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STUDIES ON THE SAVANNA VEGETATION OF THE VENEZUELAN LLANOS

I. THE USE OF ASSOCIATION-ANALYSIS

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INTRODUCTION

In the intertropical region of America there are several kinds of savannas; their distribution, composition, structure and environmental conditions have been accurately reviewed by Beard (1953). However, the tropical savanna vegetation in the New World is far less understood than other more complex types such as rain forest and mountain forests, in spite of the vast area which the formation occupies from the Tropic of Cancer in Mexico to near the Tropic of Capricorn in Bolivia and Brazil. Even the more basic generalizations about savannas, such as their primary or secondary condition, climatic or edaphic determination, and climax or fire-climax character, are subject to extremely opposing viewpoints.

If we accept as a useful physiognomic definition of savanna that given by Beard (1953), i.e. 'a community comprising a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants, of which grasses and sedges are the principal components, and with scattered shrubs, trees or palms sometimes present', we can differentiate three ecologically unrelated types of tropical savannas. The first type comprises the grasslands or palm grasslands occurring on seasonally flooded or waterlogged soils, placed correctly in Beard's (1955) classification of tropical American vegetation in the 'seasonal swamp formation-series'. The second type includes the soil-determined grassy and shrubby vegetation that replaces the rain forest in very well-drained sandy places, forming small 'lagunes' of savannas in the middle of a humid forest region, as in the so-called 'campos' of the Amazonian rain forest. The third type is formed by the savannas on non-hydromorphic soils which are the predominant physiognomy over extensive areas of tropical wet and dry climates, and which will be considered for the time being as related to specific climatic conditions as well as to certain soil or soil influencing characteristics. We refer to this third type of savanna as 'dry savanna' because it is much drier than the other two types; the soil does not remain waterlogged more than a few days following heavy rainfall, throughout the year the water table is beyond the reach of the grass roots and during the dry season the whole soil profile desiccates completely.

These three ecologically different types of savannas, included within the same vegetation class, have made this concept so wide and ill-defined that we consider it to be mainly responsible for the considerable confusion concerning the factors controlling and conditioning the occurrence of savannas.

Only few detailed studies are available on savanna vegetation in tropical America and these refer mainly to the first two types, e.g. those of Egler (1960) in Brazil, Richardson (1963) in Trinidad, Van Donselaar (1965) in Surinam and Blydenstein (1967) in Colombia. The third group on the other hand has been less analysed and its ecological interpretation remains most controversial.

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Because the dry savanna is one of the most extensive formations of the Venezuelan lowlands, it was selected for a wide ecological programme on different aspects of its vegetation and environment. Within this framework the detailed phytosociological analysis of a savanna stand was undertaken. The purpose of this work was two-fold: firstly, to acquire a more precise knowledge of the internal variability of vegetation and of the environmental factors involved, within a limited stand with rather uniform physiognomy and the same set of dominant species; secondly, to test different methods of vegetation analysis in order to select that most appropriate for this type of vegetation.

The Biological Station of Los Llanos was chosen for this study, not only because it is representative in habitat conditions and flora of an important extension of dry savannas, but also because it is a protected stand of vegetation exclusively used for research purposes.

The association-analysis method of Williams & Lambert (1959, 1960) was first selected, not only for its simplicity but also because it has been satisfactorily tested in various other plant communities. It can be used as a reference for comparing both the results of other numerical methods of classification and the complexity of the vegetation analysed.

Before presenting details of methods we give a brief outline of the entire inland plain region of Venezuela and its main vegetation and climatic characteristics as well as the significance of the particular type of savanna chosen for the analysis.

SAVANNA VEGETATION OF THE VENEZUELAN LLANOS

Regional subdivision of the Llanos by its vegetation types

The Venezuelan inland plains are known under the generic name of 'Los Llanos'. These wide expanses of about 300000 km² between the mountains of the Coastal Range and the Andes chains in the north and west, and the Orinoco river and its delta in the south and east, apart from being a vast and geologically long-enduring sedimentary basin, with poor relief and altitudes ranging from 300 m to near sea level, have few common geological, climatic or ecological traits.

As far as vegetation is concerned, at least four different regions can be recognized in the Llanos: the deciduous forest region at the piedmont of the Coastal Range; the semi-evergreen forest region at the piedmont of the Andean Range; the swampy savannas in the flood-plains of the Orinoco river and its tributaries; and the dry savanna region between the deciduous forest region and the Orinoco valley.

In the first region the Tropical Deciduous Seasonal Forest is the most extensive plant formation, while thorny woodlands of *Mimosa* and *Acacia* and savannas of *Copernicia tectorum* Mart. occupy more restricted localities. This is the driest part of the Llanos, with an annual rainfall of only 800–1000 mm and a wet season of 5–6 months. The forest structure agrees with Beard's (1955) generalized description of the plant formation, the more important forest trees being: *Spondias mombin* L., *Pterocarpus podocarpus* Blake, *Platymiscium pinnatum* (Jacq.) Dugand, *Cochlospermum vitifolium* (Willd.) Spreng. and *Tabebuia chrysantha* (Jacq.) Nich.

The semi-evergreen forest region corresponds roughly to the 'Llanos Occidentales' (western Llanos) of the geographers and its distinguishing trait is a higher, richer and wetter type of forest: the Trophephilous Rain Forest of Tamayo (1962) or Semi-Evergreen Seasonal Forest in Beard's (1955) nomenclature. In this forest only a certain proportion of trees in the upper layer remains leafless for a short time. The annual rainfall is heavier: 1400–2000 mm, and the wet season longer: 8–9 months. In drier or wetter places forest is

replaced by other formations: dry savannas on the low hills with shallow rocky soils, and humid grasslands on the lowlands with a constant high water table.

The swampy savannas occupy the wide flood plains of the Orinoco river and its tributaries, particularly in its central basin, and they remain flooded for periods of variable length during the rainy season. This region known as 'Bajo Llano' (low Llano) exhibits a topographic sequence of plant formations ranging from forests on well-drained higher sites to *Copernicia tectorum* savannas and *Paspalum fasciculatum* Willd. grasslands on heavy textured, ill-drained soils.

Finally, the dry savanna is the dominant plant formation in the area between the deciduous forest region and the Orinoco valley, reappearing in the southernmost part of the country on the other side of the swampy savanna area next to the Colombian frontier. In this region the amount of rainfall is intermediate between that of the deciduous forest and the semi-evergreen forest region, reaching from 1000 to 1400 mm, with a wet season of approximately 6 months. Gallery forests and dense groves of *Mauritia* palms along the watercourses and *Copernicia tectorum* savannas on the wetter river terraces complete the series of plant formations in this region.

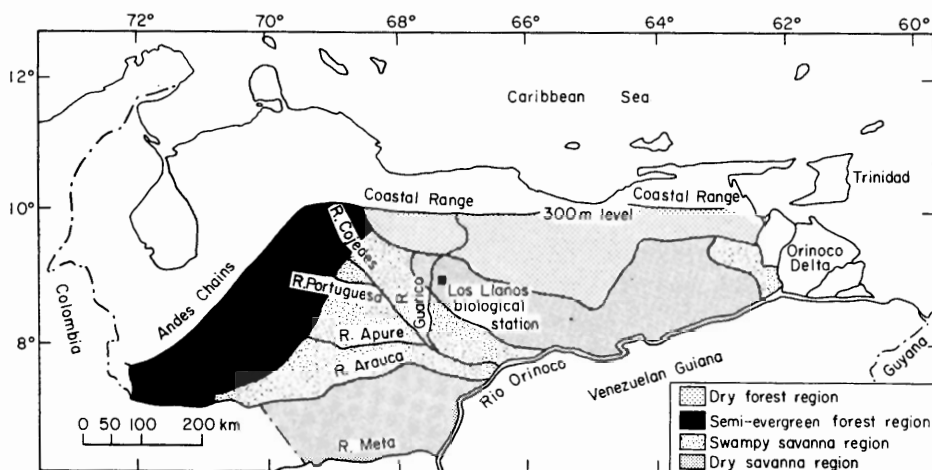


FIG. 1. Northern Venezuela showing the four vegetation regions into which the Llanos may be divided. Note the position of the Biological Station at the western border of the dry savanna region.

It may be emphasized that each of the three main plant formations predominates in a certain region of the Llanos under a peculiar hydric climate, occurring in other regions only on azonal soils where some edaphic or topographic characteristic modifies the local water balance. Thus the deciduous forest is predominant in the northern driest parts, the semi-evergreen forest in the most humid western Llanos, while the dry savanna appears in the climatically intermediate central and eastern regions. Obviously the swampy grasslands are not climatically conditioned. This regional separation of each plant formation is one line of evidence supporting the hypothesis that what we consider here as dry savanna is, like the two other types, a climatic formation (Sarmiento 1968). By use of data given by Ramia (1967) and Tamayo (1962) as well as the authors' field notes, an outline was drawn showing the four vegetation regions (Fig. 1).

Taking into account only the dry savannas inside the savanna region, it can be seen that the ecologically dominant matrix of xeromorphic grasses and sedges shows a remark-

able similarity in physiognomy and essential floristic composition throughout the area. This corresponds to Beard's (1953) 'tall bunch-grass savanna', composed of an herbaceous stratum 80–120 cm high where several species of grass of the genus *Trachypogon* are dominant, species of *Axonopus* and *Andropogon* the main co-dominant grasses and *Bulbostylis* the most important genus of xeromorphic sedges. Within this homogeneous herbaceous matrix a wide variety of physiognomic types can be differentiated varying in density and height of the woody species. This variation can be arranged in a gradient, with the pure grassland at one extreme, then an open savanna with scattered dwarf trees lower than the herbaceous canopy, followed by an increase in the density and height of the woody species to the other extreme—a closed savanna or woodland with the crowns of the medium-sized trees touching each other. Throughout the series the same woody species are found: *Curatella americana* L., *Byrsonima crassifolia* (L.) H.B.K. and *Bowdichia virgilioides* H.B.K., three species of low, gnarled, evergreen trees of very wide distribution in the savannas of tropical America. Only at the boundaries with other regions do some other woody species appear.

In the most complex physiognomic type of dry savanna, besides the low spaced trees already mentioned, appear some groves with other species of higher trees belonging to the neighbouring forest formations, such as: *Copaifera officinalis* H.B.K., *Cassia moschata* H.B.K., *Vochysia venezuelana* Stapf, *Spondias mombin* L. and *Luehea candida* (DC.) Mart. From an aerial view, this savanna looks like parkland; the groves of high trees are scattered in an herbaceous matrix dotted with low trees.

The probable relationships between these physiognomic types and their environment are not included in this paper; however, it may be noted that the physiognomic series of increasing complexity can be arranged along an edaphic gradient where the pure grasslands occupy the dry extreme and the savanna with groves the wettest one; but in reality the situation is much more complicated than this, because management, especially grazing and fire, also plays an important role.

These savannas have been used only as natural pastures for the range economy of the region. Their value as forage is very limited, since the dominant hard grasses are palatable during their early stages of growth only. Most savannas are burnt at least once a year, to allow fresh growth for grazing. The cattle in these areas are generally of the creole type, sometimes crossed with zebu, and remain almost the entire year in the lowlands where the wetter savannas provide more valuable pastures. Agriculture is confined to the forest-covered river terraces, where the soil is deeper and water supply not limiting; occasionally the dry savanna is replaced by rice fields or artificial pastures. Such poor development of agriculture is due to the low nutrient content of the acidic soils and the unfavourable physical conditions created by the iron or clay hardpan occurring near the surface.

Vegetation of Los Llanos Biological Station

The Biological Station of Los Llanos is situated 8 km south-east of the city of Calabozo, 8°56' N and 67°25' W (see Fig. 1), near to the western margin of the dry savanna region. The Station protected field has an area of about 300 ha, completely covered with natural savanna. Its maximum altitude is 100 m above sea level at the northern margin, descending gently to the south to a minimum of 92 m. Since 1960 this field has been kept free of domestic herbivores and as far as possible also from fires. However, some parts of the savanna have accidentally caught fire in various years. This partial protection from fire and exclusion of grazing for 7 years did not produce significant

changes in the density of woody species, but it led to remarkable changes in the floristic composition of the herbaceous component of the vegetation. Thus, several weeds infesting the overgrazed and greatly modified neighbourhood have shown markedly reduced cover within the Station.

The savanna pattern corresponds to the previously described 'savanna with groves'. As a whole, the scattered groves, ranging in diameter from 10 to 100 m, cover about 10% of the surface, giving the landscape a parkland appearance. Our syncological analysis was restricted to the savanna element (herbaceous matrix plus small scattered trees) of this mosaic, neglecting the groves.

The pattern of floristic variation within the savanna element is somewhat difficult to determine by simple surveying and current field observation. Although a first impression is of homogeneity, a closer study reveals that the dominant species vary in importance from site to site and frequently replace one another. The secondary species also interchange, but their minor physiognomic impact makes it still more difficult to follow their distributional pattern.

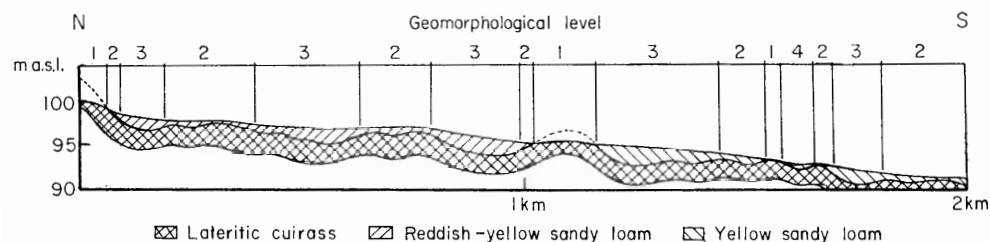


FIG. 2. North-south transect through the Biological Station field showing topographic variation, geomorphological levels and distribution of the upper sedimentary layers. For numbering of geomorphological levels see text. m a.s.l., Metres above sea level.

The major visible differences are easily correlated with outstanding soil characteristics resulting from the action of geological and geomorphological agents. From the geomorphological viewpoint the entire Station field is an ancient fluvial terrace dating probably from Pliocene or early Pleistocene; this was later uplifted and folded, giving rise to a low plateau or mesa, a few metres higher than the recent river terraces.

The alluvial sediments on the mesa surface are in three main layers: a lower one of mottled clays; an intermediate bed of iron-cemented sandy conglomerate or of pebbly sandstone; and an upper layer of sandy loams, although in the higher sites erosion has exposed directly the underlying hard bed. These three layers correspond exactly with the lateritic profiles described by Prescott & Pendleton (1952) as peculiar to some tropical regions of Africa, Asia and Australia in landscapes of similar geological history, in this case the hard horizon between sandy loams and mottled clays being an ancient lateritic cuirass.

The uppermost loose sediments, when still in place, are of two distinct types: above the 94 m level, in the northern half of the Station, a reddish-yellow sandy loam forms a layer from a few centimetres to almost 200 cm thick; and below the 94 m level, in the southern half, there is a yellow, somewhat finer sandy loam which also reaches 150-200 cm in depth (Fig. 2).

These different sedimentary beds, together with the relief arising during the faulting and folding of the original deposits, are responsible for the complex pattern of land forms found within the Station field itself. We have referred to the main land forms as 'geomorphological levels' because erosion has produced altitudinal steps, differing only in a few decimetres, which according to an ideal sequence could be arranged in the following 'catena': (1) first and highest level with gentle hills where erosion of the loose sediments has left the lateritic cuirass at the surface itself; (2) second intermediate level with shallow soils, where only 5–30 cm of loose sediments overlie the hard lateritic bed; (3) lower third level, less eroded than the previous one, with deeper soils where the sandy loams reach their maximum depth; (4) finally, and only in the lowermost part of the field covered by the yellow loams, a fourth level, formed by drainage channels where erosion has left only a few centimetres of sediments above the iron-cemented conglomerate. This pattern of land forms is scarcely visible from the ground because the gentle slopes and the presence of the small patches of forest make interpretation difficult. It was therefore examined by aerial photographs (scale 1:20000), followed by field observations. The transect sketched in Fig. 2 shows the surface geology and the sequence of land forms.

The geomorphological catena gives rise to a similar sequence of soil types. On the low hills with lateritic cuirass outcrops lithosols are found; on the gentle slopes with a shallow bed of sediments corresponding to geomorphological level 2, leaching has formed a thin but very heavy alluvial horizon which overlies the lateritic hardpan (see profile 2, Table 1). In the deeper sediments of geomorphological level 3, a more developed soil profile with wider horizons has evolved (profiles 1 and 3, Table 1); whilst corresponding to the level 4 of drainage channels is a poorly developed profile with a single sandy horizon lying directly over the lateritic cuirass (Table 1, profile 4). In all cases the soil is of the ferruginous tropical type, characterized by a low pH throughout the profile, poor nutrient and organic matter content and frequent occurrence of iron concretions in the lower horizons.

In the sites where the lateritic bed is exposed, the savanna becomes more open, the woody elements more scanty; certain species not frequent on deeper soil appear, such as *Bulbostylis conifera*, *Polycarpea corymbosa*, *Tephrosia tenella*, while others of wider ecological range become more abundant, such as *Bulbostylis capillaris*, *Diectomis fastigiata*, *Cassia cultrifolia* and *Pectis ciliaris*. This differentiation between a savanna on hard beds with their correlated lithosols, and other savannas on true soils, is easily seen by simple observation, and was the only difference in composition reported in the literature before any phytosociological work had been undertaken.

There is a second obvious difference as far as savanna composition is concerned, i.e. a narrow belt which surrounds each grove that we have named 'grove interphase'. In these interphases, with wetter edaphic and microclimatic conditions, the herbaceous layer is higher and more dense, and a number of species not commonly found in the open savanna become established; in fact, about half the species of the total list belong to the grove interphases. This belt, only a few metres wide around each area of forest, shows great variation in composition according to soil conditions, orientation with reference to the grove and the size of the grove. Even a single tree encourages the establishment of shade species of the ground flora; but on the whole these communities of more mesic shade plants are clearly distinguished from the open savanna.

A third distinction, not reported previously, became apparent during the phytosociological sampling, namely differences in the dominant species of the savannas of the northern and southern parts of the field. The main difference was that *Trachypogon*

Table 1. Analyses of four soil profiles

Profile No.	1		2		3		4	
	Group V ≥ 165 cm		Group M 30 cm		Group H 120 cm		Group E 10 cm	
Corresponding vegetation group	≥ 165 cm		30 cm		120 cm		10 cm	
Depth of lateritic hardpan	26-60		7-20		20-30		52-95	
Depth of horizon (cm)	0-9	9-26	0-7	7-20	20-30	0-5	5-21	21-52
Colour	7.5 YR	5 YR	7.5 YR	5 YR	5 YR	10 YR	10 YR	10 YR
(dry)	6/3	5/6	5/4	5/6	5/8	6/2	6/4	7/4
Texture	Sand	47.6	43.6	35.6	37.6	59.6	51.6	49.6
	Silt	22.0	22.0	24.0	16.0	22.0	20.0	18.0
	Clay	24.4	34.4	34.4	40.4	46.4	28.4	32.4
Textural class	Sandy clay loam	Sandy clay loam	Clay loam	Clay loam	Clay loam	Sandy loam	Sandy clay loam	Sandy clay loam
pH	5.35	5.05	5.10	4.80	4.80	5.10	4.80	4.75
Organic matter (%)	2.20	1.84	3.70	2.60	1.35	1.84	1.07	0.80
P (ppm)	13	9	19	15	25	10	12	15
N (%)	0.078	0.06	0.103	0.078	0.064	0.064	0.050	0.063
Ca (ppm)	242	155	315	140	78	185	139	100
K (ppm)	24	14	35	11	3	23	7	9
Na (ppm)	24	19	27	20	16	27	25	24

The soil colour refers to the Munsell Soil Color Charts. The analytical procedures follow F. E. Bear: *Chemistry of the Soil*, 3rd edn.

vestitus was always present as a dominant species in the southern part, whereas it was completely absent from the northern part. Since the various species of *Trachypogon* are rather similar in gross morphology this may explain why the distributional pattern has not been noticed before.

These were the only three distinctions which the authors were able to recognize in the savanna previous to the synecological analysis. The transitions between sites dominated by one species and by others are more or less gradual, and therefore the vegetation does not lead directly to a traditional phytosociological approach like the Zurich-Montpellier system.

COMMUNITY ANALYSIS

Methods

Three variants of normal association-analysis were tested, changing the association parameter used and the set of species considered. To obtain results which would allow extrapolation to the whole stand, the samples were placed in a restricted random way. The sampling procedure was as follows: firstly, the stand was delimited eliminating the altered zones near the borders, leaving an area of 190 ha (Fig. 8, p. 592). All the Biological Station was already divided into 1 ha squares by a grid of 100 m side, marked on the field with a numbered stake in each corner (in Fig. 8 the reticulum coordinates are designated by letters from o to m and numbers from -3 to 19). Secondly, two samples were placed at random within each 100 m unit of the grid by means of a table of random numbers. Thus a total of 380 samples were taken, two in each hectare. This stratification of samples gives a greater representation of the variation in the whole stand, without losing the statistical advantages of randomization. Each sample unit was a square of side 2 m; this area included most of the species present at each site.

The floristic data, presence/absence of vascular species, were collected between October and December 1966, the first months of the annual dry season, and therefore some therophytes and geophytes had already disappeared, but these species represent less than 5% of the total flora. In all ninety-eight species were recorded in the 380 plots, this number being reduced to ninety-one after discarding those species present in less than 1% of the samples. Nomenclature is that of Aristeguieta (1966).

In the first analysis χ^2 without Yates correction was used as the association-index, taking account only of values greater than 3.84 (corresponding to the $P = 0.05$ level). In a second program χ^2/N was used, considering in this case all the χ^2 values. The first procedure, not entirely satisfactory in theory, did not produce a classification very different from that obtained with the second program. In a third program, all the species with frequency of less than 5% were eliminated, reducing the number to fifty. Table 2 gives the list of the species included in the programs.

In every subdivision the maximum individual value of χ^2 was calculated and in the third program also the total number of 'significant' associations. For terminating the analysis two different principles were applied: a group stops subdivision when its total number of quadrats was less than ten, but if its number was ten or more, the division proceeds until no 'significant' χ^2 was found.

The programs, in FORTRAN for the IBM 360-30 computer of the Central University, were run by Miss Marta Sananes of the Computation Department of the Faculty of Sciences. The first two programs took approximately 6 h each and the third one 2 h of computing time.

Table 2. *List of the species considered in the association-analysis*

- * *Trachypogon plumosus* (Humb. & Bonpl.) Nees
 * *T. vestitus* Anders.
 * *Andropogon brevifolius* Swartz
 * *A. semiberbis* (Nees) Kunth
A. angustatus (Presl) Steud.
Leptocoryphium lanatum (H.B.K.) Nees
 * *Axonopus canescens* (Trin.) Pilger
 * *A. purpusii* (Mez) Chase
 * *A. chrysoblepharis* (Lag.) Chase
 * *Aristida capillacea* Lam.
 * *Digitaria fragilis* (Steud.) Luces
 * *Eragrostis maypurensis* (H.B.K.) Nees
Diectomis fastigiata (Swartz) H.B.K.
 * *Gymnopogon foliosus* (Willd.) Nees
 * *Hackelochloa granularis* (L.) Kuntze
Hyparrhenia rufa (Nees) Stapf
 * *Microchloa indica* (L.) Kuntze
Panicum procurrens Nees
P. hirticaule Presl
 * *Paspalum plicatulum* Michx.
 * *P. multicaule* Poir.
 * *Bulbostylis capillaris* Kunth
 * *B. junciformis* (H.B.K.) Kunth
 * *B. conifera* Kunth
 * *Bulbostylis* sp.
 * *Bulbostylis* sp.
 * *Cyperus amabilis* Vahl
 * *Dichronema ciliata* Vahl
Rhynchospora armeriodes Presl
 * *Scleria micrococca* (Liebm.) Steud.
Erichtites hieracifolia (Fischer ex Spreng.) Gris.
Eupatorium ivaeifolium L.
 * *Pectis ciliaris* L.
 * *P. carthusianorum* Less.
Spiracantha cornifolia H.B.K.
 * *Vernonia remotiflora* Rich.
 * *Cassia cultrifolia* H.B.K.
C. bauhinifolia Kunth
 * *C. hispidula* Vahl
 * *C. chamaecrista* (L.) Britton
C. tagera L.
Mimosa debilis H.B.K.
M. camporum Benth.
 * *M. tomentosa* H. & B.
Tephrosia tenella Gray
T. adunca Benth.
- * *Crotalaria stipularia* Desv.
Aeschynomene brasiliana DC.
Eriosema rufum (H.B.K.) Don
 * *Zornia reticulata* Sm.
Abrus precatorius L.
Calopogonium muconoides Desv.
 * *Indigofera pascuorum* Benth.
 * *Galactia jussieana* H.B.K.
Stylosanthes hamata (L.) Taub.
Phaseolus lathyroides L.
 * *Desmodium barbatum* (L.) Benth.
D. pachyrrhizum Vogel
Bowdichia virgilioides H.B.K.
Euphorbia glomerifera (Millsp.) Wheel.
 * *E. hyssopifolia* L.
 * *E. thymifolia* L.
 * *Phyllanthus stipulatus* (Raf.) Webster
Sebastiania corniculata (Vahl) Mull.
 * *Borreria suaveolens* Mey.
B. latifolia (Aubl.) Schum.
B. laevis (Lam.) Griseb.
 * *Borreria* sp.
 * *Diodia rigida* (H.B.K.) S. & C.
Richardia scabra L.
 * *Sida liniifolia* L.
 * *S. rhombifolia* L.
 * *Sida* sp.
 * *Hyptis suaveolens* (L.) Poit.
 * *Hyptis* sp.
 * *Cuphea micrantha* H.B.K.
Hybanthus ipecacuanha (Benth.) Baillon
Polygala monticola (St.Hil.) Steyermark
 * *Polycarpea corymbosa* (L.) Lam.
Ruellia geminiflora H.B.K.
 * *Evolvulus sericeus* Sw.
Curatella americana L.
Buchnera juncea C. & S.
Turnera ulmifolia L.
 * *Piriqueta cistoides* Mey.
Cordia curassavica (Jacq.) R. & S.
Lantana achyranthifolia Desf.
Torrubia pubescens (H.B.K.) Standley
Byrsonima crassifolia (L.) H.B.K.
Cipura paludosa Aubl.
Cochlospermum vitifolium (Willd.) Spreng.

* These species were considered in the third program.

RESULTS

Formal characteristics of the hierarchies

In the first program, with ninety-one species and uncorrected χ^2 as the division parameter, eighty-six final groups were obtained. The hierarchy shows a considerable degree of chaining, e.g. of the eighty-six divisions, thirty-three separate groups of only one member and fifteen divisions give groups of two members. The maximum individual χ^2

was taken as an indication of the group heterogeneity level, but the number of inversions makes this parameter of little value.

The second program, with the same species and utilizing as the division parameter χ^2/N , gave eighty-seven final groups arranged in a hierarchy presenting also an exaggerated degree of chaining (Figs. 3 and 4).

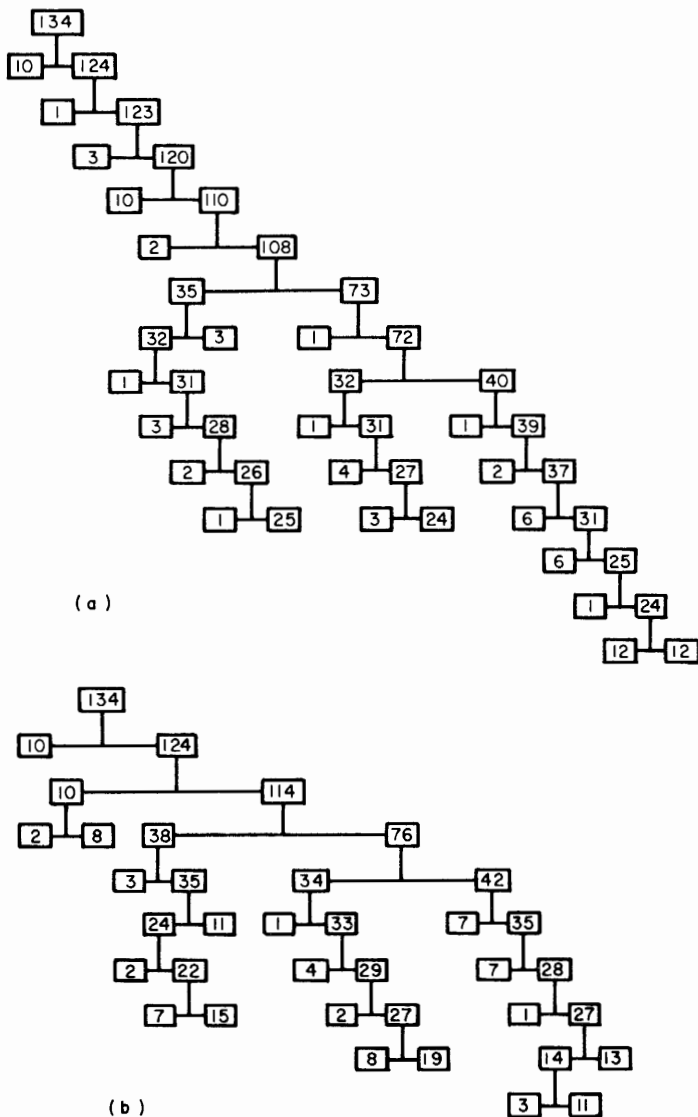


FIG. 3. Hierarchies obtained with the second and third programs of association-analysis. + *Trachypogon vestitus* branch. (a) Second program; (b) third program.

The third program utilized χ^2/N as the division parameter, considering only the fifty species with frequency higher than 5%. This figure was arbitrarily chosen for discarding the rarer species. The complete analysis gave sixty-two groups disposed in a highly chained hierarchy (Figs. 3 and 5), but are on the whole much more satisfactory formally than the preceding ones. As an heterogeneity index, besides the maximum χ^2 , the number

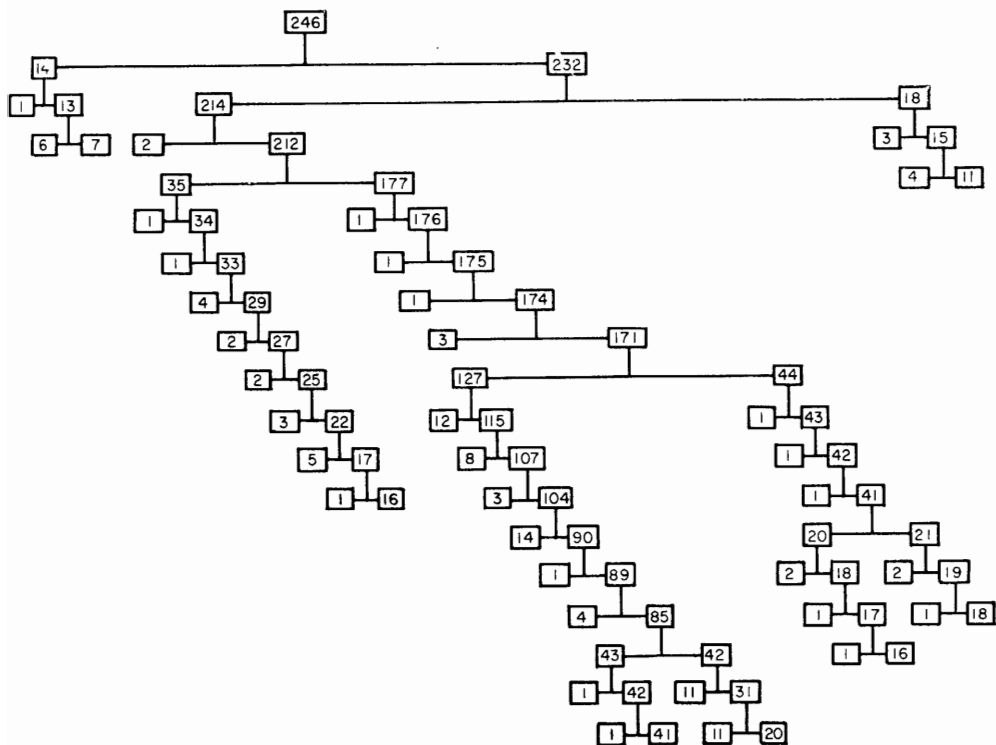


FIG. 4. Hierarchy obtained with the second program of association-analysis. — *Trachypogon vestitus* branch.

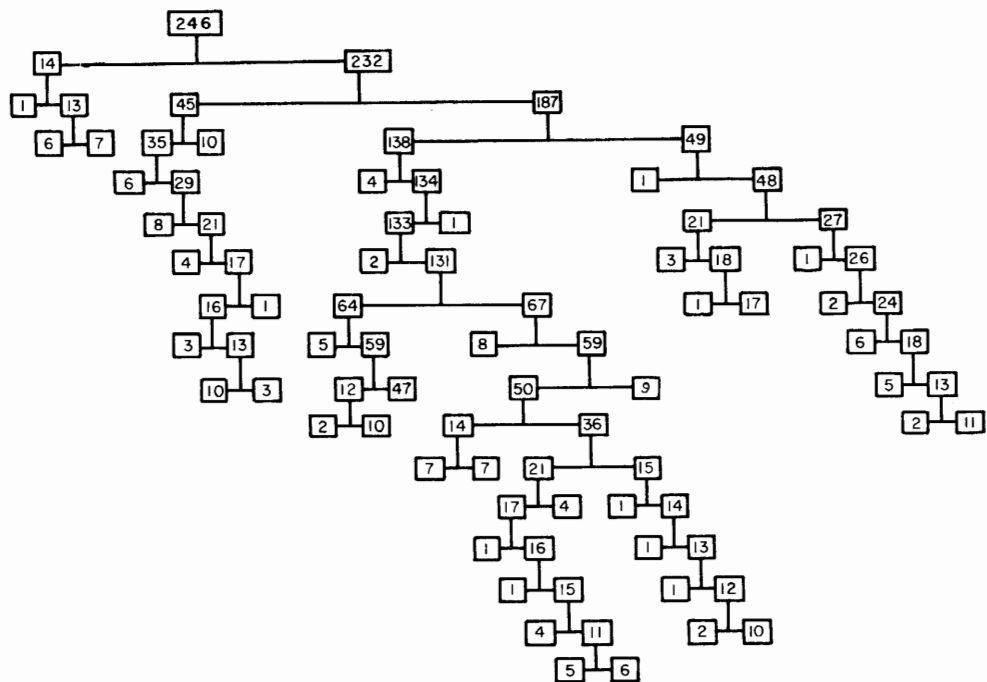


FIG. 5. Hierarchy obtained with the third program of association-analysis. — *Trachypogon vestitus* branch.

of 'significant' associations at the chosen probability level was calculated for every group. According to Lambert & Williams (1966), this index provides a better approximation to the heterogeneity level, and in this particular case, with few exceptions, it decreases as subdivisions proceed.

In comparison with the results of Williams & Lambert (1959, 1960) two features are evident in the three classifications obtained: the large number of terminal groups and correspondingly the high degree of chaining. Greig-Smith, Austin & Whitmore (1967), in

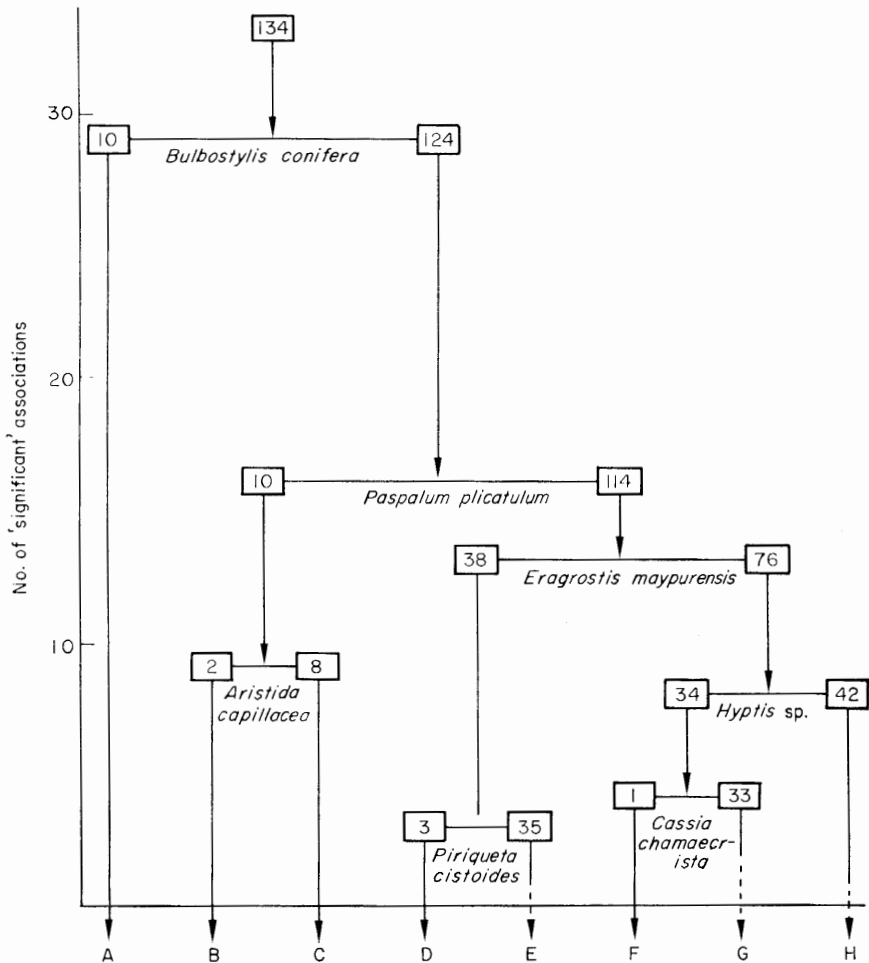


FIG. 6. The upper part of the third classification with the ecologically significant groups. The heterogeneity level is expressed as number of 'significant' associations at $P = 0.05$. + *Trachypogon vestitus* branch.

their application of association-analysis to a tropical rain forest in the British Solomon Islands, have obtained similar results: their initial set of 110 samples were grouped in twenty-six final groups disposed in a highly chained hierarchy. These two characteristics probably reflect the real complexity of the analysed vegetation but the method may not be fully adequate in a situation with so many species and no clear-cut underlying factors. Only the comparative analysis of results obtained with several classificatory methodologies can give a complete answer to this question. In any case, an ecological interpreta-

tion was attempted at the terminal level, and when no ecological significance could be assigned to these groups the hierarchy was re-examined until a significant group could be found.

On comparison of the three classifications, it is evident that the third program appreciably improved on the formal characteristics of the other two. By utilizing the number of 'significant' associations as a criterion of heterogeneity, we see a steep descent resulting from the first order division and a more gradual diminution in the subsequent steps. Thus the initial set had 109 'significant' associations (maximum $\chi^2 = 135$), this figure being reduced in the first division to twenty-nine (maximum $\chi^2 = 52$) in the positive branch and to forty-seven (maximum $\chi^2 = 90$) in the negative one. In the four successive further steps the number attained in any branch does not surpass four, with only one exception which reaches the value twelve. Figs. 6 and 7 show the heterogeneity level of those groups which are ecologically significant according to the analysis of the following section.

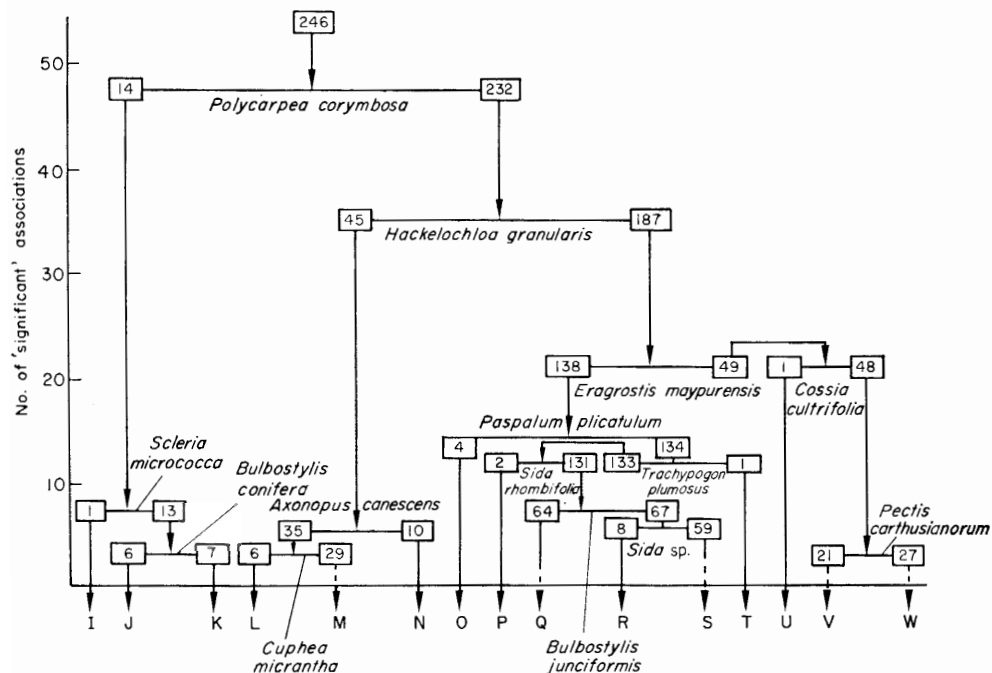


FIG. 7. The upper part of the third classification with the ecologically significant groups. The heterogeneity level is expressed as number of 'significant' associations at $P = 0.05$.
— *Trachypogon vestitus* branch.

Ecological significance

The third program was selected for assessing the ecological significance of the groups at all levels of subdivision, not only because it was the best from the formal viewpoint, but also because the classifications obtained by the three procedures were rather similar, particularly at the higher levels.

For this purpose ecological factors were sampled and assessed, within each group a number of quadrats proportional to the group size being chosen at random. The site

characteristics sampled were those which according to their pattern of distribution appear most relevant in accounting for the heterogeneity of the vegetation, i.e. topographic position; geomorphological level; total cover of the herbaceous layer; distance to the nearest grove and to the nearest isolated tree; dominant species; kind of surface sediments; depth of lateritic layer; and several soil profile features, such as depth, texture and structure of each horizon and a field estimation of the organic matter content in the humic horizon.

At every classificatory level, the coherence of groups and their differences regarding these factors were qualitatively appraised. When at least some factors were similar throughout, a particular group was considered ecologically coherent, and in this case the common factors were regarded as responsible for the group characterization.

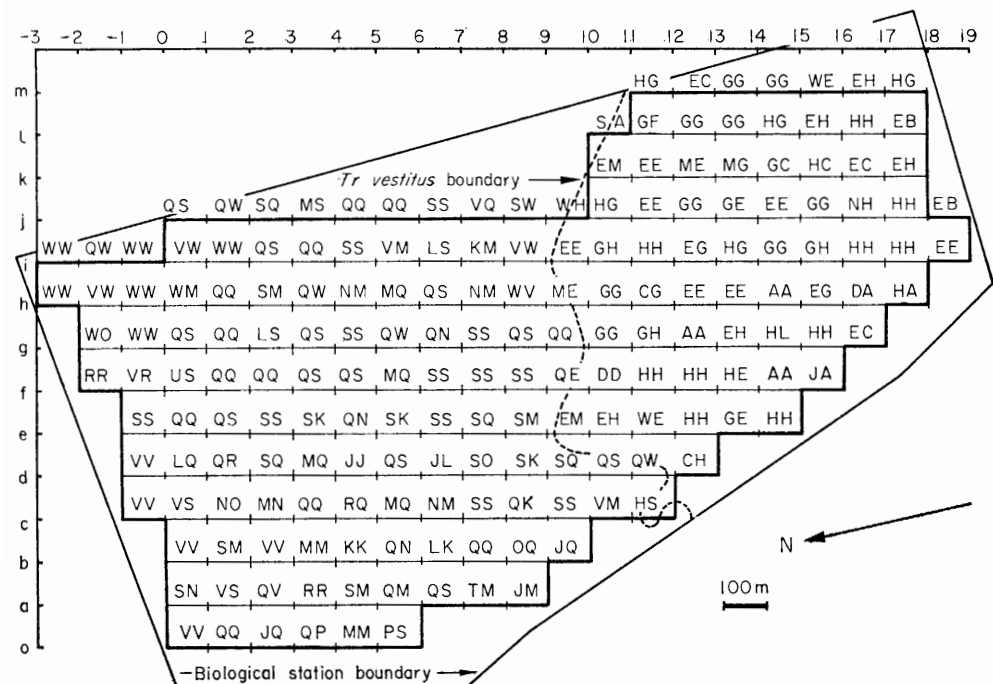


FIG. 8. Map showing the distribution of the ecologically significant groups in the field. The dotted line is the boundary between the areas of the two branches of the first order subdivision. The letters (o-m) and numbers (-3 to 19) refer to the coordinates of the sampling grid; the letters A-W refer to the ecological groupings (cf. Figs. 6 and 7) for the two quadrats in each sampling unit.

The first order division, identical in the three programs, is based on *Trachypogon vestitus*. This group delimitation is coincident with the previously mentioned separation between the savannas of the northern part of the Station, without *T. vestitus*, and those in the southern part which always have this species among the dominants. This uppermost division is the only one in the whole classification that sets apart two large and continuous areas; all the remaining subdivisions create groups whose members are scattered in the stand forming a complex patchy pattern (see Fig. 8). As already noted, these two groups differ in relative altitude, parent material of soil and geomorphological levels. In the lower southern part of the Station these three factors bring about wetter soil conditions during

the rainy season and drier ones during the rest of the year, because the heavier soils drain slowly and desiccate deeply.

When the *+T. vestitus* branch of the hierarchy (Fig. 6) is followed, all three programs separate, on the presence of *Bulbostylis conifera*, an ecologically quite homogeneous small group of ten members. In fact, this group occurs where the iron-cemented laterite is at the ground surface itself. Because of the absence of a true soil, this is the driest habitat of the southern half of the stand.

The only common factor of the *-B. conifera* group is the presence of the lateritic hardpan at a certain depth below the surface. While in the third program this group is further subdivided on *Paspalum plicatum*, in the other two programs almost the same group becomes separated, but only after two minor subdivisions forming small groups of one and three members. The *+P. plicatum* is a grove interphase group, probably conditioned by the mesic microclimate of the grove-shaded areas, but it is not uniform in soil and floristic characteristics. It is further subdivided on *Aristida capillacea* giving two final groups which differ greatly in floristic composition; the *-A. capillacea* group occurs in the interphase of the larger groves and therefore is richer in shade species.

In the *-Paspalum plicatum* branch, we start with a quadrat group of 114 characterized by two negative features: it is not linked either to the lateritic bed outcrops or to the grove interphases. In the next step this group is subdivided on *Eragrostis maypurensis* producing a sharp fall in heterogeneity level, particularly in the positive branch. In the same way, the second program also divides the *-Paspalum plicatum* group on the basis of *Eragrostis maypurensis*, but only after the intermediate separation of a small group. The *+E. maypurensis* branch, with thirty-eight quadrats and three 'significant' associations, occurs on shallow soils, where the hard lateritic horizon generally appears above 30 cm. It is further subdivided on *Piriqueta cistoides*, separating a three-membered group occurring on shallow soils of geomorphological level 2, where the soil profile is not fully differentiated into eluvial and illuvial horizons. The *-P. cistoides* group, with thirty-five quadrats and only one association, is confined to geomorphological level 4 where the soil has no differentiation of horizons (Table 1, profile 4). The remaining subdivisions of this last group do not lead to any marked decrease in heterogeneity and their ecological interpretation becomes obscure, so analysis of this branch was ceased.

The *-Eragrostis maypurensis* branch starts with an heterogeneous group of seventy-six members and eight 'significant' associations, which is subdivided on *Hyptis* sp. with a fall in heterogeneity to four associations in the positive branch and one association in the negative. The second program also makes this same subdivision, but only after the separation of a group of one member. The *+Hyptis* group occurs on geomorphological level 3, where the deep lateritic layer, generally encountered below 60 cm depth, allows the full differentiation of the soil profile, which has as its most distinctive feature a wide, heavy and massive B-horizon. A last subdivision separates on *Cassia chamaecrista* a positive one-membered group localized on an atypical site; as a consequence of this exclusion the heterogeneity level of the negative group falls to two 'significant' associations. This is the last division in the branch that could be interpreted with the available ecological data.

Finally, the *-Hyptis* group, with one 'significant' χ^2 , also occurs on well-developed deep soils, but here the B-horizon is still harder than in the previous classes, rendering drainage difficult and as a consequence the ground remains intermittently waterlogged during the rainy season.

In the ecological interpretation of the whole *+Trachypogon vestitus* branch of the

hierarchy, it can be summarized that the first subdivision separates the most different habitat: the lateritic cuirass outcrops; and the next the floristically very different grove interphase. These two steps reduce the heterogeneity level from twenty-nine to thirteen associations. The following divisions could be analysed in terms of soil depth, with a further sharp decrease in heterogeneity from thirteen to three in the shallow soil group (+ *Eragrostis maypurensis*) and from thirteen to eight in the deep soil branch (– *E. maypurensis*). The last subdivisions in the former branch are of minor ecological significance, being related to the degree of profile development, while the final subdivisions of the deep soil branch sets apart two well-defined groups according to texture and structure of the B-horizon. These properties of the illuvial horizon determine, in turn, the drainage conditions.

The other branch of the first order division, the – *Trachypogon vestitus* group (Fig. 7), with 246 quadrats and forty-seven 'significant' associations, includes all the northern part sites, where the reddish-yellow loams overlie the lateritic bed. In its first subdivision on *Polycarpea corymbosa*, a fourteen-membered positive group is disclosed, with a conspicuous fall from forty-seven to seven in the number of 'significant' χ^2 . This group, very coherent floristically as well as ecologically, occurs on the low, lateritic-capped hills of geomorphological level 1, where the driest conditions of the whole stand are found. It is further subdivided on the presence of *Scleria micrococca* isolating a one-membered group correlated with the occurrence of the very sparse trees appearing in this almost pure grassland. In a final step the + *S. micrococca* group is divided on *Bulbostylis confifera*; the positive group includes all the sites where the lateritic bed appears at the surface, while the sites grouped in the negative branch have 2 or 3 cm of sandy loam overlying the iron hardpan. Exactly the same pattern of divisions is found in the other two programs.

In the – *Polycarpea corymbosa* branch, with 232 quadrats and thirty-five associations, the only common feature is the presence of the lateritic layer at some depth beneath the surface, which permits a certain development of the soil profile. The following division on *Hackelochloa granularis* separates a coherent group of medium size with a resulting sharp decrease in heterogeneity from thirty-five to five 'significant' associations. The presence of woody species in the quadrats of the vicinity of groves are its main feature. In the other two programs a similar group appears after several minor subdivisions.

The following step sets aside, on the absence of *Axonopus canescens*, a cluster of ten quadrats correlated with the interphase of the larger sized groves. The + *A. canescens* group subdivides on *Cuphea micrantha*, giving a positive terminal group on the shallow soils of geomorphological level 2, which have a slightly differentiated thin B-horizon; and a negative terminal group on deeper soils corresponding to geomorphological level 3 where the profile shows a heavy and compact B-horizon (see Table 1, profile 2). The – *C. micrantha* group has still two 'significant' associations, but is the last one in this branch which can be interpreted ecologically in the present analysis. In the second program the + *Hackelochloa granularis* branch has an equivalent grouping, but through a much longer pathway; in the first program however this group family has no equivalent.

The – *H. granularis* group of 187 members and twenty-one associations shows neither floristic influences from groves nor is it related to the occurrence of woody species; it subdivides on *Eragrostis maypurensis*. The resulting positive group occurs on humus-poor, shallow soils where the illuvial horizon is not fully developed. From this group a small cluster of four quadrats is separated on the presence of *Paspalum plicatulum* giving a group on shallow soil distinguished by the presence of trees. The remaining

negative group separates on the absence of *Trachypogon plumosus* from a quadrat taken in a very modified site. This small group separation does not decrease the heterogeneity of the residual positive group. It subdivides again, inefficiently forming, on the presence of *Sida rhombifolia*, a two-membered group characterized by several weedy species. Finally the $-S. rhombifolia$ group of 131 quadrats undergoes an efficient subdivision on *Bulbostylis junciformis* giving two groups of comparable size. The positive one, with sixty-four members and two associations, occurs on sites where the lateritic layer, deeper than 30 cm, allows a full development of the soil profile. The analysis of this branch was not carried out further. The negative group, with sixty-seven members and six associations, separates a $+Sida$ group of eight quadrats on modified soils, and a $-Sida$ group, not yet quite homogeneous, where the pure grasslands on medium depth soils were put together.

Referring now to the hierarchy of the $-Eragrostis$ branch, we have a heterogeneous group of forty-nine quadrats and twenty-one associations, occurring on deep soils with a humus rich A-horizon and a heavy, thick and impermeable B-horizon. The next step, of minor significance, separates on the presence of *Cassia cultrifolia* one quadrat occurring in a very atypical site between two groves, but this exclusion determines in the remaining negative group a heterogeneity fall from twenty-one to three 'significant' associations. This branch subdivides into two fairly equal groups on *Pectis carthusianorum*, corresponding to the positive branch to sites where the grass cover is almost 100%, the soil rich in humus and the lateritic layer deeper than 75 cm.

In the $-P. carthusianorum$ group of twenty-seven elements and three 'significant' χ^2 , a set of quadrats of wide variation in physiognomy, ecology and floristic composition are put together. They belong to the geomorphological levels 2 or 3, and correspondingly have a full range of soil depths, from 15 to 100 cm and more; their only constant feature is the formation, inclusive in the shallower soils, of a heavy and compact B-horizon that has a similar effect on the drainage to that produced by the lateritic hardpan. Since the last subdivisions of this branch are neither formally efficient nor ecologically informative the analysis was not taken further.

In a comparison of the division of the $-Eragrostis maypurensis$ branch in the second and third programs, the similarity in pattern is apparent, but in the second program the symmetrical division on *Pectis carthusianorum* is produced only after three inefficient steps.

In short, the whole classificatory process in the $-Trachypogon vestitus$ branch discloses a compact cluster of lateritic sites in the first step, followed by the separation of the grove interphases and the plots influenced by woody species; and finally, in the third level, the division emphasizes soil depth and organic matter content. These two features are correlated, because a deeper soil maintains a closer herbaceous layer of greater productivity, which in turn determines a higher humus content. The $+Eragrostis maypurensis$ branch, with shallow, humus-poor soils, has also the greater proportion of modified or weedy savannas, probably because the bare ground left by the open savanna offers a more suitable habitat for colonization by weeds. Finally, the humus-rich, deep soil branch ($-E. maypurensis$) is subdivided according to the texture and structure of the B-horizon.

The ecological parallelism between the two branches resulting from the first order division is apparent. In fact, in both cases the first step distinguishes the quadrats occurring on the lateritic outcrops; then, in the subsequent steps, the interphase quadrats and those having woody species are separated and further subdivided by certain features linked with the presence of trees and shrubs. Similarly, a third main subdivision, based on

E. maypurensis in the two branches, gives rise to two great groups clearly characterized by a certain geomorphological level, soil depth, degree of soil profile development, humus content, total cover of the herbaceous layer and abundance of weeds. In turn, the deep soil group is subdivided on the characteristics of the illuvial horizon.

DISCUSSION

The method of association-analysis employed, particularly in the third program, produced a classification ecologically meaningful to an advanced degree of subdivision. Actually twenty-three final groups could be differentiated on the basis of the few environmental characteristics utilized in the ecological analysis.

The third program affords the best formal results, but it is also clear that there are no major differences in the overall pattern of subdivision, when only the formally efficient steps in each classification are taken into account. From the ecological viewpoint the three programs are essentially similar, but the exclusion of the less frequent species from the third method leads to a simpler division, more efficient grouping and clearer interpretation.

Another interesting fact emerging from the analysis is the great heterogeneity evident in this small stand, which from different approaches could be regarded as an homogeneous community undergoing similar pedogenetic processes and submitted to identical management. This is an indication that the tropical savanna is at least as differentiated horizontally as the temperate vegetation of the same structural complexity.

It may be also pointed out that the geomorphology was in this case the most relevant consideration involved in the separation of groups. This factor is a complex resulting from kind of surface sediments, topographic position and depth of the lateritic layer, all features which determine the characteristics of the soil horizons. It is evident that on such factors depend not only the plant water supply but also the space available for root development.

In most cases the floristic and ecological variability of the vegetation was not detectable before the analysis, but those differences already apparent, such as the lateritic cuirass and grove interphase vegetation, were also evident from the first classificatory steps.

Although this work was undertaken without any practical specified object in mind, all the differences in site conditions between the groups could be of interest from a practical point of view. It is probable that with a deeper ecological analysis all the classificatory steps could be associated with some environmental factor. The selection of the adequate level of heterogeneity will depend only on the particular interest of the utilizer; theoretically it is worth while continuing the subdivision to the final level, looking subsequently for the ecological significance of every grouping.

Since our main aim has been the ecological significance of the classification, the final level of analysis was largely determined by the usefulness of the groupings from an ecological viewpoint. Our scale of interpretation was generally coincident with the lower levels of heterogeneity, mostly between none and three 'significant' associations. Only once was the final level of heterogeneity as high as six 'significant' associations.

The main difficulties with this analysis were the high-chained hierarchies, with the corresponding separation of very small groups, and the allocation of ecologically related groups in branches far apart. The first problem is perhaps the consequence either of an insufficient sampling density or of too large a sampling unit. Indeed, most of the single-membered groups occupy sites obviously heterogeneous, and possibly a smaller unit

would have reduced variability within the sites. As regards the second difficulty, it is obviously inherent in all monothetic systems, but here was not very troublesome, because once having ascertained the ecological significance of each group, the related groups could be compared, as were the parallel groups obtained in the two branches of the first order division, e.g. the lateritic cuirass groups, the shallow soils groups.

Finally the value of the classification with reference to the whole stand was analysed, taking and classifying some additional floristic and ecological samples to see if the original allocations were correct or not. Only a few wrong classifications were found. Theoretically misclassifications may be expected, because association-analysis is not concerned with the precise allocation of all individuals, but on the differentiation of groups. The presence or absence of a key species, which permits the right allocation of a quadrat, is a matter of chance and therefore it is not reasonable to expect that a particular species will be present in all the sites with suitable conditions for its establishment. Considering this problem of a *posteriori* classification, it is desirable to start by analysing a representative sample, avoiding as far as possible the time consuming task of reclassifying the whole set of data when new sampling units are added.

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SUMMARY

The inland Venezuelan plains or 'Llanos' are grouped into four ecological regions, each one characterized by a predominant plant formation: the deciduous forest region in the north, with 800–1000 mm annual rainfall; the semi-evergreen forest region in the west, with 1400–2000 mm annual rainfall; the swampy savanna region in the flooding area of the Orinoco river system (except in the delta proper); and the dry savanna region in the central, southern and eastern parts, with 1000–1400 mm precipitation. Each plant formation occurs outside its region only on wetter or drier azonal soils.

The Biological Station of Los Llanos (8° 56' N, 67° 25' W) is a representative site of the dry savanna region. Within its 300 ha protected field, the pattern of the savanna vegetation is the most complex of all types, i.e. groves of medium-sized trees scattered in a grassland dotted with small, gnarled trees. The grassland element of this pattern has the same essential floristic composition throughout, its main dominants being xeromorphic grasses and sedges of the genera *Trachypogon*, *Axonopus*, *Andropogon* and *Bulbostylis*. *Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgilioides* are the three woody species scattered within this continuous herbaceous matrix.

A stand of 190 ha was delimited within the Station, and the savanna sampled by 380

quadrats of 4 m² disposed in a stratified random way. A direct association-analysis was performed, using three slightly different programs: (1) with χ^2 as association index and the ninety-one species with frequency greater than 1%; (2) with χ^2/N as association index and the same ninety-one species; (3) with χ^2/N and the fifty species with frequency greater than 5%. Two measures of heterogeneity were calculated: the maximum individual χ^2 and the total number of 'significant' associations at the $P = 0.05$ level.

The three hierarchies obtained have a comparable division pattern and their upper level subdivisions are similar. All three show a high degree of chaining with the corresponding separation of very small groups. Because the third program was formally the most efficient it was selected as a basis for the ecological analysis of the groups. Twenty-three final groups were correlated with different factors, such as: land form, topographic position, type of surface sediments, soil depth, development of the soil profile, humus content, drainage conditions, distance to groves. Geomorphology was the main single factor correlated with the differentiation of vegetation groups, probably because the land form is an expression of the most operative environmental influences in this area, i.e. topographic position, parent material of soil and depth of lateritic layer.

The results are discussed with emphasis on the observed heterogeneity of the vegetation and the practical utility of the classification obtained.

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