WOODY VEGETATION OF TROPICAL LOWLAND DECIDUOUS FORESTS AND MAYAN RUINS IN THE NORTH-CENTRAL YUCATAN PENINSULA, MEXICO

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ABSTRACT

Quadrats were sampled at five dry-forest and two Mayan ruin sites in the north-central Yucatan Peninsula of Mexico. A total of 149 woody species were found, and data for the 81 most important species were analyzed (Importance Values ≥1.0; DBH ≥3.0 cm). Their distribution correlates with dry season precipitation patterns (polar ordination). Average basal area is 20.2 sq. m per ha for forest sites and 28.2 sq. m per ha for ruin sites. Average density is 3344 stems per ha in forests and 1432 stems per ha on ruins. The Shannon-Weaver Diversity Index varies from 1.76 to 2.25 for forests and 0.94 to 1.25 for the two ruins. Important forest species are *Bursera simaruba, Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum,* and *Caesalpinia gaumeri.* Leguminous species are more common in the drier, western forests than in the eastern forests, but are rare on the ruins. The two Mayan ruin sites have a vegetation that is distinct from that of the central peninsula and is dominated by *Brosimum alicastrum.*

INTRODUCTION

According to the Holdridge (1967) system of vegetation classification, the Yucatan Peninsula of Mexico is dominated by dry tropical forests (Holdridge et al., 1971). Until the middle 1900s, most botanical work on the peninsula was floristic and survey-type, conducted by Lundell (1934, 1937, 1938), Millspaugh (1895, 1896, 1898), Standley (1930), and others with ties to the Carnegie Institute in Washington, D.C. Miranda (1958) divided the Yucatan forests into five types based upon woody species presence, canopy height, and deciduousness. The boundaries of his forest types correspond precisely with isohyets of increasing precipitation across the peninsula from northwest to southeast (García, 1964; Isphording, 1975). The first quantitative ecological study of a forest on the peninsula was by Thien et al. (1982) near and on the ruins of Dzibilchaltun in the very northwest of the peninsula. Others have quantified the woody vegetation of old-growth forest in the north-central peninsula (Rico-Gray et al., 1988) and have described the relationships of the local people, descendants of the Maya, to the present vegetation of the region (Rico-Gray et al., 1990; Rico-Gray and García-Franco, 1991, 1992). Whigham et al. (1990, 1991) studied a north-

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eastern forest, quantifying woody plant growth, litter production, and impacts of hurricanes. No quantitative vegetation study ofthe central peninsular forests has been published, although this is a large region under intense human pressure (Brown and Lugo, 1990; Sabogal, 1992).

Most scientific studies conducted in the region have focused on the archaeology of Mayan sites, and have spawned some ancillary descriptions of vegetation associated with ruins (Lundell, 1937; Folan et al., 1979; Orejuela, 1980; Lambert and Arnason, 1982; Peters, 1983). A paradox exists as to why the vegetation of ruin sites is often different from neighboring forest vegetation. This study describes and quantifies extant old natural forest vegetation, compares it to the vegetation on two collapsed ruins, and then compares it in general to dry tropical vegetation of the world. The variation in the peninsula's forest vegetation is then related to known climatological patterns in Yucatan.

Materials and Methods

STUDY REGION. The northern Yucatan Peninsula of Mexico (states of Campeche, Yucatán, Quintana Roo) consists of limestone bedrock of Tertiary age, flat and without surface runoff (streams are absent). The average annual temperature is 27°C, with a July average of 29°C and a January average of 24°C. The lowest recorded temperature is 6°C. Total annual precipitation across the peninsula averages 1100 mm, with a dry season from October to May (average total = 300 mm) and a wet season from June to September (average total = 800-900 mm) due to adiabatic heating. The northern peninsula has no significant topographic features to create unusual localized rainfall or temperature conditions. There is a noticeable west to east, dry to wet gradient over the peninsula (Figure 1), the prevailing winds being from the Caribbean Sea in the east. For several thousand years, an extensive Mayan civilization with enormous cities occupied the region (Morley and Brainerd, 1983). The current inhabitants of the peninsula are Mayan subsistence farmers who practice a type of slash-and-burn agriculture principally in the northern and central portion of the State of Yucatán.

Near and almost parallel to the southwestern border of the state of Yucatán is a small but topographically significant anticlinal hill range (the Puuc, 100 m maximum elevation; Isphording, 1975), which emerges from the flat landscape of the north. This range begins about 50 km from the western coastline and its fault-line is continuous for 160 km before disappearing near the southeastern border of the state of Yucatán and the state of Quintana Roo. Because it is easier for the inhabitants to cultivate the surrounding flatter land, some of the least disturbed vegetation in the north-central part of the peninsula are found on the slopes of these hills. By local estimates, forests on some slopes have grown for 50 to more than 100 years without disturbance from cultivation. This is likely a significant amount of time for recovery from disturbance, since it has been estimated that dry tropical forests generally require only 150 years for total recovery (Opler et al., 1977), and species composition may not change over that period (Miranda, 1958).

STUDY SITES. Three forest study sites 40 to 75 years old were established along the Puuc range, one at each end and one near the middle. The Calcehtok site was the western site (20°33'N, 89°54'W) near the village of Calcehtok (Figure 1). The eastern site (20°02'N, 89°04'W) was just south of the town of Tzucacab and

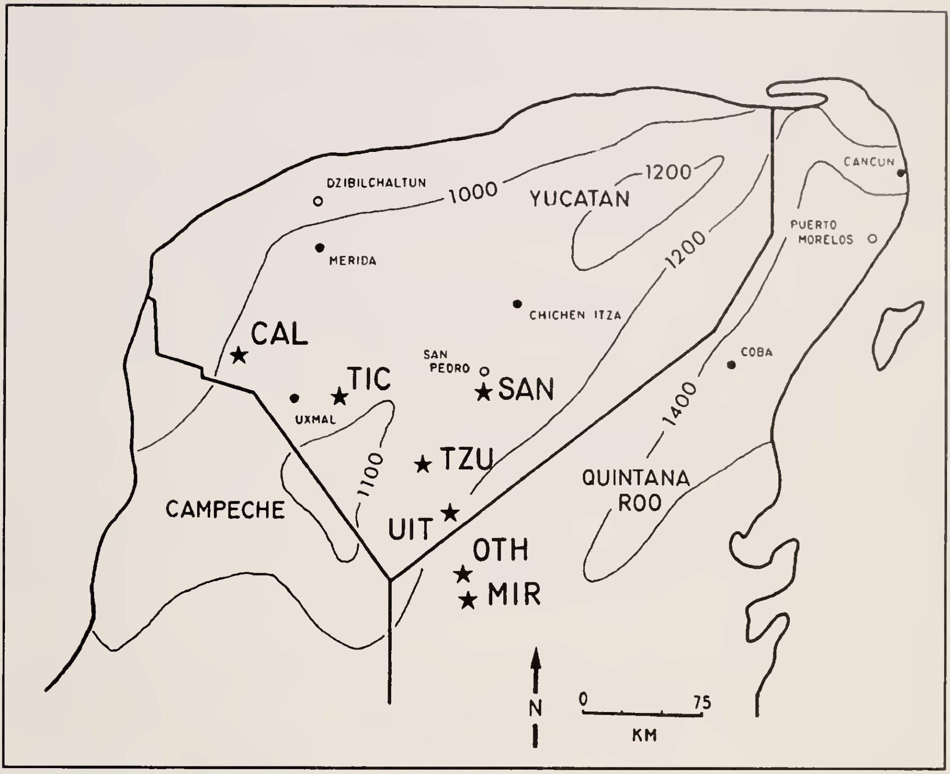

Figure 1. Map of the northern Yucatan Peninsula, Mexico, showing state boundaries, principal cities, archaeological sites (solid circles), location of the seven study sites (stars), three study sites cited in the literature (open circles), and isohyets (mm) adapted from García (1965). CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

given that name. The third site was located about equidistant between the other two (20°22'N, 89°34'W), southwest of Ticul. In addition to those sites within the Puuc, two others were studied because of their unusually old age. The Othon Blanco site (19°37'N, 89°00'W), is of older growth (more than 150 years), with a closed forest canopy and by appearance representative of the extensive forest in the east-central part of the peninsula. It is located near the village of Othon Blanco in western Quintana Roo, about the same distance (50 km) from the Tzucacab site as the distance separating the other forest sites. The San Mateo site (20°24'N, 88°49'W) was chosen for study because Rico-Gray et al. (1988) found that forests in this region show almost no evidence of human occupation or disturbance. These last two sites are on limestone substrate and a considerable distance from the Puuc area.

Two other sites were chosen because they were the least disturbed closed canopy forests found growing on the rubble of collapsed Mayan ruins. At each site the clearly visible rubble occupies an area less than 0.20 sq. km and forms small hills up to 20 m high in the otherwise flat landscape. The Uitizina ruin site (19°52'N, 88°58'W) is located 15 km southeast of the town of Tzucacab. The forests growing on the ruin are striking in their lushness, contrasting with the surrounding cattle ranches of savanna-like fields. The Mirador ruin site is approximately 5 km south from the Othon Blanco site and a considerable distance from any village or cultivated land. The structure of the closed-canopy forest around it is similar to that of the Othon Blanco site.

All seven sites were identified by local people as the oldest forests within their region. At all but the San Mateo and Mirador sites, culling of trees occurs for firewood and house construction with increasing frequency from east to west.

VEGETATION COMPOSITION AND STRUCTURE. At each site, the vegetation was sampled using sets of three 10 m × 20 m plots placed along 50 m transects. The total number of transects, and thus of plots, varied at each site from three to nine depending upon species-area curve calculations. The transects were spaced at least 25 m apart on flat land and were oriented east-west; on land with relief, the transects were oriented along the cardinal direction most parallel to the slope. The long axis of each plot was perpendicular to the transect. Within the plots, all woody stems (including coppiced stems)≥3.0 cm DBH were measured and identified with the Mayan vernacular name supplied by one or several of six remarkably knowledgeable local field assistants. To be sure of their abilities and consistency in applying names, we repeatedly collected multiple samples of sterile specimens identified by the Mayans to compare with vouchers. Very rarely were mistakes made.

Voucher collections were made for each species, most of which were eventually found with flowers or fruits. Identification to species was tedious because the flora of the peninsula is not well known. Collections were identified at Tulane University (NO), with questionable and unnamed specimens taken for scrutiny to the Field Museum (F), or the Missouri Botanical Garden (MO). Nomenclature follows the floras of Panama (Woodson and Schery, 1943-1980), Guatemala (Standley and Williams, 1946-1977), and Mexico (Standley, 1920-1926, 1930; Gómez-Pompa, 1978-; Cano et al., 1982; Sosa et al., 1985), or recent monographic studies. All vouchers have been deposited in the Tulane University Herbarium, with duplicates sent to other institutions.

For each site, Importance Values were calculated using relativized values of density, total basal area, and frequency of occurrence in the plots (Mueller-Dombois and Ellenberg, 1974). The vegetation data were analyzed using the BCORD program on the PC-ORD system (McCune, 1987). This program performs the Bray-Curtis (polar) ordination. The Euclidean dissimilarity measurement was used with endpoints selected by the variance-regression method (Beals, 1985); all other options were defaulted. The polar ordination technique was employed instead of detrended correspondence analysis and other techniques following Causton (1988); with the small number of sites, all multivariate techniques would likely give insignificantly different results. Species diversity was estimated as Richness (S), Evenness (E), and Diversity (H'). S is defined as the total number of species present, and E as H'/ln S (Pielou, 1969), where H' is $\sum(p_i \log p_i)$ (Shannon and Weaver, 1949).

RESULTS

General Vegetational Characteristics

A total of 123 plots were sampled, 99 at the five forest sites and 24 at the two ruin sites (Table 1), giving a sample area of 1.98 ha of forest and 0.48 ha on

TABLE 1. Summary of woody vegetation data from five forest sites and two ruin sites within the north-central Yucatan Peninsula, Mexico. Data are from all woody stems ≥3.0 cm DBH in 10 × 20 m plots. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin forest; MIR = Mirador ruin forest.

	CAL	TIC	TZU	SAN	OTH	UIT	MIR	FOREST*	RUIN*
Number of plots	24	9	27	12	27	12	12	99	24
Total Area Sampled (ha)	0.48	0.18	0.54	0.24	0.54	0.24	0.24	1.98	0.48
Basal Area per Stem (dm^2)	0.59	0.33	0.37	0.73	1.40	2.03	1.93	0.68	1.98
Total Basal Area (m^2/ha)	20.9	11.9	17.4	18.4	32.5	29.8	26.9	20.2	28.4
Stems/ha	3525	3611	4748	2513	2324	1467	1396	3344	1432
Stems/Plot	71	72	95	50	46	29	28	67	29
Plot Richness	13.8	15.6	21.2	18.5	15.6	8.8	8.3	16.9	8.6
Shannon-Weaver Index	1.76	2.00	2.25	2.23	2.14	0.94	1.25		
Site Richness	64	46	93	53	67	23	32	65	28
Site Evenness	0.681	0.731	0.739	0.767	0.782	0.434	0.608		
Total Tallied Stems	1692	650	2564	603	1255	352	335	6764	687

* Data are either averages or totals depending upon the parameter.

ruins. The species × area plots for the seven sites have a slope near zero after 12 plots or a sample area of 0.18-0.24 ha (Figure 2). A total of 149 species from 7451 stems ≥3.0 cm DBH were identified in one or more sites.

A summary of important vegetation parameters for the seven sites is presented in Table 1. The mean Richness of the forest sites is 65 species, whereas the ruin sites have an average of 28 species. The average Richness in each forest quadrat varies from 13.8 species at Calcehtok to 21.2 at Tzucacab, with an average of 17 for each plot over the five sites. Both of the ruin sites have fewer species in each plot (S = 8.6), and little intersite variability (alpha-diversity). The Shannon-Weaver Diversity Index is usually much higher for the forest sites (H' >2.00) than for the ruin sites (H' ca. 1.00). The density in the forest sites is much greater (3344 stems per ha) than in the ruin sites (1432 stems per ha). However, stem diameters are on average greater (15.9 cm) in ruin sites than in forest sites (9.3 cm). This translates into an average of 28.2 sq. m per ha total basal area for the two ruin sites and 20.2 sq. m per ha total basal area for the five forest sites.

Of the 149 species identified, 81 may be considered ecologically common because their Importance Values are ≥1.00 (out of a total of 100.00) in at least one of the seven study sites. The 68 remaining species are ecologically rare and were not included in these data analyses. In Appendix I, we present the frequency, density, and basal area data for the 81 common species at the seven sites; these data represent 93% of the total tallied stems. Appendix II is a list of the 68 rare species by site.

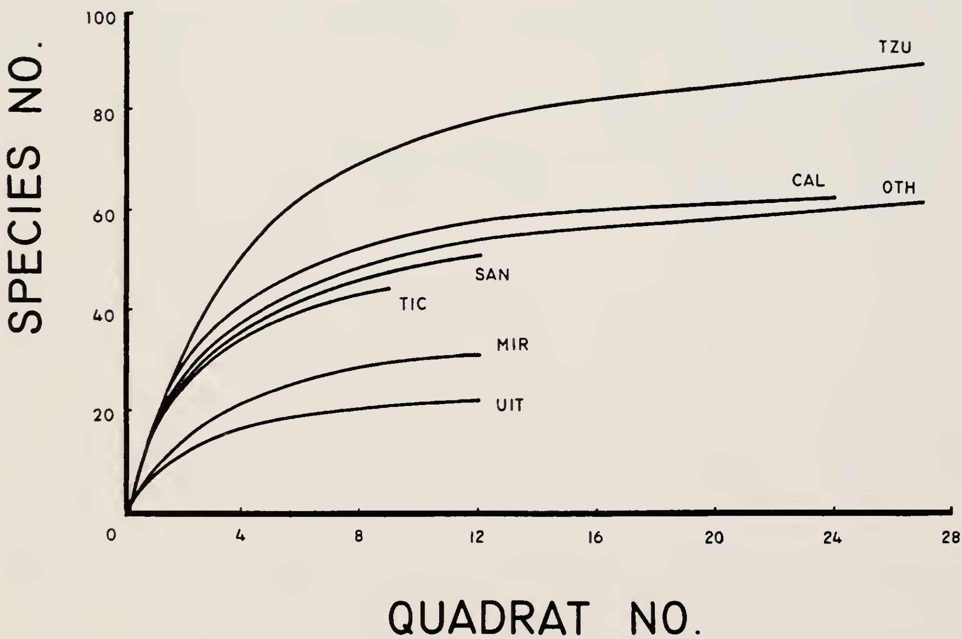

Figure 2. Species-area curves for the seven study sites in the northern Yucatan Peninsula, Mexico. The x-axis is the number of 200 sq. m quadrats sampled. The y-axis is the cumulative number of species measured. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

The ordination (Figure 3) indicates the distinctiveness of the ruin sites. The spatial position of the forest sites in the two-axis ordination corresponds exactly to a northwest to southeast transect paralleling the northern boundary of the state of Campeche (Figure 1), with Calcehtok the westernmost site and Othon Blanco the easternmost site, and the San Mateo site close to the Tzucacab site. The first two axes explain 78% of the variation in the data. No new relationships are revealed if the ruin sites are eliminated and only the five forest sites ordinated; four sites are positioned as endpoints, with the San Mateo site in the center of the two-axis plot.

Forests of Central Yucatan

Calcehtok forest.– In the Calcehtok forest, *Bursera simaruba* and *Gymnopodium floribundum* are the most frequently found woody plants; they were in 88% and

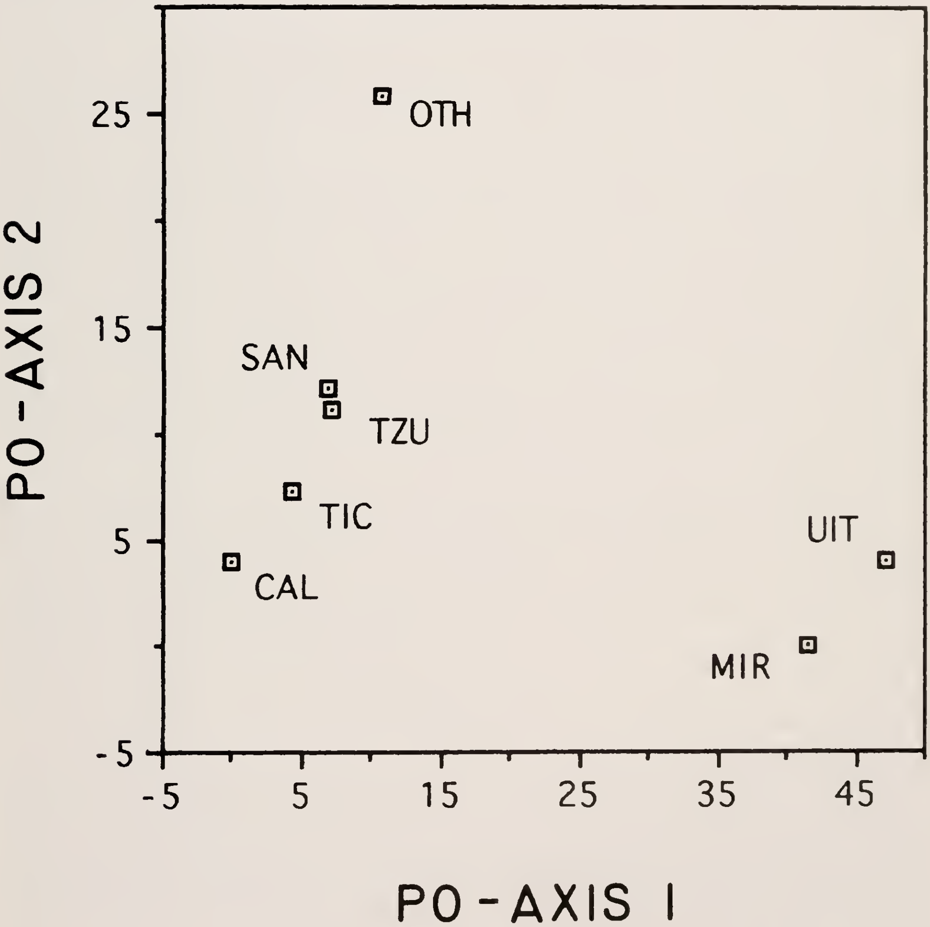

Figure 3. Polar ordination of five forest and two Mayan ruin sites in northern Yucatan Peninsula, Mexico. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; UIT = Uitizina ruin; MIR = Mirador ruin.

75% of the plots, respectively (Appendix I). *Gymnopodium floribundum, Machaonia lindeniana*, and *Bursera simaruba* are most abundant, accounting for 49% of the stems. *Caesalpinia gaumeri, Guettarda elliptica, Lysiloma bahamense,* and *Thouinia paucidentata* also have high densities, totalling 20% of the stems. They are also frequent species, found in about 70% of the plots. Together these seven species contribute 69% of the total density, and in some portions of this forest *G. floribundum* is found in large, nearly monotypic stands. *Gymnopodium floribundum* is the most abundant species and represents 26% of the density, but it contributes only a third of the total basal area, a reflection of the small average stem diameter. *Bursera simaruba* is the largest tree, with a basal area of 6.70 sq. m per ha (32% of the total). Those two species, plus *C. gaumeri* and *L. bahamense,* contribute 13.9 sq. m per ha, or 67% of the basal area. The average DBH at the site is a small 8.7 cm. The Calcehtok site is the least diverse of the forest sites (H' = 1.76), but has a relatively large total number of species (64). The canopy height varies from 8 to 15 m. *Bursera simaruba, Lysiloma bahamense,* and *Vitex gaumeri* are usually the tree species of any size in this forest.

Ticul forest.– In the Ticul forest, 650 stems were measured, and these have the lowest average diameter (6.5 cm) of any site (Table 1). *Bursera simaruba* and *Thouinia paucidentata* were found in every plot, while *Guettarda elliptica* and *Caesalpinia gaumeri* were relatively abundant, present in eight and six of the nine plots, respectively (Appendix I). *Gymnopodium floribundum* is clumped in this forest, found in four plots. These five species are the most abundant at the site, comprising 54% of the total number of stems (Table 1). Each is found at about the same density. As at the Calcehtok site, *B. simaruba* is, by a factor of three, the largest contributor (3.13 sq. m per ha or 26%) to the total basal area of 11.9 sq. m per ha. *Caesalpinia gaumeri, Piscidia piscipula,* and *Thouinia paucidentata* contribute 34% to the basal area. *Piscidia piscipula* is the largest tree at this site with a mean DBH of 12.9 cm. As in forests to the east, the Diversity Index (H' = 2.00) is significantly greater than at the Calcehtok site. The average canopy height is from 8 to 15 m, but broken with taller individual trees of *Lysiloma bahamense* and *Spondias mombin.*

Tzucacab forest.– The Tzucacab forest has the largest number of recorded species (93) and the greatest Diversity (H' = 2.25; Table 1). The six most frequent species are *Bursera simaruba, Piscidia piscipula, Diospyros cuneata, Croton reflexifolius, Lonchocarpus rugosus,* and *Coccoloba spicata* (Appendix I). *Bursera simaruba* is the most dense species with 574 stems per ha; *Croton reflexifolius* and *Diospyros cuneata* are also very abundant, yet they comprise only 29% of total density. Other relatively dense species include *Eugenia axillaris, Lonchocarpus rugosus, Lysiloma bahamense, Neea choriophylla, Piscidia piscipula,* and *Vitex gaumeri,* with a combined density of 1204 stems per ha, or 25% of the total. As in the other forests, *Bursera simaruba* is the largest contributor (3.39 sq. m per ha or 19%) to the total basal area. *Lysiloma bahamense* and *Vitex gaumeri* contribute 4.51 sq. m per ha, or 26% of the total. The ten species just mentioned make up 65% of the basal area in this forest; the other 84 species found in the Tzucacab forest contribute 35%. Average stem diameter at this site is 6.8 cm, slightly larger than in the Ticul forest. Canopy height is 15 to 25 m, broken and very plot-dependent, with no single or group of species consistently tall.

San Mateo forest.– Trees of the San Mateo forest have a mean stem diameter of 9.6 cm. This site has a high Diversity Index (H' = 2.23), very similar to that of the Tzucacab forest, and a relatively low total density of 2513 stems per ha (Table 1).

Thouinia paucidentata is most frequent (92%; Appendix I), while *Bursera simaruba* has a frequency of 83%, and *Diphysa carthagenensis, Eugenia buxifolia,* and *Piscidia piscipula* each with a frequency of 75%. *Gymnopodium floribundum* is the most commonly encountered species with 288 stems per ha, but it only accounts for 12% of the total number of stems. The other relatively abundant species, *Thouinia paucidentata, Malpighia punicifolia, Diphysa carthagenensis,* and *Eugenia buxifolia* contribute an additional 30% to the density. The total basal area of 18.4 sq. m per ha is not very different from that of the previously described sites. *Bursera simaruba* and *Caesalpinia gaumeri* are the largest trees and contribute 24% of total basal area. *Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum, Lysiloma latisiliquum,* and *Vitex gaumeri* are also significant species and about equal in their basal area contributions, a combined 34% of the total. The tallest trees in this forest reach 20 m, with *Caesalpinia gaumeri, Bursera simaruba, Talisia olivaeformis,* and *Vitex gaumeri* the usual species with an average diameter of approximately 18 cm. An occasional large crown of *Lysiloma latisiliquum* (32.5 cm average DBH) protrudes through the uneven canopy.

Othon Blanco forest.– Of all the forest sites, the Othon Blanco forest has the largest total basal area (32.5 sq. m per ha; Table 1); *Manilkara zapota* is the largest contributor (13%). *Bursera simaruba, Gymnanthes lucida, Caesalpinia gaumeri,* and *Metopium brownei* are the other major contributors to basal area (ca. 7% each; Appendix I). Six other species, *Drypetes laterifolia, Coccoloba spicata, Gymnopodium floribundum, Lysiloma latisiliquum, Psidium sartorianum,* and *Thouinia paucidentata* are also important in this forest, with a combined basal area of 24%. *Gymnanthes lucida, Drypetes laterifolia,* and *Manilkara zapota* are strikingly abundant and contribute 45% of the total number of stems (Table 1). Here, the two most widespread species are *Manilkara zapota,* found in 93% of the plots, and *Drypetes laterifolia,* found in 89% of the plots. *Gymnanthes lucida, Gymnopodium floribundum,* and *Cosmocalyx spectabilis* are also frequently encountered. *Bursera simaruba* is not so frequent as in the more western forests, here found in 44% of the plots. The Othon Blanco forest has twice the average stem basal area (1.40 sq. dm per stem, or DBH = 13.4 cm; Table 1) of any of the other forests studied. This is the only forest with a persistent, well-defined canopy and understory. The canopy height is uniformly 30 to 35 m with *Lysiloma latisiliquum* (45.6 cm DBH), *Bursera simaruba* (28.7 cm DBH), *Metopium brownei* (30.3 cm DBH), and *Spondias mombin* (31.3 DBH) the largest, most common, and tallest trees. Some individuals of *Guettarda combsii, Luehea speciosa, Piscidia piscipula, Vitex gaumeri,* and *Zuelania guidonia* are at canopy level also.

Forests on Ruins

The two ruin-associated forests are remarkable in their similar differences from the five other forest sites (Table 1). Both exhibit low Diversity, low Richness, low total density, high basal area coverage, and tall canopies (30 m). They are also similar in species composition, sharing nine species, particularly the dominant *Brosimum alicastrum* in the overstory, and *Croton lundelii* in the understory (Appendix I). *Brosimum alicastrum* is the most frequent, most dense, and largest tree in the ruin sites; it was found in all plots at both sites, accounting for 32% of the total stems encountered at the Uitizina site and 43% at the Mirador site. Trees of *Brosimum alicastrum* comprise 69% of the basal area at the Uitizina site and 50% at the Mirador, site, with average diameters of 23.9 cm and 26.9 cm, respectively. In both forests, *Croton lundelii* is the second most abundant species (Uitizina, 19%; Mirador, 17% of total density), but only in the understory. It is frequently encountered, found in 100% of the Uitizina and 75% of the Mirador plots.

Both ruin-site forests are unique in the presence of *Urera baccifera* in the understory. It is common at the Uitizina site (16% of total density) and small, with an average diameter of 3.5 cm. *Bursera simaruba* and *Thouinia paucidentata* are important overstory species at both sites, both species being larger at Uitizina. The sites differ in other overstory species. The Uitizina forest has the overstory species *Ehretia tinifolia* and *Talisia olivaeformis*, while the Mirador overstory is much richer and includes *Karwinskia humboldtiana, Chlorophora tinctoria, Spondias mombin, Piscidia piscipula,* and *Ficus cotinifolia,* all with average diameters between 38 cm and 22 cm. In addition, there are several unidentified species of large *Ficus* growing over the rubble of this ruin.

Forest Phytosociology

In Table 2 the Importance Values (I.V.) for the 81 most common species are listed by forest; to show patterns of distributions, the species are separated into eight groups. By studying only the ecologically common species (those with I.V. ≥1.0), intersite phytosociological relationships become clear. The elimination of the 68 rare species should not affect the robustness of the data; the combined Importance Values for the rare species averaged 6% across all seven forests (Table 2, bottom), and was never greater than 14%.

Of the 81 more important species in the central Yucatan forests, 13 are especially common; three (*Bursera simaruba, Thouinia paucidentata, Bunchosia swartziana*) are present in all seven forests, and one, *Spondias mombin,* is found in five forests but is likely present in all (Group I, Table 2). Of the 13 species, *Bursera simaruba* is the most important tree contributing 11% to the total Importance Value for the five forest sites and 5% of the Importance Value for the two ruin sites. Its Importance Value is highest in the westernmost forests. Eleven species were found only in the forest sites (Group II, Table 2); two of these are particularly noteworthy, *Gymnopodium floribundum* and *Caesalpinia gaumeri* having relatively high average Importance Values.

Ten species are present only in the four western forest sites at Calcehtok, Ticul, Tzucacab, and San Mateo; of them, *Guettarda elliptica, Lysiloma bahamense,* and *Neea choriophylla* are most important. Nine species are present only in the three eastern forest sites (Tzucacab, San Mateo, and Othon Blanco); two species of *Coccoloba* (*C. cozumelensis* and *C. spicata*) are the most important of these. The Tzucacab forest is a site of species distribution overlap.

The three eastern forests share eight species with one or both of the ruin sites (Group V, Table 2). Three species, *Manilkara zapota, Cosmocalyx spectabilis,* and *Gymnanthes lucida,* are present at one ruin site (Mirador) and are especially important in the very easternmost forest site (Othon Blanco).

Legumes comprise exactly one-third of the 24 species in the first two groups (Table 2). The western forests have a greater ecological Importance Value in legumes. Four of the ten Group III species (Western Species) are legumes, whereas there is only one, *Pithecellobium albicans,* in all the eastern groups (Groups IV, V, VI). In Group VII, legumes are more important in the western sites. No other distributional pattern is evident for the Group VII species; maybe each should be considered only locally important, or maybe they were present

TABLE 2. Importance Values of 81 of the more common (I.V. ≥1.0 in at least one of the seven sites) woody species (DHB ≥3.0) for five forest and two ruin sites within the north-central Yucatan Peninsula, Mexico. Importance Values were obtained from Appendix 1 using relativized density, basal area, and frequency data. *Indicates a species likely present at the site but not recorded. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; MIR = Mirador ruin forest; UIT = Uitizina ruin forest.

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
I. WIDESPREAD SPECIES (13):							
Bursera simaruba	16.00	14.35	11.98	7.30	4.38	5.39	5.22
Thouinia paucidentata	4.58	9.58	2.17	7.26	4.05	6.81	4.64
Bunchosia swartziana	0.65	1.62	0.29	1.96	2.48	0.46	2.51
Spondias mombin	*	1.71	0.35	*	1.01	2.79	1.72
Piscidia piscipula	2.48	5.78	4.28	5.21	1.82	3.30	
Pithecellobium leucospermum	1.04	0.93	0.08	0.43	0.22	0.45	
Semialarium mexicanum	0.95	0.53	1.87	2.17	1.37	0.46	
Eugenia axillaris	0.25	0.62	2.99	0.51	0.24	2.13	
Exostema caribaeum	1.27	2.38	0.74	2.44	0.15	1.04	
Bourreria pulchra	0.71	*	0.36	1.94	0.40	1.29	
Cordia gerascanthus	0.32	*	0.24	1.68	1.07	0.44	
Krugiodendron ferreum	0.49	*	0.17	0.99	1.01	0.47	
Karwinskia humboldtiana		0.90	2.74	*	0.45	*	2.80
II. FOREST-SITE SPECIES (11):							
Gymnopodium floribundum	*	13.94	6.82	0.49	7.07	5.07	
Caesalpinia gaumeri	6.63	8.66	1.71	5.83	3.82		
Lonchocarpus yucatanensis	0.30	2.48	2.37	1.48	2.03		
Acacia gaumeri	1.65	0.76	0.60	1.83	0.11		
Bauhinia divericata	0.25	1.06	0.76	0.76	0.59		
Diphysa carthagenensis	0.41	0.76	0.07	4.81	1.59		
Diospyros cuneata	0.29	*	6.35	0.23	0.32		
Erythroxylum rotundifolium	0.31	*	0.60	3.17	1.28		
Vitex gaumeri	1.47	*	5.82	3.35	0.96		
Lennea sepium	1.15	*	0.10	1.45	0.14		
Jatropha gaumeri	0.13	0.81	*	1.76	0.37		

TABLE 2. (Continued)

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
III. WESTERN FOREST SPECIES (10):							
Guettarda elliptica	3.48	6.34	0.20				
Lysiloma bahamense	7.73	1.03	7.98				
Neea choriophylla	2.27	2.62	3.22				
Cnidoscolus aconitifolius	0.75	1.71	0.15				
Pithecellobium dulce	0.21	2.34	0.22				
Diospyros anisandra	0.74	2.43	0.31				
Alvaradoa amorphoides	1.73	0.81	0.65	0.54			
Mimosa bahamensis	0.67	2.73	0.07	1.20			
Randia gaumeri	1.23	1.63	*	0.85			
Bursera schlechtendalii		0.12	1.40	0.07			
IV. EASTERN FOREST SPECIES (9):							
Pithecellobium albicans		1.62	0.34	0.45	0.44		
Coccoloba cozumelensis			1.28	3.13	1.38		
Coccoloba spicata			2.78	1.76	3.47		
Psidium sartorianum			1.14	0.21	2.64		
Luehea speciosa			1.61	0.52	1.90		
Ardisia escallonioides			0.23	1.13	0.58		
Guettarda gaumeri			0.91	2.20	0.37		
Hampea trilobata			1.99	0.97	0.86		
Malpighia punicifolia			0.19	4.79	*		
V. EASTERN FOREST AND RUIN SPECIES (8):							
Malmea depressa			1.08	1.15	2.33	2.82	1.26
Talisia olivaeformis			0.66	1.33	0.60	1.79	1.86
Drypetes laterifolia			*	0.22	8.12	1.12	1.87
Zuelania guidonia			0.66	0.82	1.36	2.39	
Eugenia buxifolia			2.12	3.92	0.22	1.02	
Nectandra coriacea			0.45		0.33	1.44	
Croton reflexifolius			4.71	1.82	2.42		0.42
Celtis iguanea			0.54	0.54	0.11		3.15

VI. Easternmost Forest Species (3):							
Manilkara zapota					10.07	1.47	
Cosmocalyx spectabilis					3.21	3.57	
Gymnanthes lucida					11.00	0.44	
VII. Miscellaneous Forest Species (16):							
Adelia oaxacana	1.06	0.69					
Colubrina reclinata	1.13	2.75					
Sideroxylon foetidissimum	1.09	2.44					
Apoplanesia paniculata	1.49						
Sebastiana adenophora	1.38						
Machaonia lindeniana	7.56			1.47			
Caesalpinia velutina	0.70			1.25	0.49		
Lysiloma latisiliquum				2.35	1.66		
Casearia corymbosa		1.01	0.45				
Colubrina greggii		0.30	1.72				
Acacia riparia		1.58					
Eugenia spp.		1.21					
Cochlospermum vitifolium				1.15		0.13	
Guettarda combsii			1.30		1.54		
Lonchocarpus rugosus			3.36		0.82		
Metopium brownei					3.48		
VIII. Ruin Species (11):							
Brosimum alicastrum		0.77			0.85	35.00	37.47
Croton lundelii						9.75	11.31
Urera baccifera						1.72	9.68
Hybanthus yucatanensis						0.89	3.53
Ficus cotinifolia						2.47	
Ficus spp.						2.94	
Chlorophora tinctoria						1.70	
Capparis indica							4.19
Capparis pachea ssp. *oxysepala*							2.99
Ehretia tinifolia							1.78
Astrocasia tremula					0.24		3.38
Total (maximum 100.00%)	91.43	95.72	86.35	96.69	94.66	98.43	96.91

but unrecorded in some sites because of their rarity or clumped distribution. The two ruin sites have eleven non-leguminous species not usually present at any of the forest sites. *Brosimum alicastrum* was the most important of these ruin-species; at both sites it makes up over 33% of the Importance Value. As stated, *Croton lundelii* and *Urera baccifera* are also important species at the ruin sites.

Discussion

Forests within the northern (above 20°N latitude) Yucatan Peninsula are clearly dry-tropical by the Holdridge (1967) classification. More specifically, the five forest sites are within four different tropical vegetation types described by Miranda (1958), and corroborate quantitatively his height- and deciduousness-based classification system. The Calcehtok and Ticul sites are in the "low-medium deciduous" forest zone of the western and central portions of the state of Yucatán (Figure 1), and have the predicted canopy height of 15 to 20 m. The San Mateo site is a "medium transition" forest with about 25 m canopy height. Adjacent to and east of this zone is Miranda's zone of "tall-medium subdeciduous" forest with a canopy of 25 to 30 m; the Tzucacab site is located within this zone. The Othon Blanco forest is near the western edge of Miranda's "tall subevergreen" forest, which covers the central and southern portions of Quintana Roo.

The increase in canopy height from northwest to southeast across the northern peninsula follows the change in species composition seen across the forest sites as identified by the ordination (Figure 3). These trends in canopy height and species composition mirror annual precipitation patterns for the peninsula presented by García (1965; Figure 1). She gives no precipitation breakdown by wet-dry seasons, but recent official maps prepared by SPP (Secretaría de Programación y Presupuesto) do give isohyets across the peninsula for both seasons from the years 1921 to 1975. Although the five forest sites are in the same isohyet (900 mm) for the wet season (May-Oct), the amount of rain in the dry season(Nov-Apr) differs considerably, from 150 mm in the west (Calcehtok forest region) to more than 300 mm in the east (Othon Blanco forest region), a result of the prevailing westerly winds from the Caribbean Sea. It is likely that during those drier months the difference in precipitation of more than 150 mm affects plant growth and produces the observed gradient in canopy height.

Past quantitative vegetation research in other areas of the peninsula supports this conclusion. Thien et al. (1982) presented data from the dry northwestern region of the peninsula, a forest site around the ruins of Dzibilchaltun (Figure 1) within Miranda's zone of "low deciduous" forest where annual rainfall is less than 700 mm. Here, canopy height ranges from 6 to 8 m. Whigham et al. (1990) described a forest on the east coast of the peninsula near Puerto Morelos, within Miranda's "tall subevergreen" forest zone with a recorded annual precipitation of about 1100 mm, although quite variable. That area has an upper canopy height of 25 m. Rico-Gray et al. (1988) worked in an old-growth forest at San Pedro, in the same area as the San Mateo forest. They recorded an annual precipitation of just under 1000 mm and a canopy height of 20 m.

The T/P (annual mean temperature/annual total precipitation) ratios for those three forests, and for forests reported on here, range from 3.7 (Dzibilchaltun) in the northwest to 2.3 (Othon Blanco) in the southeastern part of the study area, and thus are in the worldwide range for dry tropical forests as described by Murphy and Lugo (1986a). Canopy heights in the Yucatan Peninsula are typical for world dry tropical forest, varying from 8 m (Dzibilchaltun) to 35 m (Othon Blanco), and likewise woody plant Richness (DBH >ca. 2.5 cm), with a range from about 50 species (Dzibilchaltun) to 100 species (Othon Blanco). The broken nature of the canopy is a pronounced characteristic of the more western forests (Calcehtok, Ticul, Tzucacab, San Mateo), and this also was reported for the Dzibilchaltun, San Pedro, and the Puerto Morelos forests.

Over the entire northern Yucatan Peninsula the forests are characterized by several widespread species. *Bursera simaruba, Gymnopodium floribundum, Piscidia piscipula,* and *Thouinia paucidentata* are usually particularly important. As in the present study, Rico-Gray et al. (1988) and Thien et al. (1982) found the first three species to be common and dominant. There is a species composition difference corresponding to a dry-season precipitation difference of more than 150 mm across the peninsula. In the west, *Casealapinia gaumeri, Pithecellobium leucospermum, Acacia gaumeri, Bunchosia swartziana, Diospyros cuneata,* and *Vitex gaumeri* are important species in all the studied forests. The dry-season wetter forests in the eastern and northern region (within Miranda's "tall subevergreen" forest zone) have five species not usually found in the west: *Brosimum alicastrum, Drypetes laterifolia, Gymnanthes lucida, Manilkara zapota,* and *Talisia olivaeformis* (this study and Whigham et al. (1990)). Murphy and Lugo (1986b) reported that *Gymnanthes lucida* was the most common tree in a Puerto Rican dry tropical forest and it has been recognized as an important component of the Antillean flora (Miranda, 1958).

Miranda (1958) identified *Vitex gaumeri* as the "abundant" indicator tree in his "tall to medium subdeciduous" vegetation zone, and an important component of his "medium transition" forest just to the west. From the results of this study, the indicator status for *Vitex* is in doubt. Even though *Vitex gaumeri* has the highest Importance Values at the two sites (Tzucacab and San Mateo, Table 2) within the two vegetation zones just mentioned, it cannot be singled out as anything but a general "forest species." However, this study does corroborate *Manilkara* (*Achras*) *zapota* as an indicator species of the most eastern vegetation zone of "tall subperennial" species: the species was found only at the two sites (Othon Blanco and Mirador ruins) in that zone. Additional quantitative sampling of the peninsula's vegetation needs to be done to confirm other Miranda conclusions.

Could all published accounts of the northern Yucatan forests be describing aberrant vegetation so disrupted by lengthy Maya habitation that little resemblance to a native type exists? Possibly, but this is a worldwide concern in dry-tropical forests (Murphy and Lugo, 1986a). Great care was taken in this study to find the least disturbed sites in the central peninsula, but it is difficult to assess the true age of any of the peninsular forests because of incessant culling practices and coppicing (Rico-Gray and García-Franco, 1992). A few emergent trees scattered among the canopy cover may be a false indication of old age. Still, in this study, all Mayan field assistants were certain that no site had been severely cut for farming during the past 40 years, and, as noted above, some individual plots, even entire forest sites, are more than 100 years old. Miranda (1958) predicted that forest species richness and diversity would not be significantly different in the absence of humans, only that the individual trees would be larger.

Rico-Gray et al. (1988) and Thien et al. (1982) named several species as indicators of the oldest quadrats studied if found in large size and high density. These include *Bursera simaruba, Vitex gaumeri, Caesalpinia gaumeri, Piscidia piscipula,* and *Apoplanesia paniculata.* Along with *Lysiloma bahamense,* these were among the largest trees in the five forest sites analyzed for the present study. It is certain that the forests growing over the ruins were the oldest studied; the Maya viewed them with a special significance and unequivocally stated that little culling had occurred within them for many years.

The San Mateo forest of this study, and the San Pedro forest (Rico-Gray et al., 1988), are less than five km apart. Of the 51 species reported in the San Pedro forest and the 45 species in the San Mateo forest, 25 are common to both, a reflection of tropical diversity; using those 25 species to characterize the forests of this region seemed reasonable, and in total they contributed heavily to the Importance Values: 75% in the San Pedro forest and 66% in the San Mateo forest.

As for many other studies (Bartlett, 1935; Lundell, 1937; Folan et al., 1979; Lambert and Arnason, 1978, 1982), this study clearly shows that the woody vegetation growing on Mayan ruins of the Yucatan Peninsula is different from the vegetation of even adjacent forests (Figure 3). Eleven species are associated with the two ruin sites (Table 2); they contribute 55% of the Mirador site and 75% of the Uitizina site total Importance Values. Of particular significance is *Brosimum alicastrum,* which makes up more than a third of the total Importance Value at each site. It has been thought (Lundell, 1937; Bartlett, 1935), but recently challenged (Lambert and Arnason, 1978, 1982), that *Brosimum alicastrum,* among other species, is more common around ruins because it is a relict from the ancient days of Mayan cultivation. However, such species may be associated with ruins because conditions for growth on rubble are satisfactory (Miranda, 1958) and free from competition from other forest species; i.e., conditions are optimal for growth and reproduction (Lambert and Arnason, 1982). For *Brosimum,* it might be that the bat-dispersal of seeds creates high potential for establishment on ruins, which are bat roosting sites (Peters, 1983).

The Uitizina site is unique. Nine of the 13 widespread species (Table 2) are absent from the site. *Manilkara zapota,* historically a species associated with ruins (Lundell, 1937), is also absent. Oddly, this species is not important at the Mirador site (I.V. = 1.47%). *Talisia olivaeformis* was identified as another ruin-associated species by Lambert and Arnason (1978). In our study, both of the ruin sites, as well as the three most eastern forest sites (Table 2), record it in low Importance.

Conclusions

This first quantitative study of the north-central Yucatan Peninsula's dry-tropical forests corroborates Miranda's qualitative description of forest types, and clearly documents a change in species composition and height across the peninsula, with these differences likely caused by small and local differences in dry-season rainfall. Certain species (*Bursera simaruba, Thouinia paucidentata, Piscidia piscipula, Gymnopodium floribundum, Caesalpinia gaumeri*) are widespread, quantitatively important, and therefore characteric of the forests in this part of the world.

The average total basal area for all five forest sites (20.2 sq. m per ha) is low, but within the range of 17 to 40 sq. m per ha given by Murphy and Lugo (1986a) for dry-tropical forests. Likewise, the forests studied here fall within parameters from other dry-tropical forests with respect to T/P ratios, Richness, Diversity, canopy height, and structure.

The abandoned Maya ruins of the northern peninsula have a distinct vegetation dominated by *Brosimum alicastrum*, this likely due to the bouldery substrate.

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Appendix I.

Species data for five forests and two ruin sites in the north-central Yucatan Peninsula, Mexico. FREQ. = number of plots (10 × 20 m) in which the species was present. STEMS = total number, including coppiced stems, ≥3.0 cm DBH in all plots. DENSITY = stems per ha. AREA = sq. dm per ha. Species with an Importance Value ≥1.0 in at least one of the seven sites are listed. Taxa that could not be positively separated are combined.

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
CALCEHTOK FOREST (24 plots sampled)									
Acacia gaumeri Blake	8	5	54.17	21.17	*Adelia oaxacana* (Meull. Arg.) Hemsl.	4	21	43.75	15.26
Alvaradoa amorphoides Liebm.	11	18	37.50	16.74	*Apoplanesia paniculata* Presl	8	17	35.42	22.37
Bauhinia divaricata L.	2	2	4.17	0.35	*Bourreria pulchra* Millsp.	4	9	18.75	8.32
Bunchosia swartziana Griseb.	4	10	20.83	3.12	*Bursera schlechtendalii* Engl.	1	1	2.08	0.30
Bursera simaruba (L.) Sargent	21	163	339.58	669.65	*Caesalpinia gaumeri* Greenm.	13	96	200.00	214.99
Caesalpinia velutina (Br. & Rose) Standl. (or *C. violacea* (Mill.) Standl.)	4	7	14.58	10.21	*Chlorophora tinctoria* (L.) Gaudich.	1	1	2.08	0.65
Cnidoscolus aconitifolius (Mill.) Johnst.	6	6	12.50	1.69	*Colubrina reclinata* (L'Hérit.) Brongn.	7	13	27.08	10.51
Cordia gerascanthus L.	2	3	6.25	4.01	*Diospyros anisandra* Blake	5	10	20.83	2.67
Diospyros cuneata Standl.	2	3	6.25	1.76	*Diphysa carthagenensis* Jacq.	3	4	8.33	1.93
Erythroxylum rotundifolium Lunan	2	2	4.17	4.18	*Eugenia axillaris* (SW.) Willd.	2	2	4.17	0.47
Exostemma carbaeum (Jacq.) R. & S.	8	18	37.50	6.98	*Ficus* spp.	1	5	10.42	2.58
Guettarda elliptica Sw.	14	82	170.83	29.06	*Gymnopodium floribundum* Rolfe	18	436	908.33	222.31
Hybanthus yucatanensis Millsp.	1	2	4.17	0.51	*Jatropha gaumeri* Greenm.	1	1	2.08	0.71
Karwinskia humboldtiana (R.&S.) Zucc.	5	11	22.92	11.16	*Krugiodendron ferreum* (Vahl) de Wil.	3	8	16.67	1.85
Lennea sepium (Jacq.) Walp.	6	25	52.08	22.06	*Lonchocarpus yucatanensis* Pittier	2	3	6.25	2.45
Lysiloma bahamense Benth.	17	73	152.08	287.30	*Machaonia lindeniana* Baill.	15	231	481.25	94.00
Mimosa bahamensis Benth.	3	13	27.08	6.98	*Neea choriophylla* Standl.	11	30	62.50	36.06
Piscidia piscipula (L.) Sargent	10	26	54.17	60.30	*Pithecellobium albicans* (Kunth) Benth.	7	17	35.42	36.68
Pithecellobium dulce (Roxb.) Benth.	1	3	6.25	3.47	*Pithecellobium leucospermum* Brand.	5	11	22.92	20.02
Randia gaumeri Greenm. & Thompson	8	18	37.50	4.82	*Sebastiana adenophora* Pax & Hoffm. (or *S. tikalana* Lundell)	7	25	52.08	11.66
Semialarium mexicanum (Miers) Mennega	5	13	27.08	11.78	*Sideroxylon foetidissimum* Jacq. ssp. *gaumeri* (Pittier) Penn.	6	19	39.58	6.97
Thouinia paucidentata Radlk.	16	91	189.58	74.11	*Vitex gaumeri* Greenm.	6	9	18.75	43.08
TICUL FOREST (9 plots sampled)									
Acacia gaumeri Blake	2	4	22.22	2.85	*Acacia riparia* H.B.K.	3	8	44.44	16.36
Adelia oaxacana (Meull. Arg.) Hemsl.	2	3	16.67	2.26	*Alvaradoa amorphoides* Liebm.	1	3	16.67	14.73

Appendix I (Continued)

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
Bauhinia divaricata L.	3	5	27.78	3.06	*Brosimum alicastrum* Swartz	2	4	22.22	3.05
Bunchosia swartziana Griseb.	4	9	50.00	7.26	*Bursera schlechtendalii* Engl.	3	7	38.89	11.67
Bursera simaruba (L.) Sargent	9	65	366.67	313.78	*Caesalpinia gaumeri* Greenm.	6	67	372.22	134.77
Casearia corymbosa H.B.K.	3	4	22.22	3.34	*Cnidoscolus aconitifolius* (Mill.) Johnst.	5	7	38.89	5.27
Colubrina greggii S. Wats.	1	1	5.56	0.48	*Colubrina reclinata* (L'Hérit.) Brongn.	4	21	116.67	25.74
Diospyros anisandra Blake	2	29	161.11	16.63	*Diphysa carthagenensis* Jacq.	2	3	16.67	4.46
Eugenia axillaris (Sw.) Willd.	2	2	11.11	1.47	*Eugenia* sp.	3	6	33.33	6.79
Exostema caribaeum (Jacq.) R.&S.	4	18	100.00	18.04	*Guettarda elliptica* Sw.	8	63	350.00	42.85
Gymnopodium floribundum Rolfe	4	72	400.00	77.43	*Jatropha gaumeri* Greenm.	2	4	22.22	4.49
Karwinskia humboldtiana (R.&S.) Zucc.	3	18	100.00	39.25	*Lonchocarpus yucatanensis* Pittier	3	21	116.67	24.50
Lysiloma bahamense Benth.	1	2	11.11	24.62	*Mimosa bahamensis* Benth.	5	21	116.67	16.44
Neea choriophylla Standl.	5	16	88.89	21.71	*Piscidia piscipula* (L.) Sargent	7	16	88.89	116.91
Pithecellobium albicans (Kunth) Benth.	1	1	5.56	1.84	*Pithecellobium dulce* (Roxb.) Benth.	6	12	66.67	10.50
Pithecellobium leucospermum Brand.	3	3	16.67	2.13	*Randia gaumeri* Greenm. & Thompson	4	10	55.56	5.86
Semialarium mexicanum (Miers) Mennaga	1	3	16.67	4.93	*Sideroxylon foetidissimum* Jacq. ssp. *gaumeri* (Pittier) Penn.	5	17	94.44	13.28
Spondias mombin L.	1	1	5.56	50.44	*Thouinia paucidentata* Radlk.	9	87	483.33	105.65
TZUCACAB FOREST (27 plots sampled)									
Acacia gaumeri Blake	5	6	25.93	6.62	*Alvaradoa amorphoides* Liebm.	5	11	20.37	11.48
Ardisia escallonioides Schlecht. & Cham.	3	3	5.56	0.65	*Bauhinia divaricata* L.	9	13	24.07	3.22
Bourreria pulchra Millsp.	3	10	18.52	2.72	*Brosimum alicastrum* Swartz	3	5	9.26	2.57
Bursera schlechtendalii Engl.	1	1	1.85	0.16	*Bursera simaruba* (L.) Sargent	25	310	574.07	339.08
Caesalpinia gaumeri Greenm.	9	56	103.70	23.86	*Casearia corymbosa* H.B.K.	4	10	18.52	4.76
Celtis iguanea (Jacq.) Sargent	2	9	16.67	16.14	*Cnidoscolus aconitifolius* (Mill.) Johnst.	2	2	3.70	0.42
Coccoloba cozumelensis Hemsl.	11	30	55.56	13.20	*Coccoloba spicata* Lundell	20	70	129.53	36.64
Cochlospermum vitifolium (Willd.) Spreng.	10	15	27.78	19.35	*Colubrina greggii* S. Wats.	14	48	88.89	14.72
Cordia gerascanthus L.	3	3	5.56	1.42	*Cosmocalyx spectabilis* Standl.	1	1	1.85	0.44
Croton reflexifolius H.B.K.	22	184	340.74	54.28	*Diospyros anisandra* Blake	4	5	9.26	0.80
Diospyros cuneata Standl.	23	256	474.07	87.75	*Diphysa carthagenensis* Jacq.	1	1	1.85	0.19
Ehretia tinifolia L.	1	2	3.70	0.84	*Erythroxylum rotundifolium* Lunan	4	16	29.63	8.19
Eugenia axillaris (Sw.) Willd.	15	110	203.70	35.90	*Eugenia buxifolia* (Sw.) Willd.	17	62	114.80	16.75

Exostema caribaeum (Jacq.) R.&S.	5	23	42.59	7.69	*Guettarda combsii* Urban	12	32	59.26	9.86
Guettarda elliptica Sw.	2	5	9.26	0.88	*Guettarda gaumeri* Standl.	9	19	35.19	7.25
Gymnopodium floribundum Rolfe	3	15	27.78	6.36	*Hampea trilobata* Standl.	11	43	79.63	41.22
Krugiodendron ferreum (Vahl) Urban	2	3	5.56	0.62	*Lennea sepium* (Jacq.) Walp.	1	2	3.70	0.86
Lonchocarpus rugosus Benth.	21	102	188.89	42.19	*Lonchocarpus yucatanensis* Pittier	15	71	131.48	29.81
Luehea speciosa Willd.	7	48	88.89	29.93	*Lysiloma bahamense* Benth.	19	113	209.26	281.75
Malmea depressa (Baill.) Fries	9	23	42.59	13.18	*Malpighia punicifolia* L.	1	7	12.96	2.24
Mimosa bahamensis Benth.	1	1	1.85	0.15	*Nectandra coriacea* (Sw.) Griseb.	4	8	14.81	5.98
Neea choriophylla Standl.	17	99	183.33	49.22	*Piscidia piscipula* (L.) Sargent	25	104	192.59	76.73
Pithecellobium albicans (Kunth) Benth.	2	5	9.26	14.24	*Pithecellobium dulce* (Roxb.) Benth.	2	6	11.11	1.20
Pithecellobium leucospermum Brand.	1	1	1.85	0.21	*Psidium sartorianum* Nied.	9	33	61.11	9.94
Semialarium mexicanum (Miers) Mennega	17	46	85.19	14.77	*Spondias mombin* L.	3	3	5.56	7.19
Talisia olivaeformis (H.B.K.) Radlk.	7	14	25.93	3.69	*Thouinia paucidentata* Radlk.	15	58	107.41	28.44
Vitex gaumeri Greenm.	17	122	225.93	169.31	*Zuelania guidonia* (Sw.) Britt. & Millsp.	3	10	18.52	18.42
SAN MATEO FOREST (12 plots sampled)									
Acacia gaumeri Blake	4	11	58.33	25.02	*Alvaradoa amorphoides* Liebm.	2	2	8.33	7.13
Ardisia escallonioides Schlecht. & Cham.	4	6	25.00	10.79	*Bauhinia divaricata* L.	3	4	16.67	4.85
Bourreria pulchra Millsp.	6	13	54.17	17.46	*Bunchosia swartziana* Griseb.	7	13	54.17	10.52
Bursera simaruba (L.) Sargent	10	24	100.00	246.44	*Caesalpinia gaumeri* Greenm.	8	18	75.00	200.36
Caesalpinia velutina (B.&R.) Standl. (or *C. violacea* (Mill.) Standl.)	4	7	29.17	14.19	*Celtis iguanea* (Jacq.) Sargent	2	3	12.50	3.93
Coccoloba cozumelensis Hemsl.	7	19	79.17	56.95	*Coccoloba spicata* Lundell	4	9	37.50	36.46
Cordia gerascanthus L.	5	7	29.17	29.69	*Croton reflexifolius* H.B.K.	7	9	37.50	14.77
Diospyros cuneata Standl.	1	1	4.17	1.26	*Diphysa carthagenensis* Jacq.	9	43	179.17	59.80
Drypetes laterifolia (Sw.) Krug. & Urban	1	1	4.17	0.69	*Erythroxylum rotundifolium* Lunan	9	22	91.67	33.08
Eugenia axillaris (Sw.) Willd.	2	3	12.50	2.64	*Eugenia buxifolia* (Sw.) Willd.	9	38	158.33	25.82
Exostema caribaeum (Jacq.) R.&S.	8	14	58.33	25.50	*Guettarda gaumeri* Standl.	6	12	50.00	35.03
Gymnopodium floribundum Rolfe	7	69	287.50	121.67	*Hampea trilobata* Standl.	3	7	29.17	7.32
Jatropha gaumeri Greenm.	5	14	58.33	13.17	*Karwinskia humboldtiana* (R.&S.) Zucc.	1	2	8.33	10.32
Krugiodendron ferreum (Vahl) Urban	4	4	16.67	9.09	*Lennea sepium* (Jacq.) Walp.	4	8	33.33	22.26
Lonchocarpus yucatanensis Pittier	6	7	29.17	10.49	*Luehea speciosa* Willd.	1	3	12.50	11.23
Lysiloma latisiliquum (L.) Benth.	2	3	12.50	103.77	*Machaonia lindeniana* Baill.	3	13	54.17	16.57
Malmea depressa (Baill.) Fries	4	8	33.33	6.16	*Malpighia punicifolia* L.	7	43	179.17	71.78
Mimosa bahamensis Benth.	3	10	41.67	11.06	*Piscidia piscipula* (L.) Sargent	9	21	87.50	148.49
Pithecellobium albicans (Kunth) Benth.	1	2	8.33	10.07	*Pithecellobium leucospermum* Brand.	2	2	8.33	1.31
Psidium sartorianum Nied.	1	1	4.17	0.42	*Randia gaumeri* Greenm. & Thompson	3	5	20.83	6.97

APPENDIX I (Continued)

	FREQ.	STEMS	DENSITY	AREA		FREQ.	STEMS	DENSITY	AREA
Semialarium mexicanum (Miers) Mennega	5	12	50.00	41.68	*Talisia olivaeformis* (H.B.K.) Radlk.	2	4	16.67	44.74
Thouinia paucidentata Radlk.	11	52	216.67	150.81	*Vitex gaumeri* Greenm.	6	10	41.67	104.31
Zuelania guidonia (Sw.) Britt. & Millsp.	3	5	20.83	5.04					
OTHON BLANCO FOREST (27 plots sampled)									
Acacia gaumeri Blake	1	1	1.85	0.88	*Ardisia escallonioides* Schlecht. & Cham.	5	6	11.11	2.50
Astrocasia tremula (Griseb.) Webster	2	2	3.70	2.88	*Bauhinia divaricata* L.	5	6	11.11	3.09
Bourreria pulchra Millsp.	3	3	5.56	8.50	*Brosimum alicastrum* Swartz	6	11	20.37	8.61
Bunchosia swartziana Griseb.	12	39	72.22	48.54	*Bursera simaruba* (L.) Sargent	12	23	42.59	275.22
Caesalpinia gaumeri Greenm.	11	26	48.15	220.74	*Caesalpinia velutina* (Britton & Rose) Standl. (or *C. violacea* (Mill.) Standl.)	3	4	7.41	14.57
Celtis iguanaea (Jacq.) Sargent	1	1	1.85	0.16	*Coccoloba cozumelensis* Hemsl.	7	15	27.78	41.55
Coccoloba spicata Lundell	15	40	74.07	119.17	*Cochlospermum vitifolium* (Willd.) Spreng.	1	1	1.85	1.96
Cordia gerascanthus L.	6	10	18.52	32.03	*Cosmocalyx spectabilis* Standl.	17	40	74.07	78.04
Croton reflexifolius H.B.K.	15	32	59.26	37.28	*Diospyros cuneata* Standl.	2	2	3.70	10.74
Diphysa carthagenensis Jacq.	12	17	31.48	18.25	*Drypetes laterifolia* (Sw.) Krug & Urban	24	176	325.93	151.08
Erythroxylum rotundifolium Lunan	9	13	24.07	22.15	*Eugenia axillaris* (Sw.) Willd.	2	2	3.70	2.33
Eugenia buxifolia (Sw.) Willd.	2	2	3.70	0.59	*Exostema caribaeum* (Jacq.) R.&S.	1	2	3.70	1.78
Guettarda combsii Urban	8	11	20.37	60.30	*Guettarda gaumeri* Standl.	3	3	5.56	5.41
Gymnanthes lucida Swartz	21	248	459.26	268.54	*Gymnopodium floribundum* Rolfe	19	88	162.96	120.49
Hampea trilobata Standl.	7	8	14.81	8.88	*Jatropha gaumeri* Greenm.	3	3	5.56	5.65
Krugiodendron ferreum (Vahl) Urban	8	10	18.52	10.58	*Lennea sepium* (Jacq.) Walp.	1	1	1.85	3.32
Lonchocarpus rugosus Benth.	5	6	11.11	25.94	*Lonchocarpus yucatanensis* Pittier	8	24	44.44	74.15
Luehea speciosa Willd.	10	13	24.07	74.43	*Lysiloma latisiliquum* (L.) Benth.	4	4	7.41	120.79
Malmea depressa (Baill.) Fries	15	30	55.56	33.52	*Manilkara zapota* (L.) van Royen	25	144	266.67	416.19
Metopium brownei (Jacq.) Urban	11	16	29.63	213.61	*Nectandra coriacea* (Sw.) Griseb.	3	3	5.56	1.16
Piscidia piscipula (L.) Sargent	8	13	24.07	81.71	*Pithecellobium leucospermum* Brand.	1	1	1.85	10.92
Psidium sartorianum Nied.	8	35	64.81	104.72	*Semialarium mexicanum* (Miers) Mennega	9	15	27.78	25.49
Sideroxylon foetidissimum Jacq. ssp. *gaumeri* (Pittier) Penn.	1	1	1.85	1.40	*Spondias mombin* L.	4	4	7.41	56.98
Talisia olivaeformis (H.B.K.) Radlk.	4	8	14.81	6.99	*Thouinia paucidentata* Radlk.	16	41	75.93	165.44
Vitex gaumeri Greenm.	5	6	11.11	39.29	*Zuelania guidonia* (Sw.) Britt. & Millsp.	8	9	16.67	47.39

MIRADOR RUIN FOREST (12 plots sampled)

Bourreria pulchra Millsp.	2	4	16.67	17.53	*Brosimum alicastrum* Swartz	12	144	600.00	1341.83
Bunchosia swartziana Griseb.	1	1	4.17	1.60	*Bursera simaruba* (L.) Sargent	6	8	33.33	207.96
Chlorophora tinctoria (L.) Gaudich.	2	2	8.33	67.13	*Cordia geriscanthus* L.	1	1	4.17	0.13
Cosmocalyx spectabilis Standl.	5	13	54.17	47.60	*Croton lundellii* Standl.	9	58	241.67	76.48
Diospyros anisandra Blake	1	1	4.17	3.47	*Drypetes laterifolia* (Sw.) Krug & Urban	2	4	16.67	4.29
Eugenia axillaris (Sw.) Willd.	4	7	29.17	7.32	*Eugenia buxifolia* (Sw.) Willd.	2	3	12.50	4.14
Exostema caribaeum (Jacq.) R.&S.	1	4	16.67	24.66	*Ficus cotinifolia* H.B.K.	2	6	25.00	96.55
Ficus spp.	4	4	16.67	96.26	*Gymnanthes lucida* Swartz	1	1	4.17	0.38
Hybanthus yucatanensis Millsp.	2	2	8.33	1.05	*Karwinskia humboldtiana* (R.&S.) Zucc.	2	3	12.50	147.21
Krugiodendron ferreum (Vahl) Urban	1	1	4.17	2.42	*Malmea depressa* (Baill.) Fries	5	9	37.50	19.33
Manilkara zapota (L.) van Royen	3	4	16.67	4.72	*Nectandra coriacea* (Sw.) Griseb.	3	4	16.67	2.45
Piscidia piscipula (L.) Sargent	4	5	20.83	117.06	*Pithecellobium leucospermum* Brand.	1	1	4.17	0.79
Semialarium mexicanum (Miers) Mennega	1	1	4.17	2.15	*Spondias mombin* L.	3	4	16.67	111.74
Talisia olivaeformis (H.B.K.) Radlk.	4	4	16.67	9.59	*Thouinia paucidentata* Radlk.	8	17	70.83	195.82
Urera baccifera (L.) Wedd.	2	9	37.50	12.01	*Zuelania guidonia* (Sw.) Britt. & Millsp.	3	8	33.33	47.25

UITIZINA RUIN FOREST (12 plots sampled)

Astrocasia tremula (Griseb.) Webster	6	14	58.33	13.26	*Brosimum alicastrum* Swartz	12	111	462.50	2066.17
Bunchosia swartziana Griseb.	5	9	37.50	6.06	*Bursera simaruba* (L.) Sargent	5	6	25.00	273.74
Capparis indica (L.) Druce	7	19	79.17	14.73	*Capparis pachea* ssp. *oxysepala* (Radlk.) Iltis	6	9	37.50	21.00
Celtis iguanaea (Jacq.) Sargent	6	10	41.67	26.21	*Croton lundellii* Standl.	12	67	279.17	102.76
Croton reflexifolius H.B.K.	1	1	4.17	0.69	*Drypetes laterifolia* (Sw.) Krug & Urban	4	4	16.67	19.54
Ehretia tinifolia L.	2	3	12.50	76.86	*Hybanthus yucatanensis* Millsp.	7	13	54.17	6.78
Malmea depressa (Baill.) Fries	3	3	12.50	2.08	*Neea choriophylla* Standl.	1	1	4.17	1.08
Spondias mombin L.	3	5	20.83	25.85	*Talisia olivaeformis* (H.B.K.) Radlk.	3	4	16.67	40.80
Thouinia paucidentata Radlk.	6	9	37.50	168.49	*Urera baccifera* (L.) Wedd.	10	58	241.67	90.12

SUMMARY

Numbers in parentheses = percentages based on all species found at each site (Appendix I and II).

SITE	SPECIES	STEMS	AREA	SITE	SPECIES	STEMS	AREA
Calcehtok Forest	44 (69%)	1563 (92%)	2007 (96%)	Ticul Forest	36 (78%)	633 (97%)	1155 (97%)
Tzucacab Forest	54 (58%)	2263 (88%)	1575 (91%)	San Mateo Forest	45 (85%)	584 (97%)	1794 (98%)
Othon Blanco Forest	50 (75%)	1219 (97%)	3087 (95%)	Mirador Ruin Forest	30 (94%)	333 (99%)	2671 (99%)
Uitizina Ruin Forest	18 (78%)	346 (98%)	2956 (99%)				

APPENDIX II

Presence of 68 rarer species (Importance Values <1.0 in all sites) at five forest sites and two ruin sites in the north-central Yucatan Peninsula, Mexico. CAL = Calcehtok forest; TIC = Ticul forest; TZU = Tzucacab forest; SAN = San Mateo forest; OTH = Othon Blanco forest; MIR = Mirador ruin forest; UIT = Uitizina ruin forest.

	CAL	TIC	TZU	SAN	OTH	MIR	UIT
Acacia collinsii Safford	•		•	•			
Acacia dolichostachya Blake						•	•
Acacia pennatula (Schlecht. & Cham.) Benth.	•	•	•				
Adelia barbinervis Schlecht. & Cham.			•				
Agonandra obtusifolia Standl.					•		
Albizia tomentosa (Micheli) Standl.		•	•		•		
Allophyllus cominea (L.) Swartz			•				
Bauhinia ungulata L.			•				
Caesalpinia yacatanensis Greenm.			•				
Callicarpa acuminata H.B.K.			•				
Casearia randioides Lundell	•						
Casimiroa tetrameria Millsp.			•				
Cecropia obtusifolia Bertol.			•				
Cedrela odorata L.					•		
Ceiba aesculifolia (H.B.K.) Britt. & Baker	•	•		•	•		
Chiococca alba (L.) Hitch.			•				
Chrysophyllum mexicanum Brand. ex Standl.			•	•	•		
Coccoloba acopulcensis Standl.							•
Cordia dodecandra DC.					•		
Cornutia pyramidata L.			•				
Cupania glabra Sw.			•		•		
Dalbergia glabra (Mill.) Standl.	•				•		
Diospyros verae-crucis Standl.			•				
Diospyros yatesiana Standl.			•				•
Dipholis salicifolia (L.) A. DC.			•		•		
Duranta erecta L.			•				
Enterolobium cyclocarpum (Jacq.) Griseb.	•						
Erythrina americana Mill.	•	•					
Eugenia laevis var. *gaumeri* (Standl.) McVaugh			•				
Exostema mexicanum Gray			•				
Guazuma ulmifolia Lam.	•	•					
Helicteres baruensis Jacq.	•		•				
Heliocarpus americanus L.			•				
Jacquinia macrocarpa Cav.	•						
Koanophyllon albicaule (Sch. Bip. ex Klatt) K.&R.			•				
Leucaena leucocephala (Lam.) deWit			•				
Malpighia glabra L.			•				
Neomillspaughia emarginata (Gross.) Blake	•		•	•	•		
Nissolia fructicosa Jacq.			•				
Parmentiera aculeata (H.B.K.) Seem.	•						
Phyllostylon rhamnoides (Poisson) Taubert	•						
Piper sempervirens (Trel.) Lundell						•	
Pisonia aculeata L.	•	•					
Platymiscium yucatanum Standl.				•	•		
Plumeria alba L.	•						

Appendix II (Continued)

	CAL	TIC	TZU	SAN	OTH	MIR	UH
Plumeria obtusa L.					•		
Pouteria campechiana (H.B.K.) Baehni			•				•
Pouteria unilocularis (Donn. Sm.) Baehni					•		
Pseudobombax ellipticum (H.B.K.) Dugand					•		
Randia longiloba Hemsl.	•						
Randia truncata Greenm. & Thompson	•			•			
Rehdera trinervis (Blake) Moldenke			•				
Sabal mexicana Martius			•		•	•	
Senna atomaria (L.) Irwin & Barneby	•	•	•	•	•		
Senna racemosa (Mill.) Irwin & Barneby				•			
Sideroxylon obtusifolium (R.&S.) Penn.			•				
Simarouba glauca DC.			•				
Spondias purpurea L.	•						
Tabebuia rosea (Bertol.) DC.			•				
Thevetia gaumeri Hemsl.			•				
Trichilia arborea C. DC.			•				
Trichilia glabra L.			•				
Ximenia americana L.			•				
Xylosma flexuosum (H.B.K.) Hemsley			•				
Zanthoxylum caribaeum Lam.	•						
Zemenia frutescens (Mill.) Blake			•				
Unknown No. 1		•					
Unknown No. 2			•				
Totals	20	8	41	8	17	2	4