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Floristic composition, plant species abundance, and soil properties of montane savannas in the Gran Sabana, Venezuela

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Abstract

Floristic composition, species abundance, and soil properties were studied in slope, flat and disturbed savannas in the northern part of the Gran Sabana, Venezuela. All savannas presented shallow soils (<30 cm depth) with high content of sand and low content of clay. In general, the soils were poor in nutrients and strongly acidified. The major difference between the soils was the content of the stony fraction, which was significantly higher ($P<0.05$) in the slope savannas than in the flat savannas. A total of 57 dicot, 42 monocot, and 7 fern species were recorded in all studied savannas. In the flat and slope savannas predominated the monocot species, while in the disturbed savanna predominated the dicots. The families with the largest number of species were Poaceae (19.8%), Cyperaceae (13.2%), Asteraceae (10.4%) and Melastomataceae (8.5%). The number of species in the flat savannas was higher than that of the slope savannas. The lowest plant species richness was associated to slope savannas and their high content of stony fraction of the soils. The highest floristic similarity was found between slope savannas, and the lowest between disturbed savanna and slope savannas. The most abundant life forms in the studied savannas were perennial (42.4%) and annual (24.5%) herbs, followed by suffruticoses (16.0%) and shrubs (12.3%), and the less frequent was lianas (4.7%). The disturbed savanna showed the higher richness and diversity index. *Trachypogon plumosum* (Poaceae) was the most abundant species in all studied savanna.

Keywords: Life forms; Floristic composition; Soil characteristics; Species diversity; Tropical savannas

Introduction

The upland plateau of the Gran Sabana has been considered as one of the major savanna areas in South America (Sarmiento, 1983). From a general climatic point of view, this region should be covered by evergreen montane and submontane forests (Huber, 1995). However, these forests occur predominantly as patches or islands surrounded by extensive areas of savannas (Dezzeo, 1994). According to EDELCA (1986), this region is subjected to a high frequency of fire each year, and these fires are in great part started by the indigenous population. In many cases, grass savannas with huge charred standing and fallen trunks of the former forests evidence the savannization process (transformation of forest or other type of vegetation into savanna) in the region (Fölster, 1986; Huber, 1990).

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The actual vegetation cover appears as a complex mosaic consisting of several vegetation types, in which the savannas and bush vegetation dominate, and the forests appear as scattered fragments limited in extent (Fölster, 1994; Hernández, 1994). The particular climate-edaphic blend of the Gran Sabana savanna, in addition to its isolation, point to its vulnerability (Baruch, 2005). The majority of these savannas are secondary savannas, originated and maintained by repeated fires. Although open savannas are widespread throughout the Gran Sabana plateau, mainly in the north section, there is limited information about their ecological characteristics (Baruch, 2005). Soil properties and topography together with disturbances may allow understanding the patterns of plant species number and their abundance in heterogeneous environments. Small-scale disturbances in the savanna matrix could be increasing or maintaining species diversity: vegetation and diversity may be influenced by localized disturbance both in temperate and tropical grasslands (Gillson, 2004; Jentsch and Beyschlag, 2003; Overbeck and Pfadenhauer, 2007).

The objective of this study was to characterize the floristic composition and soil properties in open savannas in the northern of the Gran Sabana plateau, and to determine the relation between edaphic properties, richness, and diversity of plant species in five areas of open savanna with different topography and soil properties. Specifically, the following questions were posed: (1) Do soil properties vary according to savanna topography? and (2) Are richness, diversity, and evenness of plant species affected by relief and soil disturbance in the savannas of the Gran Sabana plateau?

Methods

Study area

The study was carried out in the Gran Sabana, an elevated plateau (800–1500 m asl) located in the Canaima National Park, in southeastern Venezuela, between 04°45′–05°30′N and 60°30′–61°22′W. The Gran Sabana belongs to the Central Guayana Province of the Guayana Region (Huber, 1994), and the potential vegetation has been defined as evergreen montane forest (Huber, 1995). The parent rocks consist of quartzitic sandstone of the Roraima Group, an assemblage of Precambrian Formations with radiometric ages between 1600 and 1700 millions years (Schubert et al., 1986). The soils are in an advanced phase of weathering, and are characterized by low pH values, deficiency of basic cations, accumulation of acidic cations and low Ca/Al ratio in the soil solution (Dezzeo and Fölster, 1994; Fölster et al., 2001).

Specifically, the fieldwork was carried out in the northern part of the Gran Sabana plateau, in the surroundings of the Estación Científica de Parupa, at 1200 m asl. The climate of this area has been considered as humid seasonal, with a short dry season (3 months) where the monthly rainfall is lower than 100 mm (Ramírez et al., 1988). However, this period cannot be considered as a pronounced dry season. The annual precipitation varies between 1815 and 3400 mm, and main monthly temperature does not vary drastically throughout the year: 19.9–21.4 °C (Ramírez et al., 1988). For the study we selected two savanna areas on flat ground (Aeropuerto and Misión) and two savanna areas on slope (Torón and Liworiwo), close to 5°42.68′N; 61°32.54′W. All selected savannas have been impacted by uncontrolled fires, and flat savannas presented small patches of old edaphic perturbations, which were caused by mechanic alteration of the soils. The characteristics of the studied savannas were as follow: (1) Torón: savanna on hill with a slight slope (approximately 25–30°) and rocky substrate. (2) Liworiwo: savanna on hill, with a strong slope (approximately 45–50°) and rocky substrate. (3) Aeropuerto: flat savanna with sandy substrate. (4) Misión: flat savanna with sandy substrate, which differs from Aeropuerto by ancient disturbance by the first encampment of monk colonists in the area. In addition, flat savannas exhibited patches of edaphic perturbation caused by mechanic alteration of soil: hollows, cavities, and/or mounds of different size (approximately from 1 up 10 m^2). All these patches were grouped as an additional area denominated in this study as "disturbed savanna".

Across each savanna area 25, 1-m^2 plots were randomly distributed. Circular plots were used to avoid the border effect of quadrate forms (Kershaw, 1975). The plots were positioned intentionally in small-perturbed patches of each selected savanna, and the collected data were placed together under the category called "disturbed savanna".

Soil analysis

At each savanna area, mineral soil was regularly sampled at six points using an auger. These points were located in the surrounding of the 25 plots of 1 m^2 delimited for vegetation analysis. Soil samples were collected only at 0–20 cm depths because of the C-horizon was found between 25–30 cm soil depths. Samples in the disturbed patches of each savanna area were not collected because of the soil in these patches was removed by mechanic effects. Each collected soil sample was weighed and oven dried (65 °C) for determination of the moisture content, chemical analyses, and estimation of the fine soil fraction (<2 mm) and coarse or stony fraction (>2 mm). The physical and chemical analysis was carried out using the fine fraction of soils.

Soil texture was determined by the hydrometer method (Day, 1965). Soil pH was measured in 1 M KCl (Thomas, 1982). Organic matter was determined by the Walkley and Black (1934) method. Total N was measured following the Kjeldahl method (Jackson, 1976). Available P was extracted according to Tiessen and Moir (1993), and colorimetrically determined (Murphy and Riley, 1962). Exchangeable K, Mg and Ca were determined by atomic-absorption spectrometry using 1N ammonium acetate as extracting solution (Thomas, 1982). Exchangeable Al was extracted with 1 M KCl solution and determined by titration with NaOH (McLean, 1965).

Plant species and life form

Plant samples of all species growing in the studied savanna areas were collected for botanical identification along a period of 2 years. Voucher samples were deposited in the Herbario Nacional de Venezuela (VEN). Plants were classified as monocots, dicots and ferns (incl. clubmosses), and they were identified to species level. Plant life forms were established according to habit, longevity, stem lignifications, height, and type of ramification. At first, plants species were classified as perennial and short-lived species. Short-lived condition was established observing a minimum of ten individuals per species during 2 years in permanent plots. Those species where more than 80% of the individuals died during the observation period were considered as short-lived or annual species. Perennial species were classified according to their habitat in herbaceous, suffruticose (herbs with somewhat woody stems), shrubs (plants that do not exceed 2–4 m high, and with woody stems divided near to the ground), and climbing (plants climbing on herbaceous species).

Vegetation analysis

At each of the 25 delimited subplots per savanna area, the species and individuals (abundance) were counted during the mid-rainy season. In the case of herbaceous species with vegetative propagation (i.e. grasses), individual plants were checked for above and/or underground root connections. The abundance of plant species was established as the number of plant species per savanna area.

Floristic similarity between savanna areas was calculated using Jaccard's index (CC) (Magurran, 1988). Similarity between savanna areas was also estimated according to the species number and their abundance (Digby and Kempton, 1987) using a cluster analysis. In this analysis linkages were determined using the method of unweighted pair-group (UPGMA), which uses arithmetic averages to evaluate the distances between clusters (StatSoft, 2001). The distances were measured as 1-Pearson *r*.

Diversity of each savanna area and for the overall community was calculated using the diversity index of Shannon–Wiener (Magurran, 1988). The relative abundance of plant species within each savanna area (equitability or evenness) was calculated as $E = H/\ln S$ (Magurran, 1988), where S is the number of plant species and H the Shannon–Wiener index of diversity.

Statistical analysis

Mean values and their standard deviations are provided throughout the presentation of similarities/differences in the texture and chemical properties of the soils among savanna areas. Statistical differences in the soils were tested using one-way ANOVA (StatSoft, 2001). Values were transformed before analysis if they did not exhibit normal distribution or variance homogeneity, following Sokal and Rohlf (1995). A Tukey honest significant difference (HSD) test was used when statistical differences ($P < 0.05$) were observed. Statistical significance of diversity indices between savanna areas was assessed using a *t*-test (Magurran, 1988). In order to establish the level of dependence between life forms and savanna areas, a log-linear analysis of frequency was performed, using two-factor tables (StatSoft, 2001).

Results

Soil properties

The soils in all studied savannas were shallow (<20–30 cm depth) and did not show the organic surface layer typical of the soils under forest in this region. One difference between the soils of the studied savannas was the content of mineral particles with diameters >2 mm (stony fraction) (Table 1). The stony fraction of the soils in Liworiwo and Torón (savannas on slope) did not differ significantly between them. But it was significantly higher ($P < 0.05$) than the stony fraction of the soils in Aeropuerto and Misión (savannas on flat ground).

One common characteristic in the soils of the studied savannas was the texture of the fine soil (fraction <2 mm), which showed high content of sand (>65%) and low content of clay (<10%) (Table 1). The soils of Misión (savanna on flat ground) and Torón (savanna on slope) belong to the sandy loam textural class, and the soils of Aeropuerto (savanna on flat ground) and Liworiwo (savanna on slope) to the loamy sand class. Although there are significant differences in

Table 1. Stony and fine soil fractions, and proportions of clay, silt, and sand (mean ± SD) in the studied areas

	Flat savannas		Slope savannas	
	Aeropuerto	Misión	Liworiwo	Torón
% Stony fraction (>2 mm)	22.2±5.1^{a}	42.2±2.9^{b}	83.2±3.0^{c}	88.6±1.5^{c}
% Fine soil (<2 mm)	77.8±5.1^{a}	57.8±2.9^{b}	16.8±3.0^{c}	11.5±1.5^{c}
% Clay	8.3±3.0^{a}	6.9±3.7^{a}	3.3±1.3^{b}	10.1±6.6^{a}
% Silt	13.3±3.0^{a}	24.4±4.2^{b}	9.2±3.4^{a}	20.4±5.6^{b}
% Sand	78.3±2.0^{a}	68.7±5.6^{b}	87.5±4.2^{c}	65.5±5.3^{b}

Different letters in rows indicate significant differences among areas (ANOVA, $P<0.05$).

Table 2. Chemical characteristics of the soils (mean ± SD) in the studied savannas

	Flat savannas		Slope savannas	
	Aeropuerto	Misión	Liworiwo	Torón
pH	4.47±0.10^{a}	4.40±0.09^{a}	4.37±0.12^{a}	4.40±0.09^{a}
Organic matter (%)	1.55±0.23^{a}	2.79±0.31^{b}	3.43±0.63^{b}	6.14±0.73^{c}
N (%)	0.05±0.00^{a}	0.09±0.02^{b}	0.11±0.02^{b}	0.18±0.02^{c}
P (μg/g)	3.04±0.50^{a}	3.98±0.92^{a}	3.55±0.33^{a}	3.91±0.52^{a}
K (cmol/kg)	0.02±0.00^{a}	0.05±0.01^{bc}	0.04±0.01^{b}	0.06±0.01^{c}
Mg (cmol/kg)	0.01±0.00^{a}	0.03±0.00^{b}	0.02±0.00^{c}	0.04±0.01^{b}
Ca (cmol/kg)	0.02±0.00^{a}	0.04±0.01^{bc}	0.03±0.00^{b}	0.05±0.01^{c}
Al (cmol/kg)	0.65±0.03^{a}	1.10±0.12^{b}	0.81±0.18^{c}	0.95±0.09^{d}

Different letters in rows indicate significant differences among savanna areas (ANOVA, $P<0.05$). The mean values of pH were calculated on the backtransformed pH concentrations.

the sand, clay and silt content between some of the studied savannas, these differences seem to be not related with their topographical position (Table 1).

In general, chemical characteristics of the soil were unfavorable and reflected a high degree of weathering of the parent material (Table 2). Soil acidity was characterized by low pH values, which were statistically similar among the savannas areas. Exchangeable Al was high and showed significant differences among the studied areas (Table 2). The levels of K, Ca, and Mg were very low and showed significant differences among some of the studied savannas. However, these differences seem to be no related with the topographical position (Table 2). The P concentrations were very low and statistically similar among the different savanna areas. The organic matter content in all soils was high and showed significant differences among the savanna areas (Table 2). The N content in the soils was relatively low, despite the high contents of organic matter (Table 2), which could also indicate low quality of the organic material.

Plant species composition, diversity, and floristic similarity

The number of species recorded in all studied savannas was 106 (Appendix 1). A total of 57 dicot (53.8%), 42 monocot (39.6%), and 7 fern (6.6%) species were recorded in all studied savannas. In the flat and slope savannas the abundance of monocot species was higher than that of the dicot species (Table 3). The highest frequency of dicots, particularly pioneer species, and six of the seven fern species were found in the disturbed savanna.

The plant families with the largest number of species (N) in the total studied area were Poaceae ($N=21$; 19.8%), Cyperaceae ($N=14$; 13.2%), Asteraceae ($N=11$; 10.4%), Melastomataceae ($N=9$; 8.5%), Polygalaceae ($N=7$; 6.6%), and Orchidaceae ($N=6$; 5.7). The most frequent genera in the studied savannas were *Rhynchospora* ($N=7$; 6.6%), *Polygala* ($N=7$; 6.6%), and *Axonopus* ($N=5$; 4.7%) (Appendix 1).

The number of species in the flat savannas (Aeropuerto and Misión) was higher than that of the slope savannas (Liworiwo and Torón) (Table 4). The savanna of Liworiwo with the largest inclination showed a lower number of plant species than the savanna of Torón with less inclination. The highest species number was found in the disturbed savanna (Table 4). According to the index of Jaccard (Table 5), the highest value of floristic similarity was found between both slope savannas (Liworiwo and Toron). The pair of flat savannas (Misión and Aeropuerto) showed also a relatively high value of floristic similarity. The results of similarity

Table 3. Number (N) and percentage (%) of plant species according to life form and taxonomic group

	Flat savannas		Slope savannas		Disturbed savanna
	Aeropuerto N (%)	Misión N (%)	Liworiwo N (%)	Torón N (%)	N (%)
Life forms					
Shrubs	2 (4.4)	0 (0)	0 (0)	1 (3.4)	13 (17.3)
Suffruticose	3 (6.7)	1 (2.3)	4 (21.1)	6 (20.7)	10 (13.3)
Lianas	1 (2.2)	0 (0)	0 (0)	0 (0)	4 (5.3)
Perennial herbs	27 (60.0)	29 (65.9)	14 (73.7)	19 (65.5)	27 (36.0)
Annual herbs	12 (26.7)	14 (31.8)	1 (5.3)	3 (10.3)	21 (28.0)
Taxonomic group					
Dicots	16 (35.6)	11 (25.0)	5 (26.3)	7 (24.1)	41 (54.7)
Monocots	27 (60.0)	31 (70.4)	14 (73.7)	22 (75.9)	28 (37.3)
Ferns	2 (4.4)	2 (4.6)	0 (0.0)	0 (0.0)	6 (8.0)

Table 4. Species richness, Shannon's diversity index, equitability, species/area ratio, abundance, and individuals/area in the studied savanna areas

	Flat savannas		Slope savannas		Disturbed savanna	Total
	Aeropuerto	Misión	Liworiwo	Torón		
Species richness	45	44	19	29	75	106
Shannon's index	2.96^{a}	2.71^{b}	1.84^{c}	2.46^{d}	3.17^{a}	3.11^{a}
Equitability	0.78	0.72	0.63	0.73	0.73	0.67
Species/area ratio	1.80	1.76	0.76	1.16	3.00	0.85
Abundance*	1802	2566	888	1880	749	7885
Individuals/area	72.1	102.6	35.5	75.2	29.9	63.1

Different letters in row indicate significant differences among savanna areas (ANOVA, $P<0.001$).
*Number of individual per 25 m^2 for each area and per 125 m^2 for the total sample.

Table 5. Floristic similarities in the studied savannas expressed as Jaccard indices

	Aeropuerto	Misión	Liworiwo	Torón	Disturbed savanna
Aeropuerto	—				
Misión	0.44	—			
Liworiwo	0.28	0.26	—		
Torón	0.32	0.30	0.50	—	
Disturbed savanna	0.38	0.30	0.19	0.23	—

taking into account the species number and their abundance (Fig. 1) showed also that the flat savannas, including disturbed savanna are more similar between them than the slope savannas.

The highest values of the Shannon's diversity indices were found in the disturbed savanna, Aeropuerto flat savanna, and in the overall sample. These values showed no significant differences. The other savanna areas showed significant differences in the Shannon's index (Table 4). The lowest value of diversity was found in the savanna with the largest slope, Liworiwo, which showed also the lowest values of richness, equitability, species/area, and individual/area (Table 4). Although Aeropuerto and disturbed savanna showed similar diversity, some important differences were found between both areas (Table 4). Richness and species/area ratio were higher in disturbed savanna plots than in Aeropuerto, whereas abundance and individual/area ratio were higher in Aeropuerto than in disturbed savanna plots.

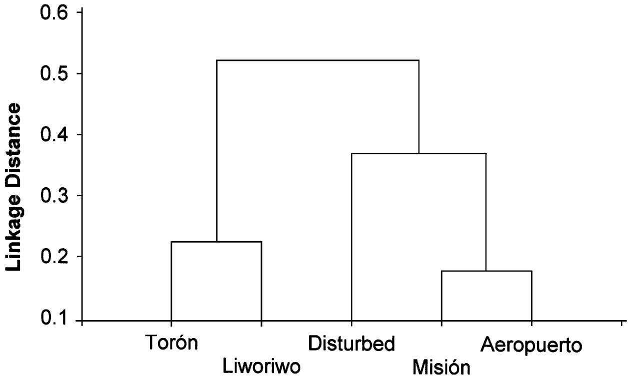

Fig. 1. Cluster analysis of savanna areas according plant species abundance.

Life forms

Life forms were significantly associated with the savanna areas (df = 16, $\chi^2 = 36.7$, $P = 0.002302$). The most abundant life form in all studied savannas was that of perennial herbs ($N = 45$, 42.4%), followed by annual herbs ($N = 26$, 24.5%), whereas the less frequent life form was the climbing ($N = 5$, 4.7%). Shrubs ($N = 13$, 12.3%) and suffruticose plants ($N = 17$, 16.0%) showed an intermediate number of species. The frequency of annual herbs was higher in the disturbed savanna and in the flat savannas than in the slope savannas (Table 3).

The abundance of plant species

The species with the highest values of absolute abundance were *Trachypogon plumosum*, *Rhynchospora caracasana*, *Hypolytrum pulchrum*, *Echinolaena inflexa*, *Rhynchospora velutina*, *Mesosetum rottboellioides* and *Panicum micranthum* in the flat savannas, and *Trachypogon plumosum*, *Axonopus* sp., *Bulbostylis paradoxa*, *Paspalum lanciflorum*, *Rhynchospora mexicana* y *Bulbostylis conifera* in the slope savannas (Appendix 1). The species with the highest values of abundance in the disturbed savanna were *Trachypogon plumosum*, *Echinolaena inflexa*, *Rhynchospora velutina*, *Paspalum lanciflorum*, and *Raddiella essembeckii*, however, *Trachypogon plumosum* exibited the highest values of abundance. According to the results, some species occur with high or intermediate number of individuals in all savanna areas, regardless of topographical position or disturbance (i.e. *Trachypogon plumosum*, *Raddiella essembeckii*, *Paspalum lanciflorum*, and *Rhynchospora velutina*).

Discussion

The soils in all studied savannas have low profundity, which has been associated with the presence of mineral layers highly resistant to weathering and with processes of fluvial erosion (Dezzeo and Fölster, 1994). The high proportion of stony fraction in slope savannas could be explained considering the erosion process associated with savannization. According to Fölster (1992) and Fölster et al. (2001), savannization is followed by a translocation of fine materials from the slopes to the valleys. Differences in organic matter among the savanna areas seem to have no relation to slope position and their absence could be related with fire frequency in the Gran Sabana Plateau. High content of C in the soils of forests and savannas of the study region has previously reported (Dezzeo and Fölster, 1994; Dezzeo et al., 2004; Fölster et al., 2001) and has been considered an effect of low microbial activity (Priess and Fölster, 2001). The highest content of organic matter in slope savannas may be related with the high proportion of stony fraction, which could limit the moisture in the soil and therefore could be associated with low microbial activity.

The values of chemical soil properties for the study areas are comparable with those reported for other savannas growing on sandy soils in the North of the Gran Sabana plateau (Chacón and Dezzeo, 2004; Dezzeo et al., 2004), but are lower than the values reported for other montane savannas on more clayed soils in the South of the Gran Sabana (Dezzeo and Fölster, 1994; Fölster et al., 2001). With the exception of the organic matter content, the chemical soil data of our montane savannas were unfavorable for plant growth in comparison with the data reported by Sarmiento (1990) for seasonal savannas of the Venezuelan Llanos growing on sandy loam soils, but were similar to the data reported by this author for seasonal savannas growing on sandy loam soils in French Guiana.

Summing up one must conclude that that the soils in all studied savannas are extremely poor in nutrients and strongly acidified. It has been presumed that this edaphic condition is one of the more important factors accounting for the presence of savannas in the tropics (Sarmiento, 1990). However, the soil nutrient condition of the studied savannas is quite similar to that reported for the forest areas of the region (Dezzeo et al., 2004; Fölster et al., 2001), and therefore such soil conditions do not seem to be a necessary determinant factor explaining the presence or absence of savannas in the Gran Sabana Plateau. According to Sarmiento (1990), climatic seasonality is one of the most essential features of a savanna ecosystem. In the study region, however, there is not well-defined rainfall seasonality (Hernández, 1994). Under such circumstances, the studied savannas could be considered as secondary formations, originated and maintained by periodic fire (cf. Overbeck and Pfadenhauer, 2007).

Plant species composition, diversity, and floristic similarity

The taxonomic comparison of the studied savannas with that of other savannas indicate floristic divergences among phytogeographical areas: (1) the plant families with the largest number of species differ from similar vegetation types (i.e. Batalha and Mantovani, 2001; Ramírez, 2003; Weiser and Pires de Godoy, 2001); however, Poaceae and Cyperaceae have been also reported as the main families in seasonal and non-seasonal savannas (Baruch, 2005; Sarmiento and Vera, 1979). (2) The most frequent genera in the studied savannas may be close to seasonal savannas (Baruch, 2005) or differ from other tropical savannas (e.g. Batalha and Mantovani, 2001; Ramia, 1967; Ramírez, 2003; Vareschi, 1968; Velásquez, 1965; Weiser and Pires de Godoy, 2001). Differences in the most abundant genera may be associated with elevation and water and nutrient availability (Baruch, 2005), that have influence upon the savanna formation.

The large number of plant species recorded in all savannas studied could be related to disturbance and the lack of a pronounced dry period in the North of the Gran Sabana Plateau. The highest frequency of pioneer species, mostly dicot and fern species, were found in the disturbed savanna. These results are comparable with those reported by Velásquez (1965) for pastures previously subjected to intensive grazing. The highest species number in the disturbed savanna may be associated with the heterogeneity of disturbance. Heterogeneity of microsites can influence the distribution and coexistence of plant species (Shmida and Wilson, 1985), and therefore can affect the floristic composition among adjacent disturbed patches. Several of the species found in the disturbed savanna places were absent in the other four savannas areas, and the most frequent species in the disturbed savanna differ from the common species reported by Rosales et al. (1997) for other degraded areas. This suggests that disturbed areas contribute substantially to the high values of richness in the savanna of the Gran Sabana Plateau. Apparently, edaphic perturbations promote the colonization of a high number of species, and increase the levels of species richness. In a similar way, small-scale disturbances maintain species diversity of temperate dry acidic grasslands (Jentsch and Beyschlag, 2003).

The similarity of savanna areas indicates that the flat savannas, including disturbed savanna plots, differ from the slope savannas. These results suggest that the topographical position and the stony fraction of the soils can be considered as important factors modulating the floristic composition and the abundance of species in the savanna vegetation, irrespectively of the highest abundance of *Trachypogon plumosum* in all the five savanna areas. The soils of slope savannas could be considered as deeply eroded and therefore could limit the number of plant species. In addition, the levels of inclination seem to affect the number of plant species. The savanna with the largest inclination show the lowest number of plant species. According to Fölster (1986), the main effect of the slope is related to the washing of soils by water, which varies with the level of the slope and soil texture. In contrast, chemical characteristics of the soil do not seem to affect floristic composition and plant species abundance for the studied savannas. Similar results have been found for a variety of cerrado physiognomies (Cruz-Ruggiero et al., 2002).

Shannon's diversity indices for the savanna studied were close to that of the savanna area of the Venezuelan Central Plain (Ramírez, 2003), which suggests that diversity indices for tropical savannas could be related to vegetation physiognomy: habitats with similar above ground appearance might converge in diversity indices values, because habitats with similar physiognomies may exhibit similar patterns of species abundance. However, there were found significant differences for the five savanna areas studied. In the disturbed savanna, the highest Shannon's diversity index does not agree with the low diversity that is to be expected in perturbed areas under successional development (Drury and Nisbet, 1973). It is known that the species diversity is affected by the richness of subordinated species (Whittaker, 1965). High diversity in the disturbed savanna can be associated with the high number of plant species and the high species/area ratio, as well as with the high richness of subordinate species and the lower number of individuals per species, which promote a relative balance in the species' dominance. The lowest values of diversity, richness, equitability, species/area, and individual/area found for the savanna with the largest slope may indicate an unbalance there in the abundance of the plant species. This is probably associated with the precarious soil properties in these areas.

Life forms

The dominance of herbaceous species in grassland communities agree with previous studies in Brasilian Cerrados (i.e. Batalha and Mantovani, 2001) and savannas (i.e. Ramírez, 2003). The lack of a pronounced dry period in the North of the Gran Sabana Plateau (Ramírez et al., 1988) seem to favor the occurrence of herbaceous species and to limit the presence of shrub and suffruticose species with adaptations to prolonged dry periods and periodical burning, which showed high diversity in the seasonal savannas of the Venezuelan Llanos (Sarmiento and Monasterio, 1983). In addition, the abundance of each life form correlated with the average values of reproductive efficiency: the most abundant life forms, annual and perennial herbs, exhibit the largest fruit set and the less abundant life form, climbing, exhibit the lowest values of fruit set (Ramírez, 2005). However, the abundance of the other life forms does not correlate with the values of fruit set. Although there is not a direct effect of average values of fruit set and the abundance of each life form, reproductive efficiency could be associated with the status of dominant life forms.

The importance of the annual herbs varies depending on the habitat. According to Sarmiento and Monasterio (1983), annual herbs are frequent in dry sites and disturbed areas. The high proportion of annual species in the disturbed savanna could be associated to the fact that high levels of perturbation tend to select short-lived species (Drury and Nisbet, 1973; MacArthur and Wilson, 1967). Most of the plant species growing on disturbed savanna are invaders, and a large proportion of these are annual species, which contribute to plant species richness as alien species increase species richness in temperate savannas (Keeley et al., 2003). In contrast, low frequency of annual herbs in the slope savannas could be associated with eroded soils, and probably with the dragging of seeds through the slope by water. In fact, patterns of species richness are best explained by species diversity of soil seed banks (Díaz-Villa et al., 2003; Tracy and Sanderson, 2000).

In conclusion, soils in all savanna studied are extremely poor in nutrients and strongly acidified. The chemical characteristics of the soil do not seem to affect floristic composition and plant species abundance for the studied savannas. However, the grassland community has a representative number of plant species which can be associated with the environmental heterogeneity. The main factors affecting plant species richness and diversity indices are disturbance and topography: the richest savanna was the disturbed one and the poorest were slope savannas. Slope topography seems to limit the number of plant species by the high proportion of stony fraction of the soil in these areas.

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Appendix 1

Please see Table A1.

Table A1. Family, plant species, life form, and their abundance (individuals/25 m^2) recorded in five savanna areas in the Gran Sabana Plateau

FAMILY Species	Life form*	Aeropuerto	Misión	Liworiwo	Torón	Disturbed savanna
ACANTHACEAE						
Justicia guianensis (N.E.Br.) Wassh.	AH					1
APOCYNACEAE						
Mandevilla benthamii (A. DC.) K. Schum.	F				4	
Mandevilla leptophylla (A. DC.) K. Schum.	L					2
ASCLEPIADACEAE						
Blepharodon nitidus (Vell.) Macbr.	L					1
Metastelma hirtella (Oliver) Leide	L					6
Ditassa bolivarensis (R.W. Holm.) Morillo	L	1				
ASTERACEAE						
Austroeupatorium inulaefolium (Kunth) R.M. King & H. Rob.	SH					1
Ayapana amygdalina (Lam.) R.M. King & H. Rob.	F					1
Baccharis leptocephala DC.	F					1
Calea nana Maguire	F			1	1	
Calea oliveri B.L. Rob. & Greenm.	F					1

Table A1. (*continued*)

FAMILY Species	Life form*	Aeropuerto	Misión	Liworiwo	Torón	Disturbed savanna
Chromolaena laevigata (Lam.) R.M. King & H. Rob.	SH	2				1
Chromolaena thurnii (B.L. Rob.) R.M. King & H. Rob.	AH					2
Lepidaploa ehretifolia (Benth.) H. Rob.	SH					3
Lepidaploa gracilis (Kunth) H. Rob.	SH					2
Trichogonia campestris Gardner	AH					2
Vernonia miersiana Gardner	F					1
CAESALPINIACEAE						
Chamaecrista devauxii Killip	F					1
CAMPANULACEAE						
Lobelia fastigiata H.B.K.	AH		1			
CLUSIACEAE						
Vismia guianensis (Aubl.) Pers.	SH					9
CYATHEACEAE (Fern)						
Cyathea villosa Willd.	PH		1			1
CYPERACEAE						
Bulbostylis conifera (Kunth) C. B. Clarke	PH	74		8	442	9
Bulbostylis lanata Kunth	PH		8			
Bulbostylis paradoxa Nees in Mart.	PH	58	38	58	176	5
Hypolytrum pulchrum H. Pfeiffer	PH	97	148	7	87	31
Lagenocarpus rigidus Nees	PH	76	71	18	74	5
Rhynchospora caracasana (Kunth) Boeckl.	PH	223	162	64	14	14
Rhynchospora curvula Griseb.	PH	11	167			3
Rhynchospora globosa (Kunth) Roem. & Schult.	PH	8	27		1	
Rhynchospora mexicana (Liebm.) Stend.	PH	19	57	17	141	
Rhynchospora pilosa (Kunth) Boeckl.	PH				2	
Rhynchospora rugosa (vahl) Gale.	PH	14	4			8
Rhynchospora velutina Nees	AH	175	376		3	132
Scleria cyperina Kunth	PH	14	5	24	96	18
Scleria distans Poir.	PH			1		29
DENNSTAEDTIACEAE (Fern)						
Lindsaea stricta (Sw.) Dryand.	PH	3				22
DROSERACEAE						
Drosera felix Steyerm. & L.B. Sm.	PH	25				
GENTIANACEAE						
Coutoubea reflexa Benth.	F					1
Curtia tenuifolia (Aubl.) Knobl.	AH	2				
Irlbachia alata (Aubl.) Mass	AH		2			2
Irlbachia caerulescens (Aubl.) griseb.	AH		1			
Irlbachia purpuracens (Aubl.) Mass	AH					1
GLEICHENIACEAE (Fern)						
Dicranopteris flexuosa (Schrad.) L. Underw.	PH		5			8
HYMENOPHYLLACEAE (Fern)						
Trichomanes cellulosum Klotzsch.	PH			1		1
LENTIBULARIACEAE						
Utricularia amethystina St. Hil.	AH	2	9			12
LOGANIACEAE						
Bonyunia minor N.E. Br.	SH	1				1

Table A1. (*continued*)

FAMILY Species	Life form*	Aeropuerto	Misión	Liworiwo	Torón	Disturbed savanna
LYCOPODIACEAE (clubmoss family)						
Lycopodiella camporum B. Ollg. & P. G. Windisch	PH					1
Lycopodiella cernua (L.) Pichi Serm.	PH	1				
Lycopodium clavatum L.	PH					1
MALPIGHIACEAE						
Byrsonima crassifolia (L.) Kunth	SH				27	2
Byrsonima verbascifolia Rich. ex Juss.	F			4	1	
MELASTOMATACEAE						
Clidemia pustulata DC.	SH					1
Clidemia sericea D. Don	F	2				11
Desmoscelis villosa (Aubl.) Naud.	AH					3
Macairea lasiophylla (Benth.) Wurdack	AH	49				8
Marcetia taxifolia (St. Hil.) DC.	SH					4
Miconia alata (Aubl.) DC.	SH					1
Miconia rufescens (Aubl.) DC.	SH					1
Microlicia benthamiana Triana ex Cogn.	F	1				
Siphanthera cordifolia (Benth.) Gleason	AH	32	44			
MYRTACEAE						
Psidium larnotteanum Cambess. In A. St.-Hil.	SH					1
OCHNACEAE						
Sauvagesia amoena Ule	F		1			
ORCHIDACEAE						
Cleistes rosea Lindl.	PH	1				
Cyrtopodium parviflorum Lindl.	PH		1			
Epidendrum ibaguense Kunth	PH	1	1			
Epidendrum secundum Sw.	PH					1
Habenaria mesodactyla Griseb.	PH		2			
Habenaria schomburgkii Lindley es Benth.	PH		1			
POACEAE						
Andropogon selloanus (Hack.) Hack.	AH					11
Aristida recurvata Kunth	AH	1			6	2
Aristida torta (Nees) Kunth	AH	99	62	1	34	24
Axonopus anceps (mez) Hitchc.	AH	76	52			16
Axonopus canescens (Nees) Pilg.	PH	18	28	8	57	2
Axonopus fissifolius (Raddi) Kuhlm.	AH		1		3	6
Axonopus flabelliformis Sw.	PH				1	
Axonopus sp.	PH	67	27	371	118	2
Echinolaena inflexa (Poir.) Chase	PH	99	161		1	3
Mesosetum rottboellioides (Kunth) Hitchc.	PH	64	143		23	3
Panicum cyanescens Nees es Trin.	PH		6			
Panicum micranthum Kunth	PH	168	82			44
Panicum stenodes Griseb.	AH	12	4			1
Paspalum lanciflorum Trin.	PH	1	224	45	216	1
Panicum nervosum Lam.	PH				1	
Raddiella esembeckii (Steud)Calderon & Söderström	PH	33	66	23	2	63
Schizachyrium sanguineum (Retz.) Alston.	AH		5			6
Schizachyrium tenerum (Nees) Kunth	AH					19
Sporobolus cubensis Hitchc.	PH	4	5			1
Thrasya trinitensis Mez	PH		1			
Trachypogon plumosum (H. & B.) Nees	PH	226	552	217	265	134
POLYGALACEAE						
Polygala adenophora DC.	AH	2				3

Table A1. (*continued*)

FAMILY Species	Life form*	Aeropuerto	Misión	Liworiwo	Torón	Disturbed savanna
Polygala appressa Benth.	PH	3				
Polygala glochidiata Kunth	AH		1			
Polygala hygrophila Kunth	PH		1			
Polygala longicaulis Kunth	AH		8			6
Polygala paniculata L.	AH					1
Polygala timotou Aubl.	AH	1	2			1
PROTEACEAE						
Roupala minima Steyerm.	F			1		
RUBIACEAE						
Borreria capitata (Ruiz & Pav.) DC.	F					1
Declieuxia fruticosa (Willd. ex Roem. & Schult.) Kuntze	F	8		19	65	14
Perama galioides (Kunth) Poir.	AH	24				3
Sabicea velutina Benth.	L					1
Sipanea galioides Wernham	F				17	6
SCROPHULARIACEAE						
Buchnera pallustris (Aublet) Sprengel	AH	3	2	1		1
SOLANACEAE						
Solanum campaniforme Roem. & Schult.	SH					1
VELLOZIACEAE						
Vellozia tubiflora (A. Rich.) Kunth	F				2	
XYRIDACEAE						
Xyris setigera F. Oliver	PH	1				

*AH: annual herb; PH: perennial herb; SH: shrub; F: fruticcose; L: liana or creeper.

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