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A Floristic Description of a Neotropical Coastal Savanna in Belize[1]

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ABSTRACT.—The diverse graminoid-dominated savannas of Central America remain poorly described. The flora and environment of a hyperseasonal coastal savanna near Sapodilla Lagoon, Stann Creek District, Belize were examined. Percent cover and frequency using plots and line transects were used to assess the community structure. We used non-metric multidimensional scaling and correlation to describe community-level variation and its environmental correlates. The flora consisted of 193 angiosperms, 2 gymnosperms, and 6 pteridophytes, and was dominated by graminoids. Species with the highest importance values were *Mesosetum filifolium*, *Paspalum pulchellum*, *Rhynchospora plumosa*, and *Rhynchospora barbata*. Woody species were scattered in dense clusters throughout the savanna, and were divided into a tall tree layer, dominated by *Pinus caribaea*, and a tree-palm-shrub layer, dominated by *Acoelorraphe wrightii* and *Byrsonima crassifolia*. Several large *Acoelorraphe wrightii*-dominated vernal pools were scattered about the landscape. Variation in species composition within the savanna correlated strongly with particular species (*Acoelorraphe wrightii* and *Paspalum pulchellum*), topography, cation exchange capacity, and copper concentration. Quantitative comparisons with another savanna studied in Belize show distinct differences in flora, structure, and dominance in spite of previously being classified as similar.

KEYWORDS.—*Acoelorraphe wrightii*; Belize; hyperseasonal savanna; flora; *Mesosetum filifolium*; non-metric multidimensional scaling; *Paspalum pulchellum*

INTRODUCTION

Savannas are among the most common ecosystems in the world. They are found on every continent except Antarctica, and cover nearly 20 percent of the earth's terrestrial surface (Cole 1986). In the Neotropics, savannas are particularly extensive, covering over 2 million km^2 (Sarmiento 1983a, Mistry 2000). Neotropical savannas have various densities of trees, palms and shrubs, but the perennial grasses and sedges are always the dominant vegetation (Beard 1953, Parsons 1955, Sarmiento 1992, Inchausti 1995). In spite of their global and regional importance, they remain poorly described.

Savannas are often at great risk of development. The relatively flat topography, ease of conversion to pasture or cropland, and accessibility to roads and highways, attract new agricultural and industrial development to lowland savannas. Projected global loss of savannas to various land uses is ~60 percent by 2100 (Sala *et al*. 2000). Therefore there is a great need for more in-depth analyses of these important ecological systems.

Savannas are widespread throughout Central America and Mexico, and thought to consist of two general types: *hyperseasonal* and *seasonal* (Beard 1953, Parsons 1955, Sarmiento 1983a, Bridgewater *et al.* 2002). Seasonal savannas, as proposed by Sarmiento (1983a), have an annual cycle with a predominantly dry season with frequent fires and a short rainy season. Hy-

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perseasonal savannas also have a predominant dry season, but during the rainy season there is an extended period of water-logging or flooding due to poor soil drainage. Nicaraguan and Honduran savannas cover nearly 11 million hectares along the Miskito Coast. Parsons (1955), in his early work on Nicaraguan savannas, showed that these vast savannas were actually mosaics, composed of gallery forests, palm thickets, swamps, and shrublands. Puig (1972) differentiated four kinds of savannas in southeastern Mexico: open tree savanna on upper topographic positions with poorly drained latisols, dense wood savannas, "Tasistales" (palm swamps), and "Encinares" (open woodlands of *Quercus oleoides).* Gómez Pompa (1973) identified another coastal savanna system in Mexico, which was dominated by the palm *Acoelorraphe wrightii* (Arecaceae). Similar variability of savannas has also been identified in Belize, Mexico's southern neighbor (Bourlière 1983, Bridgewater *et al.* 2002, Laughlin 2002, Woo 2002).

Belize lies just south of Mexico and east of Guatemala, and has a surface area of approximately 22,963 km^2 (Meerman & Sabido 2001). Rainfall in Belize varies from 1347 mm/year in the north to 4526 mm/year in the far south (Hartshorn *et al.* 1984). The majority of the landscape, stretching along the eastern Caribbean coastline and to the northwest, rises to just under 120 m, whereas in the west and southwest the elevation is for the most part between 850 m and 910 m in the Maya Mountains. There are many different community types in Belize including sub-tropical moist forest, inland marsh, sub-tropical deciduous forest, pine forest, and savanna.

The majority of the Belizean savannas are found in the lowlands and cover approximately 8.8 percent of the Belizean land surface (Meerman & Sabido 2001). They are mosaics that include broadleaf forests, oak woodlands, pine forests, and palm thickets (Parsons 1955, Sarmiento 1983a, Bridgewater *et al.* 2002). Meerman & Sabido (2001) distinguished two general types of savannas in Belize. The first type is *short-grass savanna with needle-leaved trees.* These are seasonal savannas with well-drained soils. Representing this group are the hilltop savannas of Mountain Pine Ridge in the Maya mountains and the interior lowland savannas known as "pine savanna", "pine ridge" and "pine forest". The second classification is the *short-grass savanna with shrubs* which is limited to the lowlands. This type is also known as "orchard savanna" or hyperseasonal savanna (Sarmiento 1983a, Woo 2002). A recent study of Belizean hyperseasonal savannas suggested an additional breakdown into *inland lowland hyperseasonal savanna* and *coastal lowland hyperseasonal savannas* (Woo 2002).

We described the flora of a coastal lowland hyperseasonal savanna in south central Belize, looked for relationships between vegetative composition and environmental parameters, and compared this coastal savanna to the mid-elevation savanna at Monkey Bay Biological Station (Woo 2002). The field methods used by Woo (2002) at the Monkey Bay Biological Station were replicated to ensure appropriate comparisons between these two intensively studied savannas.

Materials and Methods

Site Description

The study site is a hyperseasonal savanna, approximately 700 m by 250 m, located west of the All Pines region, in the Stann Creek District of Belize (Figure 1). There are widely scattered *Pinus caribaea, Byrsonima crassifolia* and *Curatella americana*, as well as small dense clusters of palms, pines, and broadleaf species. Six vernal pools are scattered around the savanna, the largest of which was 100 m across. Two of the pools have centers consisting of dense mats of *Eleocharis interstincta* and have standing water most of the year. The other pools are shallow with palms, sedges and grasses throughout, and have little to no water in them during the dry season. Evidence of standing water is also seen in the eastern section of the savanna; the grasses in this section have columns of mud approximately 15-25 cm high surrounding the

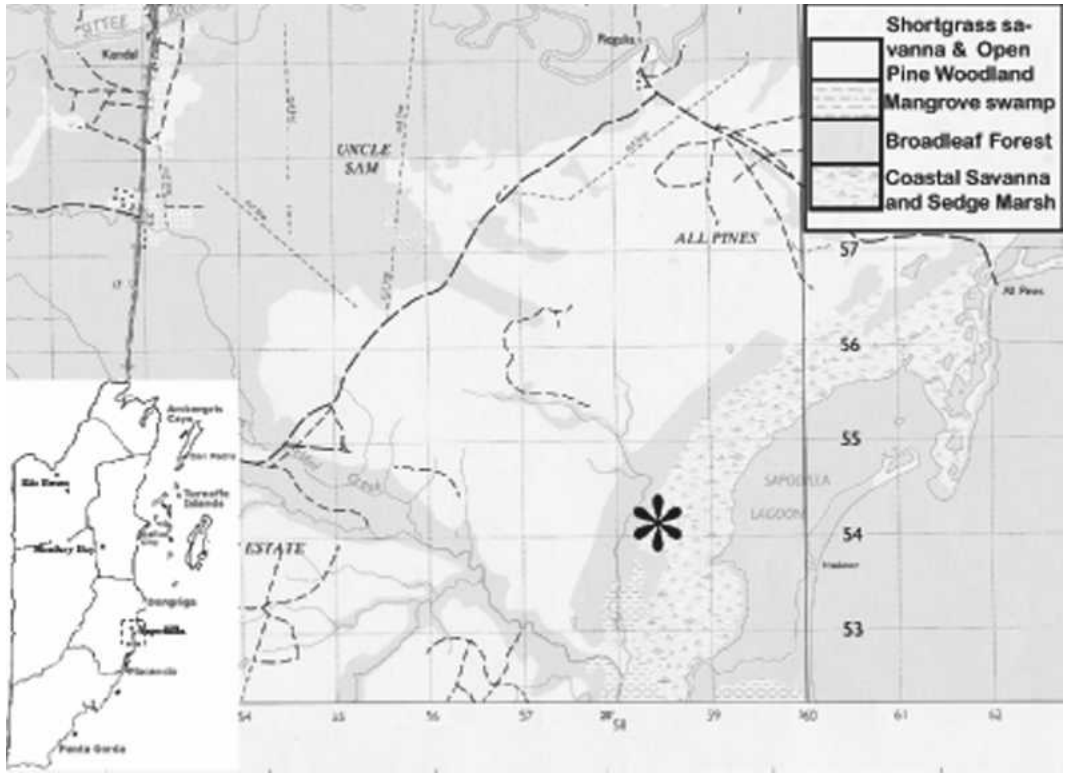

FIG. 1. Map of Belize and enlarged map of the Sapodilla Lagoon savanna site. Asterisks indicate the locations of the savannas. Topographic map extract from sheet 31/32 series E555 of Belize, Crown copyright 1993. Reproduced with the permission of the Controller of Her Majesty's Stationary Office.

base, and there are land crab burrows throughout this area.

Several types of plant communities surround the savanna. The northern side of the study site fades into open-pine woodland that persists for approximately 1 mile north of the open savanna. Beyond this the pines become less frequent as the elevation decreases and vegetation transforms into undescribed hyperseasonal savanna again. Low areas throughout these woodlands have vernal pools similar to the open savanna.

The western section is bounded by a slow moving creek and a mangrove swamp. Further west, the elevation rises and broadleaf evergreen forest predominates. West of this broadleaf ridge is a short stretch of pine forest and the All Pines savanna. The All Pines savanna is an extensive property of approximately 4452 ha, most of which is hyperseasonal savanna. Local hunters burn this extensive savanna almost yearly.

The southern section ends abruptly in a wall of evergreen broadleaf forest. To the southeast, the savanna integrates with this forest, over the course of a couple hundred meters. Finally the eastern section intermingles with palm and mangrove thickets, vernal pools, and transitions into mangrove swamp up to the edge of the mangrove forest bordering the Sapodilla Lagoon. This last area has standing water over vast portions after heavy rains and during the rainy season.

Data Collection

All data collection occurred in March, May and August 2003. The study site was prepared by marking a perimeter 15 m from the aforementioned boundaries, and establishing a reference line along a 120°

heading across the approximate center of the savanna (Figure 2). This point of reference line was divided into five 50 m sections. In each section, we established two plots at randomly selected distances northeast of the reference line and two plots at randomly selected distances southwest of the reference line. Each plot was oriented parallel to the reference line, and all plots were between 0 m and 119 m from the center reference line. In each plot corner a steel stake was permanently fixed and coordinates of the plot center were recorded with a global positioning unit (Farruggia 2004), available upon request. In each plot, six soil-core samples 4 cm in diameter were taken at each of three depths, 0-10 cm, 10-20 cm, and 30-40 cm for each plot (Figure 3). The six samples from each depth were combined, sealed and analyzed for potassium, magnesium, calcium, weak and strong bray, estimated nitrogen release, soil pH, hydrogen, cation exchange capacity, zinc, manganese, iron, copper, and percents of K, Mg, Ca, H, and organic matter (Citrus Research & Education Institute, Dangriga, Belize). Two soil profile pits were dug along the reference line, one in the east and one in the west. The approximate distance from the center of each plot to the nearest savanna edge was estimated by walking regular paces; this provided a good estimate of relative distances from the savanna edge. Topography, or relative elevation, was recorded by leveling using a transit between centers of plots as well as along the perimeter of the study site. A total of 56 environmental variables were recorded (18 soil characteristics at 3 depths, distance to edge, and relative elevation).

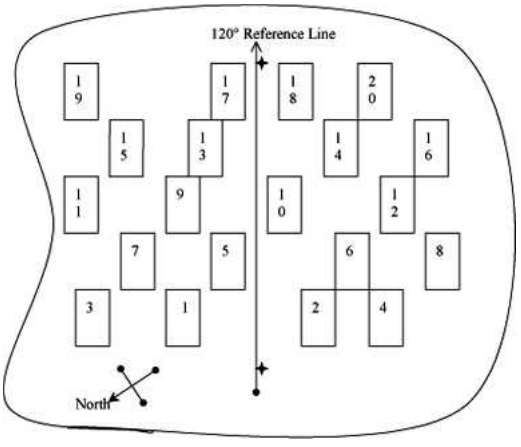

FIG. 2. Site schematic of main plot layout and point of reference line. The two black stars indicate locations of profile pits. Not to Scale

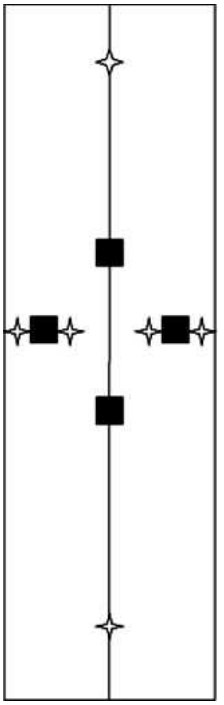

FIG. 3. Diagram of an individual 10 × 50 m main plot with four 1 × 1 m nested subplots for herbaceous cover, three horizontal 50 m transects for woody cover, and 6 points for soil cores (stars). Note: not to scale. Redrawn from Woo 2002.

Several measurements were made on the vegetation within each 10 × 50 m plot. Diameter at breast height (dbh) was measured for all trees, woody shrubs and palms greater than 1.5 m tall and ≥1cm dbh. For multi-stemmed shrubs all stems were measured. The line-intercept method (Gurevitch *et al*. 2002) was used to record the absolute cover of trees, palms and shrubs that intersected any of three parallel transects, each 50 m long, arranged along the sides and down the center of each main plot (Figure 3). For herbaceous species we established four 1 × 1 m subplots, two 2.5 m in from the midpoint of the edge transects and two along the center transect at 20 and

30 m. Percent cover for each species within each 1 × 1 m subplot was estimated visually using a modified Domin (McCune & Grace 2002) cover scale (<1, 1-5,6-10, 11-20, 21-40, 41-60, 61-80, 81-100%; Woo 2002). Plants which were found within the subplots but rooted outside were included in the cover estimates.

The entire savanna was inspected visually during each visit to identify any species that were not represented in the plots. This was carried out by walking approximately regularly spaced north-south transects across the entire site while scanning in an approximate 5 m radius. This was repeated along east-west transects. All additional species identified in these transects were added to the list of species identified in the plots to provide the flora for this savanna. Species were identified using Gentry (1993), Standley *et al.* (1946-77), Stevens *et al.* (2001), and Davidse *et al.* (1994) and confirmed with the collections at the W. S. Turrell Herbarium (MU) and Missouri Botanical Garden Herbarium (MO). Nomenclature follows that of Balick *et al.* (2000). Voucher specimens of all species found were deposited in the W. S. Turrell Herbarium (MU), and the Belize National Herbarium (BRH) in Belmopan, Belize. Species of Bromeliaceae and CITES-listed families Orchidaceae and Cycadaceae were documented using digital photography in lieu of collection.

Data Analysis

Statistical analyses of overall savanna characteristics, within-savanna variation and comparisons to other savannas were conducted using R computational software (R Development Core Team 2004) relying heavily on the vegan (Oksanen 2004) and the MASS packages (Venables & Ripley 2002) for community analyses. The R code can be found in Farruggia (2004) or is available upon request.

Overall Savanna Characteristics

The basal area and density of the woody species and palms was calculated using the dbh data, which was collected from all woody plants within the plots. The basal area for each species was calculated as the summation of all dbh records from all plots. The total area of the twenty main plots was one hectare so the units of the resulting values are cm^2/ha. The density of woody species and palms was calculated as the total number of individuals recorded in all main plots (i.e. individuals/ha).

Absolute cover for herbaceous species in each main plot was calculated by averaging each species' cover among subplots within each season, and then selecting the maximum cover for each species among all seasons. This resulted in a maximum percent cover for each species for that main plot, disregarding the seasonal differences in cover. For trees, shrubs, and palms the absolute cover data collected from the three main plot transect lines, estimated only in August, was summed among transects for each main plot. Cover for the woody and herbaceous species were then combined into one data set, and absolute frequency of species was calculated as the percentage of main plots where the species was present. Relative frequency and relative cover were calculated for each species *i* as the frequency or cover of species *i* divided by the sum of all species values. Species' importance values in this study are the averages of relative frequency plus relative cover times 100 (McCune & Grace 2002). Diversity was calculated in four ways: overall species richness, average species richness per plot, Simpson's index (Lande 1996), and the exponential form of Shannon's index (Peet 1974). Percentile confidence limits on importance values and diversity estimates were based on 10000 randomizations, resampling main plots with replacement (Davison & Hinkley 1997).

Variation within the Savanna–NMDS Ordination

Non-metric multidimensional scaling (NMDS) was used to compare main plots across the savanna. NMDS is a nonparametric dimension reduction technique which avoids the assumption of linear or unimodal response to an underlying gradient (McCune & Grace 2002). This proce-

dure is the most robust ordination analysis for community data (Grace *et al.* 2000). The general guidelines provided in McCune and Grace (2002) were followed. Species that were in only one main plot, i.e. ≤5 percent, were removed from our plot × species data matrix for the ordination analysis, as rare species have the potential to obscure general patterns in any ordination method. As the first step, we calculated the multivariate distances, or dissimilarities, between the species compositions of each plot. Oksanen (2004), McCune and Grace (2002) and Faith et al. (1987) recommend selecting a distance method that results in composition distances among plots being most strongly correlated with environmental distances among plots. On this basis we selected Bray-Curtis (Sorensen) distances. NMDS uses an iterative procedure to arrange all sites in multidimensional space, attempting to retain the compositional distances between each pair of plots. In doing so NMDS attempts to minimize the "stress", or the sum of all squared deviations between each pairwise distance and the distance in NMDS multivariate space. The graphical output is the display of these distances that result from minimizing stress and thereby attempting to retain the original distances.

The ability of NMDS to retain original distances and reduce stress depends on the number of multivariate dimensions, or axes, selected by the user (McCune and Grace 2002), with each additional dimension allowing additional stress reduction. The number of dimensions should be based on (i) interpretability of the resulting dimensions, (ii) the magnitude of the stress reduction associated with each dimension, and (iii) statistical significance (Kruskal 1964, McCune and Grace 2002). Adding an additional dimension is unwarranted if the additional stress reduction is relatively small. Following McCune and Grace (2002) the number of dimensions for the study was chosen by conducting stepwise analyses from six dimensions down to one dimension, seeking low stress. Acceptable stress levels for ecological community analysis are below 20 percent, and below 10 percent there is virtually no risk of false inference (Kruskal 1964, Clarke 1993, McCune & Grace 2002). As with any iterative solution, NMDS stress reduction can occasionally get trapped in a local minimum rather than find a global minimum. Our NMDS procedure (Oksanen 2004) has two ways to avoid this pitfall. First, its initial solution is the classic multidimensional scaling, also known as principal coordinate analysis, then it iterates to find a solution with lower stress and retains that configuration. It then selects another, random, solution and iterates to find a configuration with the lowest stress. The procedure retains the better of these two configurations, and then proceeds to the next random initial solution and iterative procedure. It repeats this a total of twenty times, the default setting in the Vegan package, each time retaining the best solution. In addition, under the *procrustes* function, it tests the stability of the final solution by comparing correlations among solutions. It then retains the solution with the lowest stress that is also relatively stable. To test the significance of each number of axes, stress in the observed data was compared to stress from NMDS ordinations of 1000 randomized plot × species percent cover data sets. The test randomized (rearranged) observed species abundances among plots for each species so that the observed abundances were all preserved, but rearranged into different plots. The *P* value was calculated as (number of stress values from randomized data ≤ the observed minimum stress + 1)/(1000) (McCune and Grace 2002).Final configuration is modified by rotating the axes so the largest distance between two plots is on the first axis, second axis has next largest and so on. This being said, NMDS axes are arbitrary; only the configuration among plots is important. Therefore we do not present any correlations between NMDS axes and environmental variables. Rather, we used vector correlations, between an environmental variable and pairs of NMDS axes, to find species-environment relationships. Vector correlations use plots as replicates and maximizes the correlation between the multidimensional configuration scores and the plot values of an environmental vari-

able. Given the large number of possible correlations and also the overly conservative nature of Bonferroni adjustments, a reasonably conservative cutoff of $P \leq 0.01$ was selected to identify relevant correlations. Relationships between NMDS axis scores and both particular species and environmental characteristics were tested with Spearman rank correlations were used with Bonferroni adjustments.

Comparison to another savanna

We compared this savanna to the nearby Monkey Bay Savanna using the data provided in Woo (2002). Jaccard's similarity index was used to compare the floras. Where quantitative data was available for species, growth forms, and diversity, comparisons to the confidence intervals from the above analyses were made.

RESULTS

Overall Savanna Characteristics

Flora.—The savanna was comprised of 193 angiosperms, 2 gymnosperms, and 6 pteridophytes (Table 1). The herbaceous layer was made up of 119 forb and graminoid species, representing 58 percent of the species. The graminoids included 33 species from the Poaceae and 27 species from the Cyperaceae. The 59 forb species were from 22 different families, and another 23 percent of the flora was made up of woody species, 15 trees and 31 shrubs. The remaining species recorded were *Acoelorraphe wrightii* (Palmae), epiphytic orchids and bromeliads, vines, ferns, and parasitic plants. Highest densities of woody species, ferns, epiphytes and vines were found in dense palm thickets, pine groves and broadleaf clusters. The N-S and E-W transects revealed that the vertical vegetation structure of the savanna consisted of 5 layers: tall-tree (>6 m), tree (6-3 m), shrub-palm (3-1.5 m), herbaceous (<1.5 m), and surface. The tall-tree layer was made up of solely *Pinus caribaea*, which was scattered evenly throughout the savanna, had a density of 10 trees per hectare, and a basal area of 1.8 m/ha (Table 2). The tree layer primarily consisted of *Byrsonima crassifolia*, found in 60 percent of the plots with a basal area of 0.45 m^2/ha. This layer also included *Curatella americana* and *Chrysobalanus icaco*, species with the next two highest basal areas. Species representing the palm-shrub layer were principally evergreen and semi-evergreen species. Unlike the tree and tall-tree layers, this layer was mainly limited to small dense clusters scattered around the savanna. Vernal pools contained the highest densities of *Acoelorraphe wrightii*, the most dense species in this category with 99 individuals/ha. The herbaceous layer was continuous throughout the entire area, with some discontinuity in the palm-shrub thickets. The surface layer was discontinuous and was made up of *Lycopodiella caroliniana*, *Drosera capillaris*, and cyanobacterial mats found around and within palm pools.

Main plot analyses

Average main plot richness was 23.55 species (95% CI: 20.6-26.05), ranging from 5 to 36 species. Simpson's diversity was 0.81 (95% CI: 0.75-0.85), and the exponential Shannon's was 8.34 species equivalents (95% CI: 7.78-9.85). A total of 90 species were recorded within the plots. There are two species which are dominant based on the calculated importance values. The most important species calculated from transects and subplots was the grass *Mesosetum filifolium*, which had an importance value of only 14.42 (95% CI: 12.17-16.58; Table 3). The next most important species was the grass *Paspalum pulchellum*, which had an importance value of 9.72 (95%CI: 8.09-11.56; Table 3). The remaining dominant species, those taxa with importance values $\geq$2, were grasses (*Mesosetum blakei*, *Dichanthelium acuminatum*, *Aristida purpurascens*), sedges (*Rhynchospora plumosa*, *Rhynchospora tenuis*, *Rhynchospora globosa*, *Rhynchospora barbata*), a parasitic vine (*Cassytha filiformis*), a palm (*Acoelorraphe wrightii*), and two trees (*Byrsonima crassifolia*, *Pinus caribaea*).

Variation within the savanna

Elevation of the main plots varied from approximately sea level (in one of the ver-

TABLE 1. Species list for Sapodilla Lagoon Savanna.

FERNS
- Blechnaceae
  - *Blechnum serrulatum* Rich.
- Dennstaedtiaceae
  - *Lindsaea lancea* (L.) Bedd.
  - *Pteridium caudatum* (L.) Maxon
- Lycopodiaceae
  - *Lycopodiella caroliniana* (L.) Pic. Serm.
  - *Lycopodiella cernua* (L.) Pic. Serm.

GYMNOSPERMS
- Pinaceae
  - *Pinus caribaea* Morelet var. *hondurensis* (Seneclauze) W.H. Barrett & Golfari
- Zamiaceae
  - *Zamia polymorpha* D. W. Stev., A. Moretti & L. Gaudio

ANGIOSPERMS
- Anacardiaceae
  - *Metopium brownei* (Jacq.) Urb.
- Annonaceae
  - *Xylopia fructescens* Aubl.
- Apocynaceae
  - *Mandevilla subsagitatta* (Ruiz & Pav.) Woodson
  - *Rhabdadenia biflora* (Jacq.) Müll. Arg.
- Araceae
  - *Syngonium angustatum* Schott
- Asteraceae
  - *Calea jamaicensis* (L.) L.
  - *Calea longipedicellata* B.L. Rob. & Greenm.
- Bignoniaceae
  - *Amphitecna breedloveii* A.H. Gentry
- Bromeliadaceae
  - *Tillandsia spp.*
- Burmanniaceae
  - *Burmannia capitata* (Walter ex J.F. Gmel.) Mart.
- Chrysobalanaceae
  - *Chrysobalanus icaco* L.
  - *Hirtella racemosa* Lam.
- Clusiacaeae
  - *Symphonia globularis* L.f.
- Combretaceae
  - *Conocarpus erecta* L.
- Convolvulaceae
  - *Evolvulus sericeus* Sw.
  - *Merremia aturensis* (H.B.K.) Hallier f.
- Cyperaceae
  - *Bulbostylis junciformis* (H.B.K.) C.B. Clarke
  - *Cyperus haspan* L.
  - *Eleocharis geniculata* (L.) Roem. & Schult.
  - *Eleocharis interstincta* (Vahl) Roem. & Schult.
  - *Fuirena camptotricha* C. Wright
  - *Lagenocarpus guianensis* Nees
  - *Rhynchospora barbata* (Vahl.) Kunth
  - *Rhynchospora cephalotes* (L.) Vahl
  - *Rhynchospora chapmanii* M.A. Curtis
  - *Rhynchospora curvula* Griesb.
  - *Rhynchospora elliottii* A. Dietrich
  - *Rhynchospora fasicularis* (Michx.) Vahl. subsp. *fascicularis*
  - *Rhynchospora filifolia* A. Gray
  - *Rhynchospora globosa* (H.B.K.) Roem. & Schult.
  - *Rhynchospora globularis* (Chapm.) Small var. *recognita* Gale
  - *Rhynchospora harperi* Small
  - *Rhynchospora holoschoenoides* (Rich.) Herter
  - *Rhynchospora oligantha* A. Gray var. *oligantha*
  - *Rhynchospora plumosa* Elliott
  - *Rhynchospora pusilla* Chapm. ex M.A. Curtis
  - *Rhynchospora rugosa* (Vahl) Gale
  - *Rhynchospora tenuis* Link
  - *Rhynchospora* sp.
  - *Scleria bracteata* Cav.
  - *Scleria ciliata* Michx.
  - *Scleria georgiana* Core
  - *Scleria tenella* Kunth
- Dilleniaceae
  - *Curatella americana* L.
  - *Davilla kunthii* A. St. Hil.
- Dioscoreaceae
  - *Dioscorea matagalpensis* Uline?
- Droseraceae
  - *Drosera capillaris* Poir.
- Eriocaulaceae
  - *Eriocaulon* sp.
- Erythroxylaceae
  - *Erythroxylum guatamalense* Lundell
- Euphorbiaceae
  - *Pera arborea* Mutis
- Fabaceae
  - *Aeschynomene histrix* Poir. var. *incana* (Vogel) Benth.
  - *Aeschynomene paniculata* Willd. ex Vogel
  - *Chamaecrista desvauxii* (Collad.) Killip var. *mollissima* (Benth.) H.S. Irwin & Barneby
  - *Chamaecrista diphylla* (L.) Greene
  - *Chamaecrista hispidula* (Vahl) H.S. Irwin & Barneby
  - *Chamaecrista kunthiana* (Schltdl. & Cham.) H.S. Irwin & Barneby
  - *Chamaecrista nictitans* (L.) Moench
  - *Clitoria falcata* Lam.
  - *Desmodium barbatum* (L.) Benth. & Oerst.
  - *Gliricidia* sp.
  - *Inga pinetorum* Pittier
  - *Macroptilium gracile* (Poepp. ex Benth.) Urb.
  - *Senna hayesiana* (Britton & Rose) H.S. Irwin & Barneby
  - *Stylosanthes guianensis* (Aubl.) Sw.
  - *Tephrosia nitens* Benth.
  - *Zornia reticulata* Sm.
- Fagaceae
  - *Quercus oleoides* Schltdl. & Cham.

TABLE 1. Continued.

Gentianaceae
Coutoubea spicata Aubl.
Schultesia guianensis (Griesb.) Benth. & Hook.f. ex Hemsl.
Iridaceae
Alophia spicata (Loes.) Goldblatt
Lamiaceae
Hyptis atrorubens Poit.
Hyptis brevipes Poit.
Hyptis conferta Pohl ex Benth.
Hyptis lantanifolia Poit.
Marsypianthes chamaedrys (Vahl) Kuntze
Lauraceae
Cassytha filiformis L.
Lentibulariaceae
Utricularia hispida Lam.
Utricularia juncea Vahl
Utricularia subulata L.
Loranthaceae
Oryctanthus cordifolius (C. Presl) Urb.
Oryctanthus spicatus (Jacq.) Eichler
Struthanthus cassythoides Millsp. ex Standl.
Malphigiaceae
Byrsonima crassifolia (L.) H.B.K.
Malvaceae
Sida linifolia Cav.
Melastomataceae
Acisanthera crassipies (Naudin) Wurdack
Acisanthera quadrata Pers.
Clidemia capitellata (Bonpl.) D. Don
Clidemia novemnervia (DC) Triana
Clidemia sericea D. Don
Miconia albicans (Sw.) Triana
Miconia ciliata (Rich.) DC
Nepsera aquatica (Aubl.) Naudin
Tococa guianensis Aubl.
Myricaceae
Myrica cerifera L.
Myrsinaceae
Myrsine floridana A. DC
Myrtaceae
Chamguava gentlei (Lundell) Landrum var. *gentlei*
Myrcia splendens (Sw.) DC
Psidium guineense Sw.
Ochnaceae
Ouratea nitida (Sw.) Engl.
Sauvagesia erecta L.
Onagraceae
Ludwigia octovalvis (Jacq.) P.H. Raven
Orchidaceae
Brassavola nodosa (L.) Lindl.
Spp. Many Sterile
Oxalidaceae
Oxalis frutescens L. subsp. *angustifolia* (H.B.K.) Lourteig
Palmae
Acoelorraphe wrightii (Griesb. & H. Wendl.) H. Wendl. ex Becc.
Passifloraceae
Passiflora foetida L.
Poaceae
Andropogon gerardii Vitman
Andropogon glomeratus (Walter) Britton, Sterns & Poggenb.
Andropogon leucostachyus H.B.K
Andropogon virginicus L.
Aristida purpurascens Poir. var. *tenuspica* (Hitchc.) Allred
Aristida tincta Trin. & Rupr.
Axonopus aureus P. Beauv.
Axonopus purpusii (Mez) Chase
Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark var. *ramosum* (Griesb.) Davidse
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *longiligulatum* (Nash) Gould & C.A. Clark
Dichanthelium strigosum (Muhl. ex Elliott) Freckmann var. *strigosum*
Dichanthelium sp.
Echinolaena gracilis Swallen
Eragrostis elliottii S. Watson
Hypogynium virgatum (Desv.) Dandy
Leptochloa virgata (L.) P. Beauv.
Leptocoryphium lanatum (H.B.K.) Nees
Mesosetum blakei Swallen
Mesosetum filifolium F.T. Hubb.
Panicum caricoides Nees ex Trin.
Panicum laxum Sw.
Panicum stenodes Griesb.
Panicum tenerum Beyr. ex Trin.
Panicum tuerckheimii Hack.
Paspalum pectinatum Nees ex Trin.
Paspalum pulchellum Kunth
Paspalum serpentinum Hochst. ex Steud.
Paspalum sp.
Sacciolepis myuros (Lam.) Chase
Schizachyrium sanguineum (Sw.) Nees ex Buse
Thrasya campylostachya (Hack.) Chase
Trachypogon spicatus (L.f.) Kuntze
Tripsacum latifolium Hitchc.
Polygalaceae
Polygala aparinoides Hook. & Arn.
Polygala hygrophila H.B.K.
Polygala incarnata L.
Polygala leptocaulis Torr. & A. Gray
Polygala longicaulis H.B.K.
Polygala variablis H.B.K.
Polygonaceae
Coccoloba sp.
Rhizophoraceae
Cassipourea elliptica (Sw.) Poir

TABLE 1. Continued.

Rubiaceae
Amaioua corymbosa H.B.K.
Chomelia protracta (Bartl. ex DC) Standl.
Coccocypselum guianense (Aubl.) K. Schum.
Diodia apiculata (Willd. ex Roem. & Schult.) K. Schum.
Guettarda combsii Urb.
Palicourea triphylla DC
Psychotria fruticetorum Standl.
Psychotria graciliflora Benth.
Psychotria hoffmannseggiana (Willd. ex Roem. & Schult.) Müll. Arg.
Psychotria nervosa Sw.
Psychotria poeppigiana Müll. Ar.
Richardia scabra L.
Spermacocce suaveolens (G. Mey.) Kuntze
Spermacocce tenuior L.
Sapindaceae
Matayba apetala (Macfad.) Radlk.
Sapotaceae
Chrysophyllum cainito L.
Scrophulariaceae
Agalinis harperi Pennell
Angelonia ciliaris B.L. Rob.
Bacopa lacertosa Standl.
Buchnera pusilla H.B.K.
Simaroubaceae
Simarouba glauca DC
Smilacaceae
Smilax velutina Killip & C.V. Morton
Smilax sp.
Solanaceae
Schwenkia americana L.
Sterculiaceae
Melochia nodiflora Sw.
Symplocaceae
Symplocos martinicensis Jacq.
Turneraceae
Piriqueta cistoides (L.) Griseb.
Turnera aromatica Arbo
Turnera pumilea L.
Verbenaceae
Citharexylum caudatum L.
Tamonea spicata Aubl.
Viscaceae
Phoradendron quadrangulare (H.B.K.) Krug & Urb.
Xyridaceae
Xyris ambigua Beyr. ex Kunth.
Xyris jupicai Rich.

nal pools), to 1.1 m along the northern edge, and on a ridge in the western section. Based on two soil profile pits (Figure 2), We found that approximately 0.6 m of mixed sand and organic material covered the underlying clay layer in the western sample, whereas in the eastern sample approximately 0.1 m of sand with very little organic material covered the clay layer. Iron oxidation (orange and red stained soils) accompanied the shallow the clay layer. A summary of the soil characteristics is published in Farruggia (2004).

Three NMDS dimensions or axes were identified using our criteria (stress = 6.07%; $P = 0.004$). This stress level suggests that the variation was well described (McCune & Grace 2002), and Spearman rank correlation between the original the Bray-Curtis distance matrix and the NMDS configuration showed that most of the variation in the original data was explained by the three dimensional NMDS ordination (Spearman $P = 0.936$).

The ordination revealed highly significant variation among plots in the importance of five species: *Acoelorraphe wrightii, Paspalum pulchellum, Mesosetum filifolium, Rhynchospora globosa* and *Xyris jupicai* (Figures 4, 5; Tables 4, 5). Soil variables, medium soil layer Copper (MCu), medium layer cation exchange (MCEC), and medium layer hydrogen (MH) were positively though weakly correlated with the *A. wrightii* gradient (Figure 4). Main plot #6 was located at the end of the *A. wrightii* gradient and had a monotypic cyperaceous center area of *Eleocharis interstincta* and the highest density of palms recorded in the savanna, making it dissimilar to all of the other main plots. MCEC and MH, in addition to shallow layer Phosphorus (SWBray), deep layer Magnesium (DMg), and deep layer cation exchange capacity (DCEC), were negatively correlated with the *Paspalum pulchellum* gradient, whereas topography showed strong positive correlation with the *P. pulchellum* gradient. The configuration associated with the third axis revealed a gradient represented by the most important species in the savanna, *Mesosetum filifolium*, and another by *Rhynchospora globosa* and *Xyris jupicai* (Figure 5). The *M. filifolium* had no corresponding environmental characteristic supporting it; however, topography was negatively related to *R. globosa* and *X. jupicai.*

TABLE 2. Woody species frequency, density and basal area.

Species	Total # of individuals	Frequency (percent of plots)	Density (trees/ha)	Ba/ha
Pinus caribaea	10	25	10	1.80
Curatella americana	5	15	5	0.01
Byrsonima crassifolia	55	60	55	0.45
Acoelorraphe wrightii	99	65	99	6.87
Erythroxylum guatamalense	5	15	5	0.00
Citharexylum caudatum	2	10	2	0.00
Chrysobalanus icaco	7	5	7	0.23
Myrsine floridana	5	10	5	0.02
Amphitecna breedlovei	8	10	8	0.01
Symplocos martinicensis	3	10	3	0.01
Chomelia protracta	4	5	4	0.00
Simarouba glauca	1	5	1	0.00
Symphonia globularis	2	10	2	0.01
Pera arborea	2	5	2	0.02
Inga pinetorum	1	5	1	0.01
Ouratea nitida	4	5	4	0.00
Cassipourea elliptica	3	5	3	0.01
Guettarda combsii	2	5	2	0.00
Matayba apetala	1	5	1	0.00
Coccoloba sp.	3	5	3	0.00
Psychotria graciliflora	4	5	4	0.02

Comparison between savannas

The Sapodilla savanna differed substantially from the Monkey Bay savanna (Woo 2002) in its floristic composition, woody species abundances, and growth form composition, but species richness differed little. Monkey Bay and Sapodilla shared only 26 percent of their flora (Jaccard Index of Similarity, J_S = 0.26). The flora of the Monkey Bay savanna (Woo 2002) contained 46 species that were not recorded for the Sapodilla savanna. In contrast there were 125 species unique to the Sapodilla savanna.

Composition and density of the woody component also differed among the two savannas. Woody species were well represented at the Monkey Bay savanna, comprising 40 percent of the total flora. Woo (2002) recorded dbh for all trees and shrubs with ≥5 cm dbh, which included six of the 33 woody species found there. She found there was a total basal area of 0.51 m^2/ha. The highest density she recorded was for *A. wrightii*, 20.2 individuals/ha and *Pinus caribaea* had a density of 14.3 individuals/ha. In the Sapodilla savanna the total basal area of the woody species with dbh ≥1 cm was 9.46 m^2/ha, for those individuals ≥5 cm it was 8.64 m^2/ha. The basal area was mainly composed of *A. wrightii* with a basal area of 6.46 m^2/ha, and a density of 99 individuals/ha. The next two highest density species at Sapodilla were *P. caribaea* with 10 individuals/ha and *B. crassifolia* with 7 individuals/ha. The woody component of Sapodilla's flora was 23 percent of the total.

These savannas also differed in their distributions of growth forms (Table 6). The total number of herbaceous species found in the Sapodilla savanna was more than twice that of the Monkey Bay site. Nonetheless, the herbaceous floras of both Monkey Bay and Sapodilla were composed of half graminoids and half forbs. Graminoids at both the Monkey Bay savanna and Sapodilla Lagoon savannas were divided evenly between Poaceae and Cyperaceae.

Woo (2002) reported diversity at the Monkey Bay savanna, using the average richness per plot. The results were similar between the two sites (Monkey Bay: average = 26.1; 95% CI: 19.4, 32.8; Sapodilla: average = 23.55; 95% CI: 20.6, 26.05).

TABLE 3. Species relative cover, relative frequency, and importance values with 95 percent confidence limits. Calculated from main plot and transect cover data.

Taxa	Rel cover	Rel freq	IV	Lwr 95% CI	Upr 95% CI
Mesosetum filifolium	24.82	4.04	14.43	12.17	16.58
Paspalum pulchellum	15.41	4.04	9.73	8.09	11.56
Rhynchospora plumosa	11.57	4.04	7.80	6.65	8.99
Rhynchospora barbata	7.10	4.04	5.57	4.41	6.87
Mesosetum blakei	4.53	2.77	3.65	2.25	5.17
Cassytha filiformis	2.96	4.04	3.50	3.16	3.85
Dichanthelium acuminatum	3.09	3.40	3.25	2.36	3.99
Byrsonima crassifolia	1.82	4.04	2.93	2.44	3.37
Acoelorraphe wrightii	2.35	3.19	2.77	1.86	3.92
Rhynchospora tenuis	2.55	2.98	2.76	1.91	3.46
Rhynchospora globosa	4.45	0.85	2.65	0.31	5.42
Pinus caribaea	2.47	2.13	2.30	1.01	3.70
Aristida purpurascens	0.83	3.19	2.01	1.48	2.59
Lycopodiella caroliniana	1.83	2.13	1.98	1.11	3.01
Drosera capillaris	0.34	3.40	1.87	1.47	2.22
Hypogynium virgatum	1.14	2.34	1.74	1.06	2.43
Paspalum serpentinum	1.83	1.28	1.55	0.57	3.05
Xyris jupicai	0.90	2.13	1.52	0.86	2.16
Scleria georgiana	0.35	2.55	1.45	0.96	1.91
Myrica cerifera	0.13	2.55	1.34	0.91	1.78
Axonopus purpusii	0.85	1.70	1.28	0.61	1.94
Acisanthera quadrata	0.17	2.34	1.25	0.77	1.73
Eleocharis interstincta	2.23	0.21	1.22	0.00	3.96
Sauvagesia erecta	0.19	2.13	1.16	0.70	1.55
Curatella americana	0.23	1.91	1.07	0.53	1.59
Dichanthelium strigosum	0.34	1.70	1.02	0.51	1.57
Rhynchospora curvula	0.96	1.06	1.01	0.25	1.92
Chamaecrista nictitans	0.37	1.06	0.71	0.23	1.37
Dichanthelium aciculare	0.10	1.28	0.69	0.24	1.14
Merremia aturensis	0.02	1.28	0.65	0.22	1.08
Polygala spp.	0.02	1.28	0.65	0.22	1.13
Utricularia subulata	0.03	1.28	0.65	0.22	1.11
Angelonia ciliaris	0.17	1.06	0.62	0.22	1.16
Andropogon leucostachyus	0.36	0.85	0.61	0.11	1.19
Evolvulus sericeus	0.05	1.06	0.56	0.21	1.01
Utricularia hispida	0.03	1.06	0.56	0.21	0.97
Leptocoryphium lanatum	0.27	0.85	0.56	0.12	1.08
Panicum tenerum	0.27	0.85	0.55	0.11	1.09
Thrasya campylostachya	0.15	0.85	0.50	0.12	0.97
Erythroxylum guatamalense	0.14	0.85	0.49	0.11	0.92
Piriqueta cistoides	0.05	0.85	0.46	0.11	0.85
Chomelia protracta	0.26	0.64	0.45	0.00	0.95
Trachypogon spicatus	0.23	0.64	0.45	0.00	1.01
Chamaecrista kunthiana	0.06	0.85	0.44	0.11	0.86
Clidemia sp.	0.02	0.85	0.44	0.11	0.82
Gliricidia sp.	0.04	0.85	0.44	0.11	0.83
Burmannia capitata	0.02	0.85	0.44	0.10	0.90
Rhynchospora rugosa	0.20	0.64	0.42	0.00	0.90
Melochia nodiflora	0.02	0.64	0.33	0.00	0.70
Cassipourea elliptica	0.07	0.43	0.25	0.00	0.60
Clidemia sericea	0.07	0.43	0.25	0.00	0.65
Myrsine floridana	0.07	0.43	0.25	0.00	0.59
Passiflora foetida	0.07	0.43	0.25	0.00	0.58
Rhynchospora chapmanii	0.07	0.43	0.25	0.00	0.61

TABLE 3. Continued.

Taxa	Rel cover	Rel freq	IV	Lwr 95% CI	Upr 95% CI
Calea longipedicellata	0.04	0.43	0.23	0.00	0.58
Chrysobalanus icaco	0.25	0.21	0.23	0.00	0.71
Ouratea nitida	0.01	0.43	0.23	0.00	0.57
Schwenkia americana	0.04	0.43	0.23	0.00	0.61
Chamaecrista diphylla	0.02	0.43	0.22	0.00	0.56
Chamaecrista desvauxii	0.14	0.21	0.18	0.00	0.55
Coccoloba sp.	0.10	0.21	0.16	0.00	0.45
Guettarda combsii	0.08	0.21	0.15	0.00	0.43
Symphonia globularis	0.08	0.21	0.15	0.00	0.43
Bulbostylis junciformis	0.07	0.21	0.14	0.00	0.44
Inga pinetorum	0.06	0.21	0.14	0.00	0.40
Pera arborea	0.07	0.21	0.14	0.00	0.41
Smilax sp.	0.06	0.21	0.14	0.00	0.41
Rhynchospora sp.	0.04	0.21	0.13	0.00	0.40
Simarouba glauca	0.05	0.21	0.13	0.00	0.39
Amaioua corymbosa	0.02	0.21	0.12	0.00	0.34
Cyperus rotundus	0.04	0.21	0.12	0.00	0.40
Hirtella racemosa	0.04	0.21	0.12	0.00	0.37
Macroptillium gracile	0.04	0.21	0.12	0.00	0.39
Scleria tenella	0.02	0.21	0.12	0.00	0.38
Spermacoce suaveolens	0.02	0.21	0.12	0.00	0.34
Zamia polymorpha	0.05	0.21	0.12	0.00	0.40
Blechnum serrulatum	0.02	0.21	0.11	0.00	0.37
Buchnera pusilla	0.00	0.21	0.11	0.00	0.36
Chamguava gentlei	0.00	0.21	0.11	0.00	0.33
Clidemia novemnervia	0.01	0.21	0.11	0.00	0.32
Paspalum pectinatum	0.00	0.21	0.11	0.00	0.33
Tamonea spicata	0.00	0.21	0.11	0.00	0.35
Unknown 1	0.00	0.21	0.11	0.00	0.33
Unknown 3	0.00	0.21	0.11	0.00	0.34
Sum	100.00	100.00			

DISCUSSION

The floristic composition recorded at the Sapodilla Lagoon savanna shares characteristics of savanna ecosystems in the Neotropics (Parsons 1955, Taylor 1963, Sarmiento & Monasterio1975, Sarmiento 1983a, Medina & Silva1990, Furley 1997, Woo 2002). Graminoid dominance in both species diversity and percent cover was an expected result from this study. In addition, two of the most common tree species at Sapodilla, *Byrsonima crassifolia* and *Curatella americana*, are considered indicator species for Neotropical savannas (Lenthal *et al.* 1999, Huber 1987). The site had low basal area and percent cover of woody species, typical for neotropical savannas (Beard 1953). The presence of palm pools was also recorded in descriptions of the Nicaraguan Miskito Coast (Parsons 1955), as well as savannas described by Puig (1972) in Mexico, Bridgewater *et al*. (2002) in northern Belize, and throughout lowland savannas of Belize (Meerman & Sabido 2001). *Acoelorraphe wrightii*, the primary element of the palm pool, is a common component of all the lowland hyperseasonal savannas throughout Belize.

Soil conditions at Sapodilla are also typical of the Yucatan Peninsula, as reported in Hartshorn *et al.* (1984). The underlying clays appear impenetrable to water, so saturation of the coarse sandy soils above occurs rather quickly during a heavy rain. The Sapodilla savanna shows evidence for heavy flooding during rain events. The palm pools, when full of water, contain extensive cyanobacterial mats. From September through December the water in the

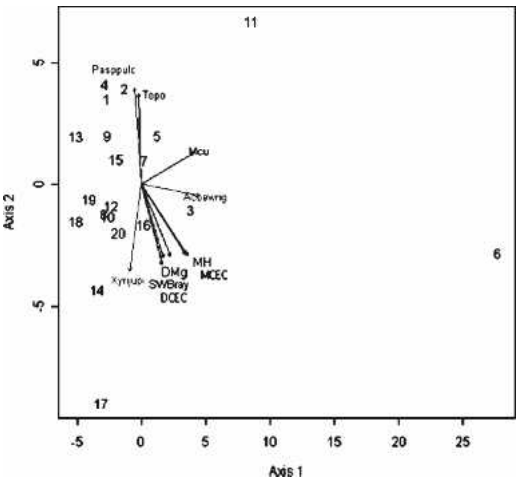

FIG. 4. First and second axes in the ordination. Numbers represent the main plots seen in the site map (Figure 2). Arrows are significant gradient vectors correlated with plots. Values in Table 4 are the correlation coefficients and level of significance for the vectors shown in the ordination. Special notation on vectors: *Paspalum pulchellum* (Pasppulc); *Acoelorraphe wrightii* (Acoewrig); *Xyris jupicai* (Xyrijupi); Topography (Topo); Medium Layer Cation Exchange Capacity (MCEC); Medium Layer Copper (Mcu); Medium Layer Hydrogen (MH); Shallow Layer Weak Bray (SWBray); Deep Layer Cation Exchange Capacity (DCEC); Deep Layer Magnesium (DMg).

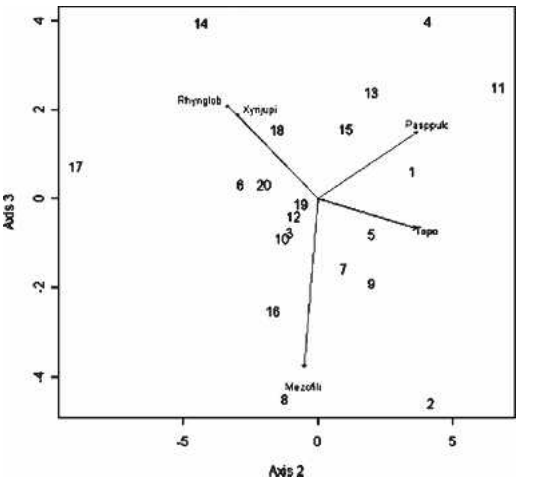

FIG. 5. Second and third axes in the ordination. Numbers represent the main plots seen in the site map (Figure 2). Arrows are significant gradient vectors correlated with plots. Values in Table 5 are the correlation coefficients and level of significance for the vectors shown in the ordination. Special notation on the vectors: *Rhynchospora globosa* (Rhynglob); *Xyris jupicai* (Xyrijupi); *Paspalum pulchellum* (Pasppulc); *Mesosetum filifolium* (Mezofili); Topography (Topo).

TABLE 4. Vector correlations of species and environmental characteristics with NMDS Axes 1 & 2.

Species	r^2	P
Paspalum pulchellum	0.63	0.001
Acoelorraphe wrightii	0.85	0.001
Xyris jupicai	0.54	0.001
Env	r^2	P
Topography	0.53	0.001
Shallow layer weak Bray	0.56	0.005
Medium layer Copper	0.73	0.001
Medium layer cation exchange capacity	0.87	0.005
Medium layer Hydrogen	0.80	0.002
Deep layer cation exchange capacity	0.56	0.003
Deep layer Magnesium	0.48	0.001

largest pool is continuous with the flooded southeastern section of the savanna. During the dry months, the impenetrable clay layer prevents ground water from rising upward, limiting water availability for most of the savanna, whereas palm pools remain quite moist throughout the dry season. Meerman and Sabido (2001) stated that palm pools remain moist not simply because they retain water but because of water moving upward through cracks in the clay layer.

Compositional differences in the NMDS ordination highlighted several distinct features. The palm pools differ from the drier sites, having high cover of both sedges and palms. *Rhynchospora globosa* (Cyperaceae) was the most dominant species only in plot 17 and grew to approximately 1.5 m tall. There was little similarity between this plot and others throughout the savanna; most others had a graminoid layer that grew only to 1 m at most. This difference may be due to its close proximity to another large palm pool; there was no evidence for extended flooding as seen in palm pools, but soil moistures may be higher in this area due to the palm pool. Another feature was seen in Plot 11, located in the pine woodland on the northern side, was composed mainly of the dominant graminoid layer, but there were far fewer sedges and an increased number of broadleaf and palm clusters. The *Mesosetum filifolium* gradient

TABLE 5. Vector correlations of species and environmental characteristics with NMDS Axes 2 & 3.

Species	r^2	*P*
Mesosetum filifolium	0.59	<0.001
Paspalum pulchellum	0.64	<0.001
Xyris jupicai	0.51	0.003
Rhynchospora globosa	0.63	<0.001
Env	r^2	P-value
Topography	0.55	0.001

TABLE 6. Comparison of vegetation types at Monkey Bay and Sapodilla Lagoon.

	Monkey Bay	Sapodilla Lagoon
Percent Herbs	60	59
Percent Woody	40	23
Numbers of species from each savanna		
Tree	13	15
Vine	5	10
Shrub	20	31
Herbs	49	119
Woody	33	46
Total	109	199
Number of species in each herbaceous category		
Graminoids	20	60
Sedges	10	27
Grasses	10	33
Forbs	29	59

discovered in the NMDS ordination did not correspond to any measured environmental variable, but since this is the most important species according to calculated importance values, the gradient is important as well.

Topography is likely the most important element of the environmental parameters gathered in this study; a strong correlation between topography and depth of the water table is likely. For example, two important middle soil layer characteristics, cation exchange capacity and percent hydrogen, typically increase with increasing soil clay content, and are negatively correlated with topography. The soil characteristics are consistent with observations in the two soil pits, which suggested that topography was most related to the thickness of the sand layer covering the clay layer. Soil drainage in sandy soils is higher than in soils with high amounts of clay, thus the sand layer may be providing habitat for species that are less suited to saturated soils. A vegetation gradient explained by topography was represented by positive correlation with *Paspalum pulchellum*, and negatively correlated with *Rhynchospora globosa* and *Xyris jupicai* (Figures 4 & 5). Slight topographic variation at small scales appears quite important in explaining within-savanna variation in soil characteristics and vegetation. It also appears important at large scales when contrasting savannas to nearby woodlands at slightly higher elevations.

Studies that have collected data on temporal changes in savanna vegetation have shown that collecting data over multiple seasons may lead to a better measure of biodiversity in these sites (Sarmiento 1983b, José & Fariñas 1991). We were not able to test temporal variation of species relative cover in wet season vs. dry in this study, due to an intentionally set fire set 15 days prior to the wet season data collection trip. The study site, as mentioned before, was selected because it is relatively remote and few people utilize the surrounding areas, and thus had a lower risk of fire. The nearby property of All Pines was sold to a foreign-owned development corporation in the summer of 2003. In Belize it is common for surveying crews to burn savannas and understory of woodlands to simplify the search for property markers. The corporation was completing a property survey during December of 2003, and consequently fires burned the study site. Another savanna that burned in the summer of 2003 was the Monkey Bay savanna (Woo 2002). By that time, most of the interior-lowland savannas had already burned, including the All Pines savanna.

Monkey Bay savanna contained more pronounced shrub and tree layers than the Sapodilla savanna, in spite of the differences in our data of woody species. The basal area of trees and shrubs was nearly 10 fold greater at the Sapodilla Lagoon site but there were half as many woody species found there. The vast difference in basal area reflects two situations simultaneously occurring at Sapodilla and not at Monkey Bay. First, the pines and other trees at Sa-

podilla are have a greater average dbh than those at Monkey Bay. This could be due to increased risk of fire and/or an early logging event at Monkey Bay. The second major difference involves *Acoelorraphe wrightii.* The shear abundance of this palm in the Sapodilla site greatly increases the basal area of the whole savanna, contributing 6.46 m^2/ha of the total 9.46 m^2/ha. Woo's study (2002) only recorded dbh for those individuals with ≥5 cm dbh. This left out a large portion of the woody vegetation in the savanna. Another survey at the Monkey Bay site, including those individuals with ≥1 cm dbh, might be expected to yield a much higher total basal area than that recorded for Sapodilla, but certainly would reflect the greater total density of woody species at Monkey Bay.

In spite of large differences between Monkey Bay and Sapodilla in the total number of species and the percent of woody species composition, the growth form distributions of the herbaceous flora were strikingly similar. The herbaceous flora at both sites was evenly split between forbs and graminoids, and the graminoids were evenly split between the Poaceae and the Cyperaceae. These ratios have not been previously reported for Central American hyperseasonal savannas, and suggest common factors controlling both sites. Such ratios may be useful in classification of savannas throughout Central America, and warrant further examination. The Jaccard index showed only 26 percent similarity between the floras of these two sites. This difference, in addition to an increased number of woody species at Monkey Bay, illustrates the dissimilarity between the Sapodilla *coastal lowland hyperseasonal savanna* and the Monkey Bay *inland lowland hyperseasonal savanna*.

Meerman and Sabido's (2001) classification of the savannas at Monkey Bay and Sapodilla as *short grass savanna with shrubs* is supported by the results of this research. The substantial differences in the density of trees and shrubs, species composition and percent growth form among the two savannas suggests that subdividing the *short grass savanna* into two subcategories, *coastal lowland hyperseasonal savanna* and *inland lowland hyperseasonal savanna*, better describes the variation seen in Belizean lowland savannas. Further baseline research needs to be done within the interior lowland hyperseasonal savannas, as seen at Monkey Bay, as well as within the coastal lowland hyperseasonal savannas, such as at the Sapodilla site. This research would provide quantitative results to further investigate the degree of heterogeneity within areas broadly classified as savannas and importance of certain species as indicators of savanna in Belize.

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