relative homeostasis in the grove units, where there is a tendency to maintain the present height-class structure, regardless of changes in the number of individuals.

In the 1970 census, stem height distribution in the groves was relatively similar to that of isolated stems, as observed on comparing the histograms of *Cochlospermum vitifolium* and *Bowdichia virgilioides* (Figs. 1, 2). However, after 7 yr, the occurrence of small size-classes was definitely higher in isolated stems, indicating that seed germination, seedling survival success, and/or establishment differed between groves and isolated populations.

Protection affects big and small individuals. Comparing the maximum height of isolated stems with that of grove stems, we may observe that in 1970 the maximum height of isolated stems was less than that of stems growing in clusters. However, after 7 yr isolated individuals of *Cochlospermum vitifolium* and *Curatella americana* were as tall as or even taller than those growing in clusters.

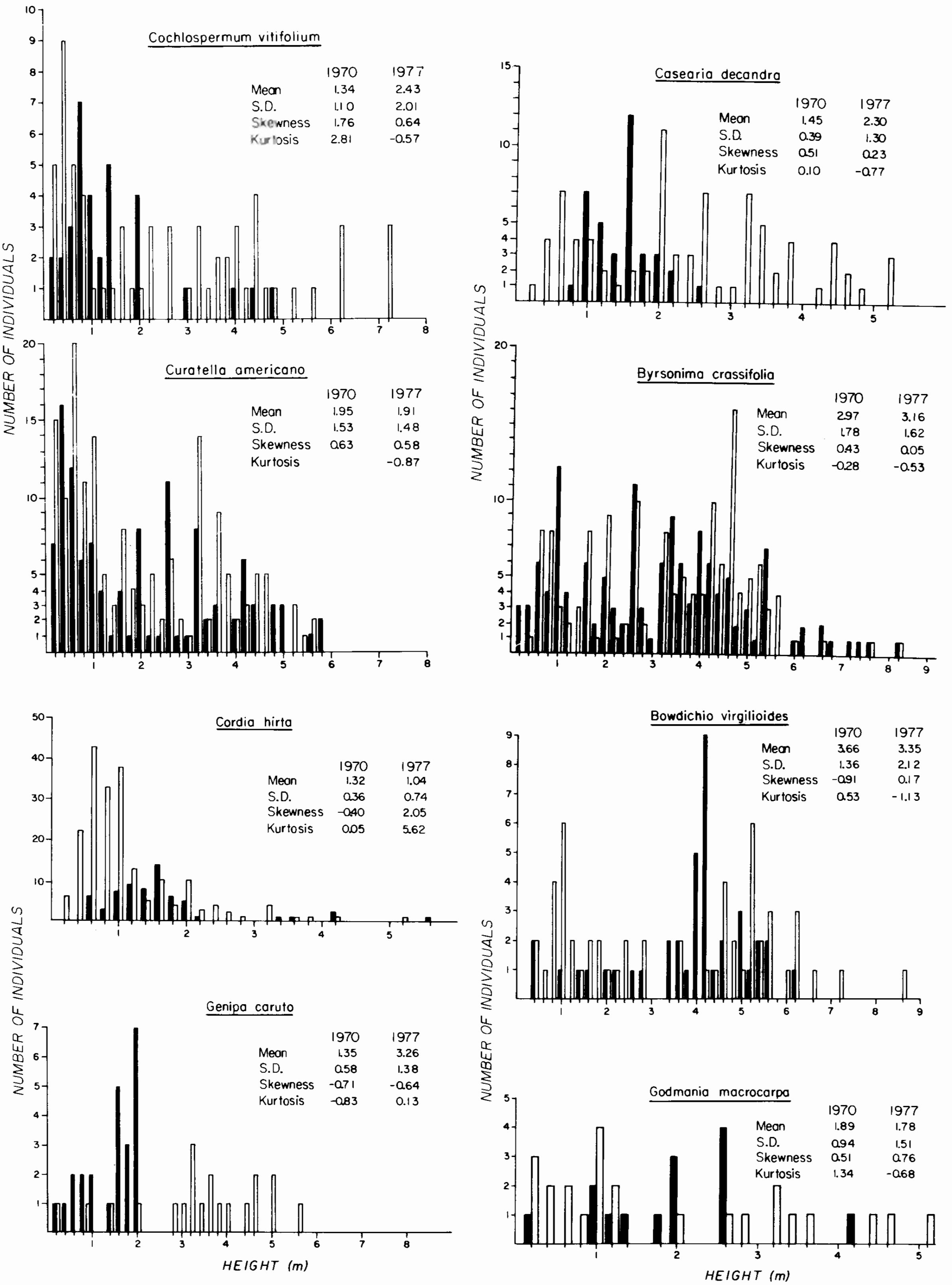

FIG. 2. Height distribution of stems in groves for the 1970 (■) and 1977 (□) censuses in a protected plot (3 ha) at the Biological Station of the Plains, Calabozo, Venezuela.

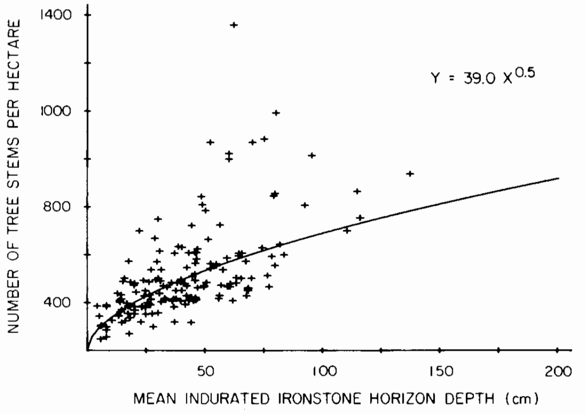

FIG. 3. Number of tree stems per hectare as a function of mean depth of the indurated ironstone in the 190-ha *Trachypogon* savanna reserve at the Biological Station of the Plains, Calabozo, Venezuela. Regression was calculated using a regression program (Hewlett-Packard General Statistics Volume 1 No. 09825-15001). $r = .77$; $P < .01$; $F = 164.2$.

The shape of the frequency distributions for all stems shows that in 1977, species such as *Cochlospermum vitifolium, Curatella americana, Bowdichia virgilioides, Godmania macrocarpa, Casearia decandra,* and *Guettarda elliptica* had an antimode in the middle-sized stem classes, preceded by a large small-stem class, which suggests a resurgence of the stem population after protection.

Association between tree stem density and indurated ironstone depth

The tree stem density data (number of tree stems per hectare) in the 190-ha contiguous plots of the savanna reserve, as a function of the mean depth (in centimetres) of the indurated ironstone horizon (mean of the four corner values), are shown in Fig. 3. The Kendall coefficient of rank correlation (Sokal and Rohlf 1969, Siegel 1976) between these variables ($\tau = 0.135$) was statistically significant ($Z = 2.770$ at $P = .01$) for 190 pairs of observations (SD = 0.049). These results indicate that tree stem density is positively correlated with indurated ironstone depth.

Tree invasion in response to mechanical disruption of ironstone

The results indicate that the dynamite altered the outcrops according to their hardness. Thus, the harder ironstone, which had no apparent interstitial channels, was fragmented. On the other hand, the channeled outcrops not only suffered fragmentation, but also a considerable mass of indurated ironstone was blown out, and cavities of ≈20 L were produced. These cavities were progressively filled with soil and litter from tree leaves. Therefore in a year, seeds of *Curatella americana* are able to germinate and develop; after 3–4 yr *Cochlospermum vitifolium* and *Genipa caruto* are still in the seedling stage, but plants of *Curatella americana* have developed into trees of ≈3 m in height with many lower branches. At this stage individuals develop with no severe competition, as the grass layer growing over the cuirass is loose, and its competitive effect seems to be relatively unimportant.

The slight increase in the number of species may indicate that additional modifications can occur in the outcrops before new sets of species appear, as the hardpan covers relatively extensive areas and prevents tree root penetration.

DISCUSSION

Under conditions of regular annual burning in the *Trachypogon* savanna, the groves and the grassland matrix are in equilibrium. Comparing aerial photographs taken in 1950 with field conditions in 1961, Blydenstein (1962) observed that the area occupied by the groves had not changed appreciably. One of the main reasons for this equilibrium seems to be the "belt of fire resistant species" that surrounds the groves (Tamayo 1977). Absence of combustible fuel also minimizes the chance of fire encroaching on the groves. The characteristic species of this "belt," *Curatella americana, Bowdichia virgilioides,* and *Byrsonima crassifolia,* are all fire tolerant. Their large stems are protected by a thick, corky bark, and their buried rootstocks are capable of rapid resprouting. These species act as firebreaks and thus provide fire protection to seedlings.

Since fire modifies the woody layer of the *Trachypogon* savannas, their physiognomic characteristics have been affected by the recurrent action of the flames. However, after protection, species in the burned savannas have not been eliminated or replaced. The increases recorded are accounted for by the invasion of local savanna species previously absent from a particular plot. These results resemble those recorded for the cerrado vegetation at Emas (Pirassununga, São Paulo, Brazil), which after 30 yr of protection does not show the slightest trace of invasion by forest species, although a forest does exist nearby (Eiten 1972).

Standing in contrast are the observations made in protected savannas of West Africa. In a Guinea savanna of the Ivory Coast, Menaut (1977) observed that after 13 yr of protection, new species from the surrounding forest were invading the vegetation in an irreversible process. A similar example was observed in a savanna of northeast Ghana, where under experimental conditions it was noted that the invading species were peculiar to the dry forest (Brookman-Amissah et al. 1980).

During the 16 yr of fire suppression, the savanna was invaded by trees, and the population density increased. Groves formed from existing isolated individuals, and the grassy layer surrounding the formerly isolated trees was replaced by a herbaceous layer typical of the groves. While these observations indicate that environmental changes produced establishment of new species, the existence of isolated trees does not guarantee the formation of groves.

All new species invading the plot must derive from seeds, whereas changes in the population density of the pioneer species resulted from both seeds and spreading clones. The height-class histograms confirm that young shoots grow very rapidly.

We may question the ability of tree species to establish in a site and compete with the savanna vegetation. Tree seedling suppression by the herbaceous layers does not seem to be a limiting factor in tree growth; therefore it is possible to observe seedlings growing throughout the grass canopy. At the beginning of the wet season, dry matter previously produced by the grasses is rapidly decomposed (San José and Medina 1976). There might also be a temporary decrease in competition between the grass and developing tree seedlings.

The grass matrix may be a quite favorable location for seedling establishment, since the number of isolated tree stems increased 14.6-fold against 3.7-fold in the groves. Fire elimination produced a drastic change in the height distribution of isolated trees but not in the height distribution of grove individuals. Although the base saturation level, organic matter, and nutrient content are relatively lower in the grassland soil than in the grove soil (San José and García-Miragaya 1979), the results indicate that savanna tree invasion of the infertile grassland does not depend solely on nutrient availability. Thus under burned conditions, the grassland matrix only sustains sclerophyllous species. In the absence of fire, deciduous trees such as *Godmania macrocarpa, Genipa caruto,* and *Cochlospermum vitifolium* invade. This indicates that the soil is fertile enough to sustain these more nutrient-demanding species. Evidence for this has been presented by Montes and Medina (1977).

Nurse trees seem to favor seedling establishment in the savanna. Their shade is harmful to the grass layer, which competes with the seedlings, and this is replaced by a herbaceous layer typical of the groves. In some cases there seem to be some allelopathic substances around the groves, which form an "inhibition belt" for the grasses. These substances might also prove important in reducing seed predation, a hypothesis presented by Salgado-Labouriau (1973) for the cerrado vegetation.

Pioneer trees may be enriching the soil beneath them by providing a source of nutrients for tree-seedling invasion. In the Neotropical savanna, trees such as *Byrsonima crassifolia* gradually enrich the surface soil by producing a nutrient concentration in the surrounding area and incorporating these nutrients into an enlarged plant–litter–soil nutrient cycle (Kellman 1979). In the *Trachypogon* savanna, the nutrient cycle seems to make nutrients readily available to the establishing seedlings, since the grove litter is decomposed during the following wet season (Medina and Zelwer 1972). In addition, the areas beneath the groves may also receive preferential seed input because they are chosen as resting and nesting sites by seed-dispersing animals. On the other hand, seed and seedling predation beneath the scattered "nurse trees" may be lower than in the groves.

The results indicate that the protected *Trachypogon* savanna is presently changing towards a denser arboreal community. In only 16 yr the total number of tree stems increased 5.6-fold. At the Biological Station it was observed that the woody species might soon cover the area and that groves are expanding and increasing in number at a fast rate. Nevertheless, the superficial indurated ironstone layer prevents tree colonization in the area occupied by the *Trachypogon* savanna. Examples of homologous vegetation are found in West Africa, described by Schnell (1976). In a dense forest, he found savanna "islands" growing on outcrops of indurated ironstone cuirass, and noted, "it seems that these cuirass fossils favour the evolution of the vegetation towards a savanna" (Schnell 1976: 140).

Although the available information does not allow us to forecast the exact course of any further change, we may assume that where there are no active edaphic limitations, fire prevents tree colonization, and under protection the area will progressively become a woodland savanna. When the indurated ironstone horizon is close to the surface, trees grow in any cracks that are present. Therefore, groves and scattered trees are present when cracks are numerous and close together, but when cracks are dispersed, trees remain isolated individuals in a grass matrix, and they will not form groves. Where the ironstone outcrop is not faulted with cracks, tree growth is impeded, and the area is covered by grassfield (open savanna). These areas will not be invaded by trees, even if fire is absent.

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