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A CLASSIFICATION AND ORDINATION OF THE TREE COMMUNITY OF TIKAL NATIONAL PARK, PETÉN, GUATEMALA

Mark D. Schulze[1] [2] and David F. Whitacre[2]

ABSTRACT

We studied tropical forest composition and structure in relation to topographic and edaphic variation, with the goal of understanding the factors that determine species distributions and the degree to which species composition can be predicted by local environmental conditions. We sampled the tree community of Tikal National Park in Petén, Guatemala, using 294 sample plots of 0.041 ha each, totaling 12.1 ha, placed systematically along topographic gradients. In addition to recording tree and sapling occurrences, we took data on environmental factors, vegetation structure, and disturbance history. Indirect and direct gradient analyses were performed (using DCA and CCA, respectively) to investigate variation along a predominant topographic/edaphic gradient and along gradients of disturbance and light availability. We used TWINSPAN analysis and ranked sorting of samples by environmental variables to produce a forest type classification practical for field use. Individual species distributions were examined with respect to edaphic conditions, understory light availability, and natural forest disturbance. Though topographic relief is moderate in the area, several edaphic factors varied strongly and predictably, though not monotonically, from hillcrests to low-lying depressions, and exerted a predominant influence on tree community composition. Most tree species distributions were strongly correlated with topography and associated edaphic conditions, and distribution patterns were consistent among widely separated topographic gradients, suggesting that environmental conditions, rather than historical events, were largely responsible for these patterns. Many of the less shade-tolerant species also showed positive relationships with natural disturbance history and degree of canopy opening. Treefall gaps have different functional significance for regeneration at different points along the topographic/forest type continuum, due to correlated differences in canopy height, canopy evenness, and light penetration. Hence, many species that appear to depend on treefall gaps for colonization and recruitment in upland portions of the continuum, are less confined in their exploitation of lower regions of the gradient, where canopy discontinuities may provide sufficient light for seedling persistence and recruitment. Thus many highly light-demanding species were not associated with treefall gaps, and appeared capable of colonizing relatively open lowland forests. Distribution patterns and disturbance/light responses are discussed for individual species, which are provisionally placed into ecological guilds based on apparent tolerances for light levels and edaphic and other environmental factors. In Tikal, much of the natural variation in forest composition and structure can be related to topography and edaphic conditions.

RESUMEN

Con el objeto de entender los factores que determinan la distribución de especies y el nivel en que la composición de especies puede ser predecida por condiciones ambientales locales, nosostros

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[1] Current Address: 208 Mueller Lab, Department of Biology, Pennsylvania State University, University Park PA 16802, U.S.A.
[2] The Peregrine Fund, 566 West Flying Hawk Lane, Boise ID 83709, U.S.A.

SCHULZE, M. D., and D. F. WHITACRE. 1999. A classification and ordination of the tree community of Tikal National Park, Petén, Guatemala. Bull. Florida Mus. Nat. Hist. 41(3): 169-297.

estudiamos la composición y estructura del bosque tropical en relación a variaciones topográficas y edáficas. Muestreamos la comunidad de árboles del Parque Nacional Tikal en Petén, Guatemala, mediante el uso de 294 sitios de muestreos de 0.041 ha cada uno, totalizando 12.1 ha, colocadas sisemáticamente a lo largo de gradientes topográficos. Además de registrar la ocurrencia de árboles y renovales, también recolectamos información sobre factores ambientales, estructura vegetal e historia de alteraciones. Se realizaron análisis de gradiente directos e indirectos (usando DCA y CCA, respectivamente) con el objeto de investigar la variación a lo largo de los gradientes topográficos/edáficos predominantes, y a lo largo de gradientes de alteración y disponibilidad de luz. Produjimos un sistema de clasificación de tipos de bosque para uso práctico en el campo mediante el análisis y ordenamiento de las muestras de acuerdo a variables ambientales y usando TWINSPAN. La distribución de cada especie fue examinada con respecto a las condiciones edáficas, a la disponibilidad de luz, y a las alteraciones naturales del bosque. Aún cuando el relieve topográfico es moderado en el área de estudio, varios factores edáficos mostraron una fuerte y predecible variación desde las cimas a los valles, y aunque esta no fue monotónica, impuso una influencia predominante en la composición de la comunidad arbórea. La distribución de la mayor parte de las especies arbóreas estuvo fuertemente correlacionada con la topografía y condiciones edáficas asociadas, siendo los patrones de distribución similares entre gradientes topográficos separados. Estos resultados sugieren que condiciones ambientales, más que eventos históricos, fueron mayormente las responsables de estos patrones. Varias de las especies menos tolerantes de sombra también mostraron correlaciones positivas con la historia de alteraciones naturales y el grado de apertura del dosel. La significación funcional para la regeneración de los claros producidos por árboles caídos, fue diferente a lo largo del gradiente topográfico y del tipo de bosque, debido a diferencias correlacionadas con la altura y homogeneidad del dosel y con la penetración de luz. Debido a esto, varias especies que parecen depender de los claros de árboles caídos para la colonización y desarrollo de renovales en las porciones de tierras altas, están menos restringidas en las regiones bajas del gradiente topográfico, donde las discontinuidades del dosel pueden proveer suficiente luz para la persistencia de plántulas y el desarrollo de renovales. Así, muchas especies con una alta demanda de luz no estuvieron asociadas con los claros de árboles caídos y aparecieron capaces de colonizar áreas relativamente abiertas del bosque de tierras bajas. En este trabajo, los patrones de distribución y de respuesta al disturbio y a la presencia de luz se discuten a nivel de especies, las que son puestas provisionalmente en agrupaciones ecológicas basadas en la tolerancia aparente a los niveles de luz y a caracteres edáficos y a otros factores ambientales. En Tikal la mayor parte de la variación natural de la composición y estructura del bosque, puede ser relacionada a las condiciones topográficas y edáficas.

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INTRODUCTION

"If the traveler notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colors are around him, but he rarely sees any one of them repeated. Time after time he goes toward a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, til on another occasion he stumbles into one on accident" (Wallace 1878). As Alfred Russel Wallace noted, two of the more distinctive characteristics of many tropical and subtropical forests are high tree species richness and a high ratio of "rare" species to common species in a given patch of forest (Hubbell 1979; Hubbell and Foster 1986b). One of the fundamental ecological questions pertaining to tropical forests continues to be–what are the mechanisms that facilitate coexistence of so many tree species? Ironically, it is the high species diversity itself that has hampered investigations of the forces structuring tropical plant communities; adequate sample sizes for the majority of tree species are often hard to obtain, and patterns of species occurrence are difficult to discern amidst constant variation in species composition.

The niche diversification paradigm, although invoked in early explanations of tropical plant diversity (e.g. Ashton 1969), has been largely abandoned for tropical forests, owing to the belief that small scale environmental variability in lowland tropical areas is not sufficient to allow niche divergence of such a large number of species. Hubbell and Foster (1986a) found that the coexistence of tree species on Barro Colorado Island (BCI) in Panama was best explained by stochastic processes and argued that adequate niche segregation to permit species coexistence was highly unlikely in tropical tree communities, because high species diversity results in largely unpredictable species identity of neighboring individuals, rendering competitive niche divergence improbable. Stochastic processes conveniently explain species coexistence, but do not adequately explain observations of distinct species distribution patterns and patterns of species co-occurrence. More recently Hubbell and Foster (1990) found evidence of weak density dependent selection for many of the trees on BCI, suggesting that, as hypothesized by Janzen (1970) and Connell (1971), increased sapling mortality rates under conspecifics may play a role in preventing competitive exclusion. Stochastic processes clearly play a role in shaping tropical tree communities, but some question whether random processes are the principal forces in community dynamics (Terborgh et al. 1996).

Other workers have emphasized treefall gaps as a major influence on tree species composition and diversity in tropical forests (Ricklefs 1977; Denslow 1980, 1984, and 1987; Orians 1982; Pickett 1983; Brokaw 1985; Brandani et al. 1988; Nuñez-Farfán et al. 1988). Much attention has focused, with limited success, on defining ecological guilds of tropical tree species based on their modes of exploitation of treefall gaps. The one undisputed dichotomy in gap exploitation is between pioneer and non-pioneer species. Some authors also recognize an intermediate group of long-lived pioneer species (Whitmore 1992; Finegan 1996), or large gap specialists (Denslow 1980). This long-lived pioneer class has not yet been adequately defined with regard to life history attributes, but is a first step in recognizing the considerable variation represented within the catch-all 'climax' or 'mature forest' species category (Finegan 1996). The pioneer/non-pioneer dichotomy essentially serves only to separate a handful of tree species from the remaining hundreds of species within a given community. It is increasingly recognized that light environments (Chazdon and Fetcher 1984; Chazdon 1988; Canham et al. 1990) and species response patterns to light are more varied than implied by the above dichotomy or even the pioneer/long-lived pioneer/mature forest species trichotomy (Welden et al. 1991; Clark and Clark 1992).

Topographic and edaphic gradients have long been recognized as important influences on species composition and structure of forest tree communities (e.g Whittaker 1956, 1960). However in the tropics, after some early attempts to relate plant species distributions to edaphic variation (e.g. Lundell 1937, Ashton 1969), consideration of small-scale topographic and edaphic variation, until recently, was largely absent from studies of tropical forest composition and community structure. There is now ample evidence to support the hypothesis that edaphic mosaics significantly increase the species diversity of tropical forests (Gentry 1981). Furthermore, it is clear that even small-scale variation in topography or edaphic conditions can have a profound effect on plant species distributions in many, if not most, tropical forests (Furley 1979; Lescure and Boulet 1985; Lieberman et al. 1985b; Hubbell and Foster 1986b; Kahn 1987; Basnet 1992; Johnston 1992; Steege et al. 1993; Oliveira-Filho et al. 1994; ter Tuomisto et al. 1994; Clark et al. 1995). Even with renewed research interest in edaphic associations of tropical plants, our understanding of community responses to environmental gradients in the tropics still lags far behind that in the north-temperate zone, where gradient analysis is a well-developed tradition (e.g. Bray and Curtis 1957; Whittaker 1967). The majority of studies published to date have focused on a small subset of the woody flora (e.g. palms–Kahn 1987; Clark et al. 1995), or on non-woody taxa (Tuomisto et al. 1994). There have been few community-level studies of tree species responses to edaphic gradients in the tropics, and even less is known about the interactive effects on vegetation of edaphic and other environmental factors, including variation in light availability, over topographic gradients.

With an understanding of the patterns of spatial heterogeneity in species occurrence within tropical forests, and of the processes underlying these patterns, we would be better able to predict the long-term effects of human activities in these forests and to inform conservation and management efforts. The ecological associations of even most economically valuable tree species are not known with precision, and it is not known whether species responses to disturbance will vary under different edaphic conditions. In our study area, efforts to maximize conservation of forest biota in the human-impacted buffer and multiple use zones within the Maya Biosphere Reserve serve as another example of the need to understand species responses to natural environmental variation. In this region agricultural activities are focused in certain portions of the topographic continuum, and remnant forest patches therefore rarely include these portions of the vegetation continuum; this may result in local extirpations of plant and animal species restricted to these habitats.

In the work reported here we attempt to document tree species responses to both edaphic conditions and light availability as a means of understanding patterns of variation in forest structure and composition. We attempt to understand the degree to which species distribution patterns are predictable and to evaluate mechanisms potentially contributing to tree species richness. We divide the vegetation continuum into a functional forest type classification, providing a basis for quantitative study of variation in plant and animal communities along the predominant environmental gradient. Additionally we present a provisional guild classification of tree species in the Tikal region, incorporating both light and edaphic tolerances, and responses to natural disturbance.

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Nicholas Brokaw served as an early mentor to M. Schulze and was an inspiration for the research reported here.

STUDY AREA

Tikal National Park lies in the northeastern corner of the department of Petén, Guatemala at 17° N latitude. The forest here is classified as Subtropical Moist (Holdridge 1971) or Tropical Semi-deciduous (Pennington and Sarukhan 1968), with annual rainfall of 1,300–1,500 mm and a pronounced dry season from February through May. The Tikal area is significantly drier than subtropical moist forest in northwestern Belize, just 70 miles to the northeast (Brokaw and Mallory 1993). While tree species diversity is considerably lower in northeastern Petén than in wetter tropical forest at lower latitudes in Central and South America, it is still extremely high relative to temperate zone forests, and the forest is subject to similar dynamic processes as those of true rain forests farther south. Brokaw and Mallory (1993) estimated between 250 and 300 tree species for the Rio Bravo area of northwestern Belize. We believe the figure to be somewhat lower for Tikal National Park as it represents a smaller area (57,600 vs 82,000 ha) with less topographic diversity and rainfall than Rio Bravo, but a conservative estimate of the total tree list for Tikal is over 200 tree species. In our study we sampled 142 tree species and observed 185.

The entire study region may have been deforested at the peak of Mayan occupation of the area, ca. 1000 years ago, during which time some species may have been locally extirpated and the relative abundances of the remaining species may have been temporarily or permanently shifted. Despite this history of large-scale disturbance, the forest can be considered mature, and has undoubtedly achieved some form of equilibrium, with respect to structure, composition, and patterns of species abundance. Although as recently as the 1960s portions of Tikal National Park were subjected to low intensity logging, the forest areas that we sampled lacked evidence of logging disturbance.

Topographic variation is not extreme in Tikal National Park, with the lowest areas being 160 m and the highest 400 m above sea level. With the exception of a large karst area in the northwestern one-eighth of the park, where slopes exceeding 25° are common, the hills in Tikal are relatively gentle, often standing only 30 m above nearby lowland basins. In contrast, the variation in vegetation character can be drastic even over short distances. Tall-canopied, open-understoried, palm-rich forest can be found within a few hundred meters of low, nearly impenetrable, xerophytic scrub swamp forest (Fig. 1).

Soils in Tikal National Park are all limestone-derived clays but vary considerably in texture from the upper regions of slopes, referred to hereafter as "upland" sites, to the low-lying depressions known locally as "bajos." In addition to clay content and texture, other significant differences between the soils are in the depth, degree of weathering, pH, mineral and organic matter content, and amount of rock fragments present. Soils in uplands are usually shallow and of moderate clay content, with a high percentage of limestone fragments, providing good to excessive drainage. In the lowest lying areas the soil is consistently more than 70 cm deep (often >140 cm) and clay-rich, with few or no rocks in the upper 70 cm; the combination of nearly pure clay soil and low topographic position results in poor drainage in the wet season and edaphic drought in the dry season, as the water present in the soil is bound strongly to clay particles.

In this manner topography and associated edaphic characteristics combine to create impressive changes in the vegetation over short distances. As soil characters and topographic position are strongly correlated, vegetation characteristics are typically similar along the same regions of the topographic gradient at different sites, tempting designation of "forest types." Development of a forest type classification system provides a practical means to compare species distributions, forest structure, and microclimate along what is in reality a vegetative continuum, and hence is fundamental to any phytosociological analysis.

METHODS

We used a relatively small plot size (0.041 ha) to adequately sample the tree community despite patchy species distributions, and to capture the full range of topographic variation in our study area. This allowed us to distribute plots over a 17 km by 9 km portion of Tikal National Park. Small sample plots provide more quantitative data with tighter connections between vegetation samples and environmental variables than do the less labor-intensive, point-based nearest individual or presence/absence sampling techniques (Clark et al. 1995). In 1992, we used circular plots to sample trees ≥7.5 cm dbh, and belt transects of 1.76 m x 20 m for sampling trees < 7.5 cm dbh, and >1 m tall. Plots were regularly spaced at predetermined locations along transects that were sited in a stratified random fashion, and along (50 m from) a series of archeological transects that bisect Tikal National Park from north to south and east to west. Inter-plot distances ranged from 100 m to 300 m. A total of 201 plots were sampled in 1992, yielding a total area of 7.6 ha.

In 1993 a streamlined supplemental sampling was completed on 93 plots also of 0.041 ha but in a more practical shape, 10 m x 41 m. These plots were spaced 100 m apart along well-developed topographic gradients that were selected on a topographic map. Despite differences in plot shape between 1992 and 1993 samples, we detected no differences in the number of stems recorded per plot by the two methods and therefore treated the samples as equivalent.

Our methods of plot placement were not strictly random. We felt that an even and widespread sampling of Tikal National Park would be more useful than a truly random sample, and opted for a stratified random design. Gauch (1982) makes a strong case that random placement of study plots is rarely achieved by plant ecologists, and that systematic placement is often a better approach to sampling. To avoid observer bias in plot selection, we determined plot locations before entering the field.

For each 0.041 ha plot in 1992, all trees ≥ 7.5 cm in diameter at breast height (dbh = 1.3 m) were measured, identified to species, surveyed for presence of aeroids or epiphytes on the trunk and in the canopy, and for vines > 2.5 cm in diameter (for the palm *Cryosophila stauracantha* all individuals with a trunk reaching breast height were recorded, regardless of dbh). Our 7.5 cm cut-off differs from the traditional minimum diameter limit of 10 cm, but it was considered more appropriate in our area, since in some vegetation types trees of >10 cm dbh were only sparsely scattered amongst a sea of saplings and stunted trees. When an individual could not be identified to species in the field, a sample was collected if possible.

Three measures of canopy height were taken per plot, using a Haga clinometer and measuring tape: that of the tallest tree in the plot, modal height of the upper canopy surface, and the lowest point of the upper canopy surface within the plot. Evenness of the canopy surface was classified into one of four categories: even, even with emergents, uneven, or broken. Soil depth was recorded at three locations 10 m apart in each plot. Two devices were used for this measurement: a 70 cm long, pointed-tipped rebar staff pounded in with a five pound mallet, and a 140 cm long auger. The maximum soil depth was considered to be that at which penetration of the rebar probe was halted, or at which the substrate changed to whitish decomposed limestone in the case of the auger. To supplement these readings, soil pits were excavated to the level of un-decomposed limestone fragments (c horizon), or 140 cm if no such layer was encountered, in 80 of the 201 plots. Slope and aspect were recorded for each plot using a clinometer and compass, and one of eighteen topographic positions was assigned (Table 1).

We collected soil samples from 15 cm to 30 cm depth at the center of each sample plot. These were evaluated by a single observer, using the feel method

Table 1. Correspondence between topographic positions, 18 topographic position codes used to describe them, and 11 recognized forest types and their codes.

Topographic Code	Description	Forest Code	Forest Type Name
1	hilltop	1	Dry Upland forest
2	upper 1/3 of hill	1	" "
3	rolling upland with Mayan house mounds or rock outcrops	1	" "
4	middle 1/3 of hill, or rolling upland without rock	2	Standard Upland forest
5	lower 1/3 of hill	2	" "
6	upper 1/3 of slope, with ravine, "shelf" or other mesic factor	2	" "
7	middle 1/3 of slope, with ravine, "shelf" or other mesic factor	3	Mesic Upland forest (1)
8	lower 1/3 of slope, with ravine, "shelf" or other mesic factor	3	" "
9	upland plain, not adjacent to low-lying area	4	Mesic Upland forest (2)
10	upland plain, adjacent to low-lying area	4	" "
11	elevated depression surrounded by upland forest	*	Cohune forest
12	base of hill	5	Hillbase forest
13	low-lying area 200-300 m from upland area, slope detectable	6	Sabal forest
14	low-lying area >300 - 500 m from upland area, slope detectable	6	" "
15	low-lying area >400 m from upland area and < 800 m from upland	7	Transitional forest
16	low-lying area > 800 m from upland area (periphery of Bajo depression)	8	Tall Scrub Swamp
17	low-lying area, > 1 km from upland area (central portion of Bajo depression)	9	Low Scrub Swamp
18	low-lying area with standing water in dry season	10	Mesic Bajo Forest
18	" "	11	True Swamp

* Due to its rarity at Tikal, Cohune Forest was not given a forest type code.

(Foth 1972) for clay content and texture, and visual inspection for rock content. We assigned each of the variables a value using an 11-point scale (0–10). The laboratory of la Dirección Tecnica de Riego y Avenamiento in Guatemala City subjected a subset of 72 samples to quantitative analyses. Textural ratings based on the feel method were highly correlated with percent clay in laboratory analyses ($r^2 = 0.84$, $p = 0.000$) and when regressed on lab textures (adj. $r^2 = 0.71$ and $p = 0.1 \times 10^{-14}$). Based on this high correlation, we used our manual textural ranking rather than laboratory results in ordinations, allowing us to use 201 samples rather than 72.

For each plot all treefall gaps intersecting the plot, and those within 10 m of the perimeter, were recorded and their length and width estimated. Young gaps were recognized using Brokaw's (1982) criteria: holes in the forest canopy down to a minimum height of 2 m. For older gaps (equivalent to "building-phase" forest) boundaries were judged as the point of discontinuity between the upper surface of regenerating vegetation and the surrounding intact canopy. To gain some insight into the relative ages of gaps, the height range and modal height of regenerating vegetation were estimated, and all fallen trees in the gap were estimated for diameter and placed into one of five categories based on their degree of decomposition. We used this same system to record all fallen trees within sample plots whether or not a canopy gap was currently present.

Disturbance history of each plot was rated with respect to three variables: disturbance type (natural, human-induced or uncertain), age since disturbance (0 to 2 yrs, 2+ to 5 yrs, 5+ to 10 yrs, and 10+ yrs) and intensity (none, light, moderate, and heavy, based on the size of disturbance and percent of plot affected). Determination of past disturbances was based only on structural evidence (i.e. presence of large diameter logs, stumps, uniform canopy noticeably lower than surrounding forest indicating regenerating gap, etc.) and not on floristic composition. This avoided the circularity of using suspected pioneer species as indicators of past disturbance. Time since disturbance was gauged using the modal height and diameter of vegetation within the disturbed area, and degree of decomposition of the fallen trees or stumps. For calibration of this somewhat subjective aging technique we used personal observations of regeneration in gaps of known age and the decomposition states of stumps of known age, in addition to published accounts of regeneration and decomposition rates (Lang and Knight 1977). Since only structural evidence was admissible in this classification we were only able to identify disturbances in the range of 0-20 years old. Older disturbances, or smaller disturbances leaving evidence for a shorter duration, were not recorded, although in many plots that lacked this concrete evidence species composition indicated that a disturbance had occurred.

The understory subsample was an arm's width (176 cm) transect 20 m long across the diameter of the circular sample plot, following an east to west compass line. On this transect all plants $\geq$ 1 m tall and < 7.5 cm dbh were identified, grouped into one of three diameter classes (0–2.49 cm, $\geq$ 2.5–4.99 cm, $\geq$ 5.0–7.5 cm), and their height estimated. All vines intersecting the transect (at height $\leq$ 2 m) were recorded and placed in diameter classes (as above) but were not identified. Dead standing vegetation was recorded in the same way as live vegetation. Dead hanging vegetation 2 m or lower was recorded in one of the three diameter classes. Often a mass of dead hanging vegetation was encountered, rather than one or two easily measurable branches. In this case we estimated the equivalent number of individuals 25 cm long, of each of the three diameter classes, that were contained in the mass. We also recorded ground cover density using a sighting tube with cross-hairs to make 25 presence/absence readings ("hits" on green foliage). These were taken parallel to the transect line, but 1 m to the side in order to avoid the effects of trampling. To supplement measurements of ground cover density, we visually estimated the percentage of total ground cover accounted for by monocotyledonous plants (primarily grasses and sedges).

Canopy cover was recorded using a spherical densiometer (Lemmon 1957). Five readings were taken, one at the center of the arms-width transect, and one each at 5 m and 10 m in both directions along the transect line. Limited sampling of understory light intensity was conducted using hemispherical photographs at sites in each topographic position lacking any signs of recent (within 15 years) canopy disturbance. Photographs were digitized and analyzed using Hemiphot (ter Steege 1996) for canopy cover and relative light intensity. These measures do not correspond with vegetation sampling plots, but provide more precise estimates of average understory light intensity than do densiometer readings.

For the 1993 sampling we omitted many of the measurements taken in 1992, as the main purpose of this effort was to increase our sample size for trees larger than 7.5 cm dbh, which were sampled in the same manner as the year before. Understory vegetation was not sampled. Topographic position, slope and modal canopy height (visual estimate), were recorded for each plot. A soil sample was also taken. Disturbance history and gap occurrence were recorded, although sizes of treefall gaps were not quantified.

DATA ANALYSIS

Plant species data analyzed were the number of individuals per species per 0.041 ha plot (for trees of 7.5 cm diameter or greater), and the number of individuals per 20 m x 1.76 m transect for trees at least 1 m in height but < 7.5 cm diameter.

Ordinations

Ordinations were performed using CANOCO (ter Braak 1987a), including its subroutines for Detrended Correspondence Analysis (DCA, Hill 1979a) and Canonical Correspondence Analysis (CCA). Vegetation classifications were produced by a nested sorting of samples by topographic and edaphic variables and were then compared to a species-based classification using two-way indicator species analysis (TWINSPAN, Hill 1979b) and to the first axis scores produced by DCA ordination of samples.

For all ordinations, species with fewer than five individuals encountered in the sampling were omitted from the ordination and those with fewer than 15 were made passive, i.e. their positions were plotted in ordination space but did not enter into the ordination calculations. Several species displayed bimodal distributions, having abundance peaks along two distinct portions of the predominant environmental gradient. Such bimodality violates a primary assumption of both DCA and CCA (Jongman et al. 1987; ter Braak 1987b), namely that species show unimodal responses across coenoclines. To prevent such bimodal species from skewing ordinations, we split each such species into two "pseudo-species" for all full-gradient ordinations (14 species were split into pseudo-species). Ten samples were eliminated from the primary ordinations as outliers; these samples were all from highly disturbed areas. The final DCA ordination of the full gradient included 283 samples, 98 active species and 17 passive species.

Indirect gradient analysis

Our initial analysis utilized Detrended Correspondence Analysis (DCA) for an unconstrained ordination of samples and species. The purpose of this ordination was to reveal patterns within the data set using an objective method and to provide a means of evaluating constrained ordinations produced by CCA and forest type classifications. Detrending by second-order polynomial and by segments yielded similar results—we chose to use detrending by segments for the final ordinations. Species were scaled as weighted mean sample scores and samples as weighted mean species scores.

Direct gradient analyses

In addition to these unconstrained ordinations (indirect gradient analyses) we used CCA to directly examine the association between patterns of tree species composition and patterns of environmental variation at Tikal. Environmental variables were incorporated into CCA as described below, and were centered and standardized prior to analyses.

Physical factors.— After initial examination of environmental variables we decided to use only four such variables for analysis of the large tree data: topographic position (18-point ordinal scale), soil clay content (11-point ordinal scale), soil rock fragment content (11-point ordinal scale), and slope (degrees). Our ordinal ranking of clay content was highly correlated with percent clay content as determined by lab analysis of 72 samples (Pearson correlation coef. = 0.844, $p < 0.001$). Although we collected data on soil depth for 201 samples, comparison of our depth measures with actual depth revealed by soil pits eroded our confidence in this index. Furthermore, comparison of soil pit depths and soil texture indicated that soil depth and clay content were closely correlated (Pearson correlation coef. = 0.854, $p < 0.001$) with deep, clay-rich soils occurring in low-lying areas and shallower soils, lower in clay, occurring in upland sites. Slope aspect had no detectable effect on vegetation and was omitted from consideration.

Natural disturbance history.— Recent human disturbance was not a significant factor in any of the plots; in this study "disturbance" therefore refers to natural canopy openings from treefalls. In the initial CCA ordination, data on disturbance and degree of canopy opening were not included. In later analyses, variables reflecting disturbance history and degree of canopy opening were used as primary variables, with topography, soil texture, soil rock content, and slope included as covariables, in order to remove their effects and allow focus on the primary (disturbance) variables. Using Monte Carlo tests we evaluated the significance of six variables reflecting canopy disturbance and understory environment: intensity of canopy disturbance, age of canopy disturbance, number of gaps per plot, total gap area within the 0.04 ha plot, mean canopy height, and percent canopy opening (mean). Following forward selection of disturbance and light intensity variables, we used CCA to examine the relation between disturbance history and light availability and distributions of juvenile trees (<7.5 cm dbh) and treelets (arborescent plants that do not attain diameters ≥10 cm). For adult trees only the intensity and age of canopy disturbances were used as primary variables, with the four environmental variables as covariables, as current light environment may have little relation to conditions present during the establishment and recruitment of adults.

Forest Type Classification

In our preliminary designation of forest types we used a hierarchical sorting of samples based on four environmental variables in the following order: topographic position, soil clay content, slope, and soil rock content. All samples were sorted first by topographic position, and then within each topographic class by soil clay content, followed by slope and finally rock content. The relative importance given to these four environmental variables was based on the strength of correlation of each variable with species data, as determined by CANOCO (Monte Carlo significance tests and length of lines in biplots). This hierarchical sorting yielded a sample ordering consistent with that obtained from the first axis of the CCA ordination. From the hierarchical ordering we grouped samples into 11 forest "types." Breakpoints between these 11 forest types coincided with breakpoints between the original 18 topographic positions. To a large degree, forest type designation was merely a condensation of topographic positions, but information on species composition was also considered in arriving at groupings of the 18 topographic positions into 11 groups that reflected observable differences in the forest along the topographic gradient.

The above method of forest type classification is straightforward and relies primarily on topographic and environmental data, but it does require some subjectivity in the actual dividing of the sample sequence into forest types. For this reason we felt it necessary to compare this classification to an independent, objective grouping of species and samples. To achieve this, we applied TWINSPAN to the full data set and then to two subsets (upland and low-lying sites) to classify samples into "pseudo-forest types" based on species composition. Classifications resulting from TWINSPAN were compared to the hierarchical classification described above, which was in turn compared to sample ordering produced by the first axis sample scores of the DCA ordination, to insure consistency between forest type designations and patterns of sample distribution in ordination space.

Distribution Patterns For Individual Species

To supplement the full community ordinations provided by DCA and CCA, we examined individual species abundance patterns along the topographic gradient. After testing several methods, we favored grouping samples into the 11 final forest types/topographic zones. Using the mean number of occurrences of each species per sample (with standard error) in each forest type, we were able to study distribution patterns of adults and juveniles in greater detail, and adequately represent bimodal distributions.

Tests of Responses to Light and Natural Disturbance

Our goals in this portion of the study were to: (1) test the hypothesis that the impact of gaps and other canopy disturbance on understory light environments (as revealed by tree regeneration patterns) varies with topography, (2) determine whether there are some species that require high light intensity for regeneration, but for which most regeneration does not occur in treefall gaps, (3) compare associations of saplings versus adult trees of a given species with disturbance and light conditions, to see whether different conditions are required for attainment of sapling and adult size, (4) assign tree species to response guilds with respect to disturbance and light environment, and (5) determine whether small-scale differences in canopy opening (e.g. between <10% and 10–20% canopy opening) have an effect on species distribution within a habitat type.

Tests of the effects of canopy opening, disturbance history, and topographic position were accomplished using multiple random permutation procedure Chi-square tests (MRPP, Berry and Mielke 1986) and analysis of variance, using SYSTAT (1990, SYSTAT, Inc.) MGLH Model statements. For the analysis of variance tests of disturbance, those sites receiving a disturbance intensity rank of zero or "low" were combined into a single "undisturbed" group, and sites with "medium" or "high" disturbance were combined into a "disturbed" group. For degree of canopy opening, two cut-points were selected to divide the resulting distribution into three groups with approximately equal sample sizes (0–10%, >10–20% and >20% canopy opening); this variable was log-transformed prior to ANOVA.

Each species distribution was subjected to a Chi-square goodness of fit test, to test numbers of trees observed in samples of each class of disturbance history and canopy opening against that expected under the null hypothesis of no correlation between these variables and species distribution. Juvenile and large tree ($\geq$ 7.5 cm dbh) data were tested separately. For chi-square tests of disturbance and canopy opening effects, we divided samples into three groups reflecting positions on the dominant topographic gradient, with one group comprising upland samples, another group transitional/hill-base samples, and the third group samples in low-lying areas that experienced periodic inundation. We used the same two disturbance classes as above. For analyses of juvenile distributions, disturbances of all ages were included, while for large tree analyses only disturbances with estimated ages of 5 years or more were used.

In each portion of the topographic gradient, Chi-square tests utilized two classes of canopy opening: "relatively open" and "relatively closed." In the upland and transitional areas, only a few samples had >20% canopy opening; hence "open" sites were those with >10% opening, while "closed" sites were those with 10% opening or less. In contrast, in low-lying sites, no samples had less than 10% canopy opening while many exceeded 20%; hence, in this sample group, "open" sites were those with greater than 20% opening and "closed" sites were those with 10–20% opening.

Wherever multiple comparisons were made, we maintained table-wise significance at stated levels by using a simultaneous Bonferroni procedure (Rice 1989) to adjust rejection regions. However, we have discussed results for both Chi-square and ANOVA tests that were not significant after Bonferroni adjustments, but were significant prior to such correction (alpha ≤ 0.05). These marginally significant results are clearly distinguished from statistically significant results (after Bonferroni) in both tables and text.

RESULTS AND DISCUSSION

The Predominant Environmental Gradient

Although the topographic gradient in Tikal is modest, several physical factors are strongly correlated with it and with one another, and this complex factor gradient proves to exert a strong influence on the vegetation. Figure 2 depicts the manner in which several physical factors vary along the topographic gradient, while Figure 3 depicts intercorrelations among these factors. Percent clay, organic matter content, and pH were all highly correlated with one another and with topographic position (linear regression of clay on topographic position $r^2=56.4$, $p = 0.31\text{x}10^{-13}$). Organic matter and pH were positively correlated with one another (linear regression $r^2 = 17.5$, $p = 0.31\text{x}10^{-3}$) and negatively correlated with clay content (linear regression $r^2 = 47.9$, $p = 0.23\text{x}10^{-10}$ o.m./clay; $r^2 = 40.1$, $p = 0.4\text{x}10^{-8}$ pH/clay), so that organic matter decreases and pH drops as one moves into regions of higher clay content. Clay content is strongly related to topographic position, being low in upland sites and dramatically higher in low-lying areas. Rockiness is higher in upland than in low-lying sites, while soil depth is shallow on upland sites (ranging from 20 m to 70 cm) and generally deep in low-lying sites (often >1.4 m).

The net result is that organic matter and pH are high in well-drained upland sites, which also feature shallow, rocky soil that is low in clay content; in contrast, organic matter, pH, and rockiness are low in low-lying sites, which feature deep, rock-free, clay-rich soils. Observations indicate that drainage is generally good on upland sites, which do not accumulate standing water. In contrast, low-lying areas may be inundated for weeks at a time during the rainy season (with some areas being subject to strong currents of flowing water), while their high clay contents and visible cracking suggest that edaphic drought may occur during the dry season.

In sum, we feel that the environment for plants along the topographic continuum may be characterized as follows: (1) on the upper reaches of slopes (Dry Upland Forest), soils and topographic features result in good to excessive drainage and probably some dry season drought stress for plants, nutrient availability is probably not limiting, and pH is moderate; (2) in upland areas occurring lower on the gradient (Standard and Mesic Upland Forests) deeper soils with relatively low clay and high rock content provide moderate moisture conditions throughout the year, relatively high nutrient availability, and moderate pH; (3) low-lying areas near the bases of slopes (Hill-base and Sabal Forests) appear to experience wet season soil saturation but not excessive waterlogging, and dry season drought is not extreme, while nutrient availability and pH are probably not much lower than in upland areas; (4) areas on the edges of lowland depressions (Transitional Forest) experience some wet season inundation as well as dry season drought, and soils show signs of gleying and are lower in nutrient content and pH than soils higher up on the gradient; (5) soils in lowland depressions (Tall and Low Scrub Swamp) experience extreme wet season inundation and extreme dry season edaphic drought, are highly gleyed, and may have nutrient and acidity levels that limit plant growth; (6) in the lowest lying areas (Mesic Bajo) soil characters are similar to those in Scrub Swamp, but dry season drought may be ameliorated by the proximity of the dry season water table to the soil surface.

Ordination Results

The first axis of the full-gradient ordinations of samples and species produced by DCA (Figs. 4–7) corresponded well with topographic position, with upland samples grouped at the left and samples farther to the right belonging to increasingly lower regions of the topographic gradient (passive correlation of topography, clay content, rock content and slope with first axis = 0.792). The species plot (Fig. 5) was consistent with this interpretation. Species generally restricted to xerophytic swamps or transitional forest are located in the right portion of the graph, while species with abundance peaks in lowland forests but not common in the extreme xerophytic swamps are located in the lower center region. Species occurring in Upland Forest but with abundance peaks in more mesic transitional lowland forests are found in the center of the graph, while at the left hand extreme appears a group of species occurring most commonly in upland sites.

The second axis in this ordination (Fig. 4) separated lowland samples into mesic swamp sites in the upper right of the graph and the xerophytic Scrub Swamp sites in the lower right. This axis accounted for variation between extreme lowland sites, hence upland sites are tightly clustered on the left of the plot. Amplifying the left-hand portion of this plot (Fig. 6) makes it clear that the DCA ordination did separate upland sites into drier sites occupying the upper portions of slopes [on left] and wetter upland sites lower on the topographic gradient and with deeper, more clay-rich soils [on right]). In the biplot of species centroids (Fig. 7), species to the left of *Malmea depressa* were all more abundant in drier upland samples, with species like *Gymnanthes lucida*, *Drypetes lateriflora* and *Thouinia paucidentata* poorly represented in wet upland samples. Conversely, the species on the right side were significantly more common in lower, more mesic areas of the upland topographic gradient.

DCA was also performed on understory samples of treelets and tree juveniles, which resulted in virtually identical ordering of samples and species to the DCA of trees >7.5 cm dbh; hence, ordination plots are not pictured here. Eigenvalues for the first two axes were also similar to those for the ordination of adults (first axis = 0.735, second axis = 0.471); and passive correlation with topographic position, clay content, rock content and slope showed a strong association of the first axis (0.789) with these variables, and the second axis was weakly correlated (0.286). The percent variance in species composition accounted for by the first two axes was low (first axis = 9.2%, second axis 5.9%).

The CCA ordination using the four primary environmental variables showed that topographic position and soil composition were significantly associated with the variation in species composition between samples (Fig. 8). The first axis was largely related to topographic position and the second to soil traits. Monte Carlo significance tests of environmental variables showed topography (p = 0.01) and clay content (p = 0.03) significant at the 0.05 level. Rock content and slope were not significant at the 0.05 level after fitting of topographic position and clay content but were included as they seemed to enhance the ordination. Monte Carlo significance testing of the overall ordination and the first ordination axis (p = 0.01 both tests), as well as the close correspondence of these direct ordination results with the indirect ordinations above, indicate the significance of this ordination, despite the fact that it accounted for a low percentage of the total variance in the species data. Tree species distribution in our study area is of a characteristically patchy nature, there are a large number of rare species, and our data set includes a relatively large number of small samples (mean number of individuals per sample = 30). All of the above factors produce a large amount of inter-sample species variation which is not explained by environmental conditions. In addition, much of the variation in species composition is due to the disturbance history of each plot. Hence, it should be expected that a constrained ordination such as CCA will only account for a small percentage of the variance within a large data set, and this is typical of the technique (Jongman et al. 1987).

Although results are not pictured here, constrained ordination of understory vegetation (treelets, shrubs and tree saplings) produced an ordering of samples and species similar to that provided by CCA for trees >7.5 cm dbh This sapling ordination also showed that species composition was significantly related to variation in topography and clay content, although the first two axes only accounted for a fraction of the total species variance (first axis = 6.1%, second axis = 0.8%). Eigenvalues and species-environment correlations, respectively, were as follows: first axis = 0.490, second axis = 0.055; first axis = 0.867, second axis = 0.551. Monte Carlo significance testing of topography (p = 0.01) and clay (p = 0.04) again showed a significant correlation between these two environmental variables and patterns of variance in species composition. In the CCA ordination of juveniles along disturbance and light intensity gradients (Fig. 9), only percent canopy opening (p = 0.01) and total area of gap and building phase forest within the plot ($p = 0.03$) were found by Monte Carlo testing to be significantly correlated with variance in species composition after fitting the four environmental covariables. In Figure 9, species associated with high understory light intensity but not with treefall gaps were clustered in the lower right of the graph. These species are primarily those that were abundant in the relatively open, low-lying, or 'bajo' forests, but that were not commonly found in treefall gaps in Upland Forest. Species clustered in the upper central portion of the plot showed positive correlations with both treefall gaps and understory light intensity, while species clustered at the upper left of the graph showed strong positive correlations with treefall gaps, but not with current light intensity. The remaining species in the lower left showed no association, or negative correlation, with both light intensity and treefall gaps.

For trees $\geq$ 7.5 cm dbh (Fig. 10), the correlation of canopy disturbance with species composition was weaker in our data set than for juveniles (Monte Carlo significance testing of environmental variables: disturbance age–$p = 0.07$, disturbance intensity–$p = 0.10$). This was likely due to the fact that many of the trees sampled were substantially older than the maximum age of canopy disturbance that we were able to document. Hence, for an older tree the lack of evidence of canopy disturbance in the vicinity does not preclude the possibility that the individual became established or recruited to adult size in a treefall gap. Despite the limitations of our data, the CCA ordination did distinguish species with strong treefall gap associations from less light-demanding species, with gap-associated species (including several pioneer species) clustered at the upper right of the plot (Fig. 10).

TWINSPAN Results Compared to Nested Sorting of Samples

Using TWINSPAN to achieve simultaneous sorting of samples encompassing the full topographic continuum did not produce meaningful sample groupings. However, when upland and lowland samples were separately classified, TWINSPAN recognized two upland and six lowland groups for a total of eight "forest types." In comparison, our nested ordering of samples by topography and soil characteristics produced four upland (including the rare cohune upland) and seven lowland (considering Mesic Bajo and True Swamp as separate types) sample groups. Of the 152 lowland samples, 92% were placed in the same groups by TWINSPAN and our nested sorting technique. Of the lowland samples classified differently by the two techniques, 62% were classified as either Transitional or Mesic Bajo by the nested sorting technique. We found that these samples were not consistently separated from one another by TWINSPAN, nor were they placed into two categories corresponding to those of the nested sorting method. Rather, both "types" were included together in each of several TWINSPAN groupings; some samples were allocated to TWINSPAN groups corresponding to our Sabal and Tall Scrub Swamp categories and TWINSPAN separated the remaining samples into four small groups.

The above result is not surprising, as there were substantial similarities in species composition between these samples. The failure of TWINSPAN to separate these two forest types may result from intrinsic problems in the divisive method of this analysis (van Groenewoud 1992) and from limitations on the number of indicator species used per analysis. None of the samples classified as Transitional Forest by the nested sorting occupied portions of the topographic gradient adjacent to samples classified as Wet Scrub Swamp. Additionally, several tree species, such as *Pithecellobium belizensis* and *Lonchocarpus guatemalensis* were found in plots we classified as Wet Scrub Swamp but not in those we classified as Transitional Forest. Therefore, we felt that combining samples of these two types as suggested by TWINSPAN would lead to less clarity than that provided by our nested topographic sorting in this case.

The differences in the classification of upland samples by the two techniques is largely due to the relative degree of splitting resulting from the two methods. To compare the three primary upland sample groups resulting from nested sorting with the two groups generated by TWINSPAN, we combined these three into two groups, based on topographic position. Grouped in this way, 92% of the 141 upland samples were placed in the same groups by both techniques. The indirect ordination of samples by DCA supported division of upland samples into three groups (Fig. 6), and the ordering produced by the first axis DCA scores is highly correlated with that produced by the nested sorting (Spearman correlation coef. = 0.902, $p = 0.000$).

To summarize, both TWINSPAN and ordinations generally supported the division into forest "types" resulting from our nested sorting on topographic position and soil factors, but differed in some details. Our final classification rests mainly upon the results of the nested sorting, and designates 11 forest types, including four upland types. Due to a large sample size for Upland Wet forest sites, for subsequent analyses we have divided this forest type into two subgroups based on topographic position. In addition, Swamp and Mesic Bajo sites have been lumped for analyses due to low sample sizes and high similarity in structure and composition between these forest types. One forest type, Cohune Forest, was only documented in one small area of Tikal, and has therefore been omitted from further analyses.

Forest Types

Any classification of forest types is artificial, but a good classification can be useful in comparing tree species distributions, vegetation structure, microenvironment, and other attributes along what is actually a continuum of variation. Moreover, classification is a prerequisite to many kinds of ecological research, as sampling must take into account the underlying vegetation continuum in order to facilitate valid choice of replicate sample plots and to define valid comparison units and scope of inference. Lundell (1937) classified the vegetation of northern Petén into three primary forest types,: two upland forest types, Ramonal and Zapotal (including Caobal association) and lowland wooded swamp (Akalches). Using quantitative data on forest structure and composition we were able to recognize several upland and lowland vegetation types. In this section we summarize the structural variation of vegetation along the topographic gradient in Tikal and then describe and compare the 11 forest types recognized by our classification with respect to structural and environmental traits, characteristic species, patterns of species diversity, and rates and types of dynamic processes influencing the sub-canopy light environment. The forest types are listed in order of their occurrence along an idealized topographic gradient (Fig. 11). Wherever appropriate, we have conformed to the terminology of Brokaw and Mallory (1993) in naming forest associations.

There was a pronounced decrease in canopy height and basal area along the topographic gradient, from well-developed Upland Forest through low, dense Scrub Swamp forest in the low-lying depressions (Table 2, Figs. 12 and 14). The principal exception to this pattern occurred in the Mesic Bajo and True Swamp types, which occur lower down on the topographic gradient than Scrub Swamp, but are taller and have greater basal area than the Scrub Swamp. Canopy opening, density of dead standing stems and live stem density (>1 m tall, >7.5 cm dbh), mirrored the above pattern, with the highest values occurring in Low Scrub Swamp, and decreasing values with increasing elevation along the topographic gradient (Table 2, Fig. 12). However, the density of stems >10 cm dbh was virtually the same across the gradient, though small stems accounted for a larger percentage of total stems in lowland forests than in upland portions of the gradient (Fig. 13). Conversely, stems >30 cm dbh accounted for up to 68% of the basal area (of stems >7.5 cm) in Upland Forest, while contributing less than 30% of the basal area in Scrub Swamp (Fig. 14). Mesic lowland forests (Hill-base, Sabal, Transitional and Mesic Bajo) displayed intermediate values with a high density of 10–30 cm dbh stems and scattered large individuals (Fig. 14).

Vine density increased from upland to lowland portions of the gradient (Table 2, Fig. 12). However, the size distribution of vines varied considerably between lowland forest types, with Scrub Swamp areas dominated by small vines (<2.5 cm diameter), and Hill-base, Sabal, and Mesic Bajo forest displaying a high ratio of large to small vines (Table 2). Dead hanging vegetation was dramatically more abundant in the understory of lowland forest areas than in upland, a result of the higher densities of live understory vegetation in these forest types (Fig. 12). Similarly, ground cover (stems <1 m tall) was much higher in lower than upper regions of the topographic gradient, with the exception of Mesic Bajo and True Swamp in which standing water for much of the year probably reduces seedling density and lower light prohibits the growth of grasses and sedges (Table 2, Fig. 12). In Scrub Swamp, sedges accounted for the overwhelming majority of ground level stems (Table 2, Fig. 12).

Species diversity did not decrease from Upland Forest to lowland areas, although one might predict such a decrease from the trend of decreasing canopy height and increasingly broken structure along the topographic gradient, and the harsh edaphic extremes found in the low-lying depressions. Instead, species richness (Fig. 15) and dominance (not pictured) were roughly equal between Dry Upland Forest and Low Scrub Swamp, which are at or near (when Mesic Bajo occurs below Scrub Swamp) the endpoints of most topographic gradients in Tikal (Fig. 11). However, the high stem density in Scrub Swamp relative to that typical of upland forest types might counteract the environmental conditions that promote low diversity, due to the density effect on species diversity (Denslow 1996). The highest number of species per unit area was found in the more mesic lowland

Table 2. Structural and environmental variation along a topographic gradient, Tikal, Guatemala. Means and standard errors are given for each of ten forest types.

	D.U. avg	D.U. se	U.S. avg	U.S. se	MU.1 avg	MU.1 se	MU.2 avg	MU.2 se	H. avg	H. se	S. avg	S. se	T. avg	T. se	T.S.S avg	T.S.S se	L.S.S. avg	L.S.S se	M.B. avg	M.B. se
Maximum canopy hgt (m)	26.8	*0.7*	26.7	*0.8*	25.0	*0.8*	25.8	*0.5*	24.8	*1.0*	23.1	*1.1*	18.6	*1.0*	18.8	*0.9*	12.1	*0.8*	19.0	*2.2*
Mean canopy hgt (m)	20.6	*0.5*	20.8	*0.7*	19.7	*0.6*	19.9	*0.4*	17.8	*0.8*	17.2	*0.5*	14.5	*0.7*	12.7	*0.9*	10.1	*0.5*	13.3	*1.4*
Minimum canopy hgt (m)	15.6	*0.5*	16.9	*0.7*	15.2	*0.7*	15.2	*0.4*	13.0	*0.7*	12.9	*0.6*	10.9	*0.7*	9.1	*1.1*	8.1	*0.3*	9.9	*1.1*
Mean canopy opening (%)	8.9	*0.6*	7.6	*0.6*	8.7	*0.6*	8.5	*0.5*	10.3	*0.8*	12.1	*0.9*	14.1	*1.8*	19.3	*0.7*	28.6	*2.3*	15.2	*1.2*
Average standard deviation of canopy opening (%)	1.7	*0.2*	2.0	*0.2*	2.1	*0.3*	2.4	*0.3*	2.6	*0.4*	3.2	*0.4*	4.8	*1.1*	4.7	*0.8*	6.4	*0.9*	3.9	*1.1*
Basal area (cm^2 per plot)	14468		11438		9850		10748		8878		8517		9511		8301		8173		7693	
Stem density (>2m tall)	500		474		400		430		398		430		570		675		1331		503	
# treefall gaps in plot	0.5	*0.2*	0.5	*0.1*	0.5	*0.1*	0.5	*0.1*	0.9	*0.2*	0.7	*0.2*	1.5	*0.3*	1.4	*0.3*	0.2	*0.2*	1.1	*0.5*
% of plot covered by gap or building phase forest	0.2	*0.1*	0.3	*0.1*	0.3	*0.1*	0.2	*0.1*	0.5	*0.1*	0.2	*0.1*	0.4	*0.1*	0.3	*0.1*	0.1	*0.1*	0.3	*0.1*
Tot. area of gap/building phase forest within 10 m radius of plot boundary (m^2)	15.3	*6.3*	25.8	*9.7*	28.6	*9.2*	24.3	*6.5*	35.1	*14.0*	37.5	*19.4*	30.5	*8.6*	73.4	*25.2*	4.8	*4.6*	27.5	*12.2*
Average size of treefall gaps (m^2)	119.3	1276	91.9	*85.1*	109.9	*60.9*	151.8	*169.2*	119.3	*127.8*	156.3	*123.8*	66.8	*94.9*	106.9	*90.7*	43.8	*32.5*	70.1	*96.5*
# trees leaning > 25 degrees off vertical per plot	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.1	*0.1*	2.7	*0.7*	2.9	*0.6*	2.2	*0.6*	2.7	*0.6*	1.5	*0.6*	6.1	*1.0*
# dead hanging branches 0-2.49 cm diameter *	9.6	*2.1*	4.9	*1.7*	6.4	*1.7*	6.3	*1.3*	8.7	*2.8*	11.6	*2.9*	27.2	*13.2*	21.5	*5.0*	52.8	*11.7*	60.0	*24.2*
# dead hanging branches 2.5-4.99 cm diameter *	1.0	*0.4*	0.6	*0.4*	1.3	*0.6*	1.5	*0.7*	1.0	*0.5*	2.3	*0.8*	2.4	*1.5*	3.1	*1.7*	3.9	*1.0*	2.8	*1.5*
# dead hanging branches 5 cm+ diameter *	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.1	*0.1*	0.2	*0.2*	0.5	*0.4*	0.5	*0.5*	0.0	*0.0*	0.5	*0.5*	0.0	*0.0*
Total # dead hanging branches *	10.7	*2.2*	5.5	*1.7*	7.7	*1.9*	7.9	*1.7*	9.9	*3.2*	14.4	*3.0*	30.1	*13.9*	24.5	*5.5*	57.2	*11.9*	62.8	*24.3*

	D.U. avg	D.U. se	U.S. avg	U.S. se	MU.1 avg	MU.1 se	MU.2 avg	MU.2 se	H. avg	H. se	S. avg	S. se	T. avg	T. se	T.S.S avg	T.S.S se	L.S.S. avg	L.S.S se	M.B. avg	M.B. se
# dead standing stems 0-7.5 cm dbh *	1.9	0.3	1.2	0.4	1.7	0.4	1.5	0.3	0.7	0.2	1.3	0.4	1.6	0.9	3.0	0.7	4.7	0.8	2.0	0.4
Percentage of ground cover accounted for by monocots (grass & sedges)	0.2	0.1	0.8	0.6	2.1	0.9	0.6	0.3	11.2	3.1	26.5	3.0	21.9	3.5	19.1	6.1	99.3	5.8	32.0	5.5
Percent ground cover	16.4	1.3	17.5	1.4	18.5	2.2	14.1	1.4	20.9	2.9	16.3	2.2	21.7	4.0	26.7	4.0	38.2	3.9	15.6	2.6
# vines 0-2.49 cm diameter - understory *	8.7	1.6	7.1	1.5	8.3	1.7	6.2	0.9	12.5	3.2	9.5	1.5	16.6	6.6	18.2	4.0	13.3	2.3	32.3	7.7
# vines 2.5-4.99 cm diameter- understory *	1.3	0.3	0.8	0.3	2.1	0.7	1.5	0.4	4.3	0.9	3.6	1.1	2.5	1.0	2.5	0.7	1.2	0.4	4.3	1.2
# vines 5 cm+ diameter - understory *	0.3	0.1	0.2	0.1	0.0	0.0	0.7	0.4	0.7	0.2	2.1	1.0	0.1	0.1	0.1	0.1	0.0	0.0	0.4	0.2
Total # of vines *	10.3	1.7	8.1	1.6	10.5	2.1	8.4	1.2	17.5	4.1	15.2	2.2	19.3	7.5	20.8	4.3	14.5	2.4	37.0	8.2
# trees per plot with 1-2 vines 0-2.5 cm diameter	4.4	0.6	4.2	0.7	5.0	0.6	5.0	0.3	5.1	0.7	5.1	0.8	6.1	0.6	15.9	10.1	3.5	0.7	5.2	0.9
# trees per plot with 3-5 vines 0-2.5 cm diameter	1.8	0.3	1.5	0.3	2.2	0.3	2.2	0.2	3.3	0.6	2.5	0.3	3.9	0.7	3.5	0.9	0.5	0.2	6.1	2.2
# trees per plot with 6-10 vines 0-2.5 cm diameter	0.8	0.2	0.4	0.1	1.4	0.4	1.0	0.2	1.8	0.3	1.6	0.3	2.2	0.8	0.9	0.4	0.0	0.0	3.0	0.7
# trees per plot with >10 vines 0-2.5 cm diameter	0.1	0.1	0.1	0.1	0.8	0.4	0.3	0.1	1.9	0.4	1.0	0.2	0.6	0.4	0.8	0.4	0.0	0.0	2.4	0.9
# trees per plot with 1-2 vines >2.5 cm diameter	0.4	0.1	0.2	0.1	1.0	0.2	0.5	0.1	1.0	0.4	0.3	0.2	1.0	0.3	1.9	0.5	0.0	0.0	1.0	0.3
# trees per plot with >2 vines >2.5 cm diameter	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.0	0.3	0.1	0.1	0.1	0.0	0.0	0.2	0.2	0.0	0.0	0.2	0.2
# trees per plot with small (<20 cm diameter) epiphytes on trunk	0.2	0.1	0.4	0.1	0.2	0.1	0.4	0.1	0.5	0.2	0.3	0.1	1.4	0.5	3.2	0.5	5.5	1.0	2.8	0.8

	D.U. avg	D.U. se	U.S. avg	U.S. se	MU.1 avg	MU.1 se	MU.2 avg	MU.2 se	H. avg	H. se	S. avg	S. se	T. avg	T. se	T.S.S avg	T.S.S se	L.S.S. avg	L.S.S se	M.B. avg	M.B. se
# trees per plot with aeroids on trunk	0.2	*0.1*	0.6	*0.2*	1.0	*0.3*	0.9	*0.2*	0.9	*0.4*	1.2	*0.5*	0.1	*0.1*	0.3	*0.2*	0.0	*0.0*	0.2	*0.1*
# trees per plot with large (>20 cm diameter) epiphytes on trunk	0.2	*0.1*	0.2	*0.1*	0.3	*0.1*	0.2	*0.1*	0.6	*0.2*	0.9	*0.3*	0.9	*0.3*	2.5	*0.6*	16.1	*1.4*	3.4	*1.2*
# trees per plot with large (>20 cm diameter) epiphytes in crown	7.4	*0.8*	5.2	*0.7*	3.3	*0.6*	3.6	*0.4*	2.7	*0.5*	1.9	*0.6*	3.5	*0.7*	3.0	*0.9*	2.4	*0.6*	4.2	*1.9*
Degree slope of land	9.0	*1.2*	7.9	*1.6*	6.5	*1.0*	2.9	*0.3*	1.6	*0.5*	1.1	*0.1*	0.5	*0.3*	0.0	*0.0*	0.0	*0.0*	0.1	*0.1*
Mean soil clay content	4.5	*0.5*	4.9	*0.6*	5.7	*0.5*	5.7	*0.3*	9.0	*0.4*	9.9	*0.1*	10.0	*0.0*	9.9	*0.1*	10.0	*0.0*	10.0	*0.0*
Mean soil rock content	3.0	*0.4*	2.3	*0.4*	2.4	*0.4*	2.0	*0.3*	0.4	*0.2*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*	0.0	*0.0*
Soil depth (cm)	40.7	*3.4*	45.4	*5.3*	52.2	*6.3*	54.8	*5.4*	105.3	*21.5*	143.0	*0.0*	143.0	*0.0*	143.0	*0.0*	143.0	*0.0*	143.0	*0.0*

Forest type codes are as follows: D.U.=Dry Upland Forest; U.S.=Upland Standard Forest; MU.1&MU.2=Mesic Upland Forest; H.=Hillbase Forest; S.=Sabal Forest; T.=Transitional Forest; T.S.S.=Tall Scrub Swamp; L.S.S.=Low Scrub Swamp; M.B.=Mesic Bajo.

* = unit area of 35.2 m^2

All other area based measures are per 0.041 ha.

Table 3. Degree of overlap in species composition between forest types, Tikal, Guatemala.*

	D.U.F.	U.S.F.	M.U.1	M.U.2	H.F.	S.F.	T.F.	T.S.S.	L.S.S.	M.B.
Dry Upland Forest	-	16	15	15	11	10	8	5	1	3
Upland Standard For.	77	-	17	17	14	11	10	5	1	4
Mesic Upland Forest 1	76	76	-	17	14	12	11	5	1	4
Mesic Upland Forest 2	77	78	82	-	15	13	11	5	1	4
Hillbase Forest	64	70	70	73	-	15	11	5	1	6
Sabal Forest	64	63	73	75	72	-	11	6	1	8
Transitional Forest	63	60	68	70	65	69	-	6	1	8
Tall Scrub Swamp	47	49	46	53	49	52	73	-	12	9
Low Scrub Swamp	30	31	30	38	39	45	58	68	-	7
Mesic Bajo	46	48	49	43	53	62	62	58	52	-

* The upper half of the table gives the number of tree species in common between forest type pairs, out of the 20 most abundant species per forest type. The bottom portion of the table depicts the percentage similarity (% of species found in one forest type that were found in both) between total species lists between forest type pairs.

forests, Sabal and Transitional, which include both upland species that are unable to persist in more extreme lowland conditions, as well as lowland species that only rarely colonize Upland Forest. Forest types that were close together on the topographic continuum had a much greater overlap in species composition than those that occurred farther apart, as would be predicted by the relative similarity of environmental conditions in adjacent topographic zones and the greater probability of seed exchange between spatially contiguous stands (Table 3). At the extreme, only 30% of the total number of species found in either Dry Upland or Low Scrub Swamp were recorded in both forest types.

Dry Upland Forest

Environmental factors and vegetation structure

This forest type (Fig. 16) occurs on the higher portions of slopes or in other rocky upland areas such as those with small Maya structures, and is particularly distinctive on tall and steep slopes. Dry Upland Forest corresponds roughly with Lundell's (1937) Ramonal. Here the combination of rapid surface drainage with shallow, rocky soils underlain by porous limestone, creates relatively dry conditions compared to other upland areas, and moisture stress is undoubtedly amplified during the dry season, especially in drought years. The shallow soils also limit vertical root penetration, favoring species with shallow, spreading root systems, and in extreme sites may favor subcanopy species over those which attain large sizes, especially on the steeper slopes. Exposure to higher winds no doubt exacerbates drought stress for trees and, combined with shallow soils, may result in higher treefall rates, at least of major windthrows and treefalls involving more than one individual. However, through conditioning, trees on ridges may be more resistant to wind than are individuals on lower ground (Basnet et al. 1992).

We did not record a high rate of large treefalls (Table 2–gaps), but the largest disturbance events are typically rare in tropical forests (Sanford et al. 1986, Hartshorn 1980). However, the only gap that we recorded larger than 500 m^2 was on such a ridgetop in Dry Upland Forest. The aforementioned factors would explain the somewhat lower canopy height recorded on the more exposed hilltops and upper slopes (mean = 15.5 m upper slopes, 20.6 m Dry Upland overall), than in Standard Upland Forest (mean = 20.8 m).

The upper canopy surface in Dry Upland Forest is generally relatively even, but in the more extreme situations the canopy is thin, with apparently fewer canopy leaves above a given point on the forest floor than in Upland Forest on lower, less exposed sites. This appears to result in higher ambient light levels in the understory of such exposed Dry Upland sites. However, this type of variation in canopy cover was only moderately well reflected by densiometer readings (Table 2–canopy opening) and was under-represented in our sampling, as we used no direct measure of light intensity. Under intact canopy cover, light intensity was higher in Dry Upland hemispherical photo samples than in Standard Upland samples (one-way ANOVA, $p = 0.0001$; est. total site factor Dry Upland = 0.2, Upland Standard = 0.13 ; difference significant in Tukey's pairwise comparison). Vine density in non-gap-influenced areas was typically equal to or slightly lower than that of the Standard Upland Forest (Table 2).

Characteristic species

The most readily apparent distinction between this forest type and Standard Upland or Mesic Upland, is the dominance of *Piper psilorrachis* in the understory along with a high density of tree saplings (Fig. 13), and the relative rarity of the understory palm *Cryosophila stauracantha* (Appendix 2). A few species that were widespread in all Upland Forest types reached their highest abundance in Dry Upland Forest, most notably *Brosimum alicastrum, Trichilia minutiflora, Talisia olivaeformis, Pouteria campechiana, Malmea depressa, Manilkara zapota*, and *Pouteria reticulata. Nectandra coriacea*, uncommon in other upland areas, was a major component of the subcanopy of Dry Upland Forest (Fig. 30). Several species that were abundant in other upland areas also occurred in dry forest, but were consistently less abundant in this topographic range, including *Pouteria amygdalina, Pseudolmedia oxyphyllaria, Wimmeria concolor, Casearia bartlettii*, and *Sebastiana longicuspis*. In less exposed sites, the points outlined above are typically the extent of differences between Dry Upland and other Upland forest types. It is important to note that *Brosimum alicastrum* and *Talisia olivaeformis* are abundant in all dry rocky upland areas and are not limited to ruin sites. The observation of high densities of these and other species at ruin sites has resulted in speculation that the Maya favored them for economic purposes (Lundell 1937). Although these species may have been cultivated by the Maya and may have had a considerable advantage over other species in the large-scale forest succession that followed the collapse of the Maya, our findings indicate that for *Brosimum* and *Talisia* current distribution patterns are related to topographic/edaphic conditions, not directly to historical events.

In the more exposed hilltops and upper slopes, a number of species that occurred in some low-lying regions of the topographic gradient, but were rare in mesic upland sites, were consistently present and often densely distributed, producing a bimodal distribution pattern across the overall topographic continuum (Fig. 30). Included in this list are: *Gymnanthes lucida, Thouinia paucidentata, Drypetes lateriflora, Amyris elemifera, Coccoloba acapulcensis, Gaussia maya,* and *Talisia floresii*. This bimodal pattern is interesting as it highlights similarities in edaphic drought conditions and light availability between Dry Upland Forest and Transitional and Tall Scrub Swamp forest. *Ceiba aesculifolia, Diospyros campechiana,* and *Bernoullia flammea,* although rare throughout Tikal National Park, were consistently seen only in Dry Upland Forest.

Upland Standard Forest

Environmental factors and vegetation structure

This forest type (Fig. 17) is widespread, covering the majority of rolling upland country and lower regions of slopes, where drainage is good but not excessive as it is in Dry Upland Forest. Soils in these areas are on average slightly deeper than under Dry Upland Forest but much shallower, lower in clay, and rockier than in the deep, clay-rich soils of low-lying sites (Fig. 2, Table 2). This is the tallest forest type, with the exception of the rare Cohune palm type, and on average has the most open understory. Average emergent canopy height was 27 m and average canopy height 21 m. Vine density was usually relatively low, on average only seven trees per plot (20%) having vines on them, and heavily laden trees were infrequent (Table 2). Sapling density is moderate (Fig. 13).

Species composition

The family Sapotaceae dominates in this forest type, with *Pouteria reticulata, P. amygdalina, P. campechiana, P. durlandii, Manilkara zapota,* and *Mastichodendron foetidessimum*. Other common trees are *Wimmeria concolor, Brosimum alicastrum, Pseudolmedia oxyphyllaria, Trichilia minutiflora, T. moschata, T. pallida, Blomia prisca, Simira salvadorensis, Aspidosperma cruenta, Pimenta dioica, Acacia dolichostachya,* and *Protium copal*. In some areas *Cedrela mexicana, Spondias mombin,* and *Lonchocarpus castilloi* are abundant emergents, probably reflecting a large, old disturbance event. *Sabal mauritiiformis* is often abundant as a canopy palm but does not dominate or have a major effect on canopy structure as it does in Sabal Forest.

The primary differences between this forest and Dry Upland described above are that: (1) the ratio of abundance of common dry upland species such as *Brosimum* and *Trichilia minutiflora,* to "mesic" upland species such as *Pouteria amygdalina* and *Pseudolmedia* is more equal, (2) species such as *Gymnanthes lucida, Drypetes lateriflora* and *Nectandra coriacea* (common in Upland Dry) are virtually absent, and (3) *Cryosophila stauracantha* dominates the understory, with *Piper psilorrachis* abundant but of secondary importance (compare Figs. 16 and 17).

Mesic Upland Forest

Environmental factors and vegetation structure

The third distinguishable upland association (Fig. 18) occurs in some particularly mesic situations such as (1) ravines or shelves on the lower portions of slopes, (2) flat areas of elevated upland, and (3) low-lying, yet still upland areas found in regions of gradual topographic transition from upland to lowland areas. While forests in these three situations have many shared characteristics and are combined here under a single forest type, in some of the analyses we found it more enlightening to distinguish the former from the latter two. In the gently sloping, low-lying upland areas, and to a lesser degree the flat but more elevated areas, the vegetation often took on a resemblance to Transitional Forest, although the species composition was primarily of upland, shade-tolerant species. The soil in these areas was lower in clay content and higher in rocks and organic matter than that of Transitional Forest areas, but may still be subjected to periods of saturation, although not inundation, in the wet season, as occurs in Transitional forest. In these lower-lying Mesic Upland areas, stem diameter distributions were also skewed towards smaller classes (10–30 cm dbh) compared to other Upland forests (Figs. 13 and 14). In contrast, Mesic Upland Forest in the more cove-like situations did not differ materially in structure from the Standard Upland Forest type (Table 2). The Zapotal of Lundell (1937) encompasses both Standard and Mesic Upland Forest.

Species composition

The following patchily distributed species were locally abundant in this forest type, whereas they were infrequent or rare in drier upland sites: *Annona cherimoya, Cymbopetalum penduliflorum, Ouratea lucens, Exothea paniculata, Zanthoxylum procerum, Matayba oppositifolia, Hirtella americana,* and *Stemmadenia Donnel-smithii.* Widely distributed species reaching their peak abundance in these mesic upland areas included: *Pouteria amygdalina, Wimmeria concolor, Pseudolmedia oxyphyllaria, Casearia barlettii, Sebastiana longicuspis* and *Cordia gerascanthus.* Other species, such as *Pouteria durlandii, Simira salvadorensis, Protium copal, Ampelocera hottlei* and *Vatairea lundellii,* while reaching peak abundance in the more mesic Hill-base and Sabal forests, occurred substantially more frequently in Mesic Upland than in the drier upland types. *Cryosophila stauracantha* dominates the understory while *Piper psilorrachis* is only sparsely distributed (Fig. 18).

Cohune Palm Upland Forest

Environmental factors and vegetation structure

This forest type, named for the palm that dominates it, *Orbignya cohune*, is rare in Tikal; it was encountered only in one location during the sampling. However, in wetter regions of Petén and neighboring Belize this forest type is much more common, and occurs in a number of topographic situations (Brokaw and Mallory 1993, M. Schulze pers.obs.). The grove of Cohune forest that we sampled occurs in a shallow depression on a shelf-like area some 30 m above surrounding lowlands on a pronounced ridge which rose tens of meters above. The soil in this depression had a higher clay content than that in the adjacent upland areas and was deeper. However, the soil was more friable and of a darker brown color than the compacted and seasonally xeric Scrub Swamp soils. The location of this depression on a relatively high, well-drained ridge presumably helps prevent excessive waterlogging of the soil in the wet season. Also, the location along the side of a tall, steep slope may result in available dry season water being concentrated here through surface and subsurface flow from the slopes above.

To summarize, the edaphic conditions here would appear to be highly mesic for Tikal, but without excessive drought or waterlogging. In the Rio Bravo region of northern Belize, Brokaw and Mallory (1993) found *Orbignya cohune* most abundant on mesic but well-drained soils, and in lower densities in less mesic sites. A similar pattern can be seen in western Petén, which is wetter than both Tikal and Rio Bravo (M. Schulze, pers.obs). The more limited distribution of cohune in Tikal is likely due to the drier climate here than in the above locations.

The Cohune palm forest was slightly taller than other Upland forest types, with modal canopy height averaging 22 m and emergent trees averaging 30 m tall. Structurally, Cohune Upland has many features in common with Hill-base and Sabal forest. The canopy is uneven and small light gaps, particularly under concentrations of canopy palms, are frequent. As in Hill-base and Sabal forest, leaning but living trees occur at a higher rate here than in other upland areas (Fig. 12), probably due to unstable soil conditions; this may contribute to canopy openings and light availability. The mean number of treefall gaps per sample was also slightly higher in this forest type than in other upland areas. The understory in Cohune Upland is typically open and palm-dominated (by *Orbignya* and *Sabal* juveniles, and *Cryosophila* adults) although vine density can be locally high.

Species composition

In terms of species composition, this forest is closely related to Hill-base and Sabal forests, with which it shares its most abundant species, such as *Trophis racemosa, Pouteria durlandii, Licaria peckii, Guarea glabra, Quararibea funebris, Spondias mombin,* and *Ampelocera hottlei.* The main attribute separating Cohune forest from Hill-base and Sabal forests is the abundance of the Cohune palm itself.

Hill-base Forest

Environmental factors and vegetation structure

This forest type (Fig. 19) occurs at the bases of larger hills, in a narrow zone up to 100–150 m from areas of upland relief. The degree of variation from typical Upland forest depends on the size of the hill and on the surrounding topographic matrix, i.e. whether the hill base is only a relatively narrow valley between two upland areas, or is at the transition to a large, low-lying ("Bajo") area. In the first situation, the forest is only slightly different than Standard Upland Forest, the most obvious difference being a higher density of vines and a lower, more irregular, canopy in the Hill-base forest. At the bases of large hills and at hill bases on the edges of large depressions, or bajos, the vegetation differs strikingly from Standard Upland Forest in both structure and species composition.

Canopy height averaged 18 m and was often very uneven, while emergent height averaged 25 m (Fig. 12, Table 2). Vine density in this forest type is high; most trees have at least a few large woody vines in their canopies, and frequently as many as half of the canopy trees are vine-laden to the extent that significant crown shading is caused by the foliage of the vines (Table 2). While this increased density of vines results in a denser understory, the growth of shrubs and tree saplings usually is not much denser in Hill-base than in Upland Forest (Fig. 19, Table 2).

Several factors may influence the patterns of species composition observed in Hill-base areas. The soils at hill bases are generally deeper than in upland areas, and there is little rock debris in the upper layers of the soil. In many cases the upper soil is only slightly lower in clay content than is soil associated with Xerophytic Scrub Swamp Forest, which occurs farther down the topographic gradient. However, as in the Cohune Palm Forest, the soil is darker and more friable than are the compacted Scrub Swamp soils.

In soil pits dug at hill bases, there was a rocky layer at a depth of 50–60 cm. Therefore, while the soils at hill bases may drain poorly during periods of inundation in a similar manner to Scrub Swamp soils, this effect is probably moderated by the more porous and texturally diverse sub-soil layer. The periods of inundation are also undoubtedly much shorter and less severe in this topographic region due simply to higher elevation. The soil textural qualities mentioned above probably also ameliorate effects of dry season moisture stress. Low-lying areas at hill bases are subject to more extreme surface and sub-surface water flow during rainy season flood periods than are upland areas (M. Schulze pers. obs.). This water flow would be expected to have a destabilizing effect on trees rooted in these soils, and it is reasonable to expect a higher treefall rate in these areas (cf. Denslow 1980). We observed slightly more treefall gaps in Hill-base forest than in Upland forest types. In addition to completely fallen trees in Hill-base Forest, there were a large number of live trees that are leaning at angles of at least 25–45°, often one-third of the trees in a plot, while in upland areas these leaning trees are numerically insignificant (Table 2, Fig. 12). Presumably this high incidence of leaning trees is a result of strong water flows during the rainy season. These leaning trees often create openings in the canopy up to 30 m^2 in area which are functionally equivalent to small treefall gaps in their effects on the understory light environment, and contribute greatly to the general unevenness and low stature of the canopy in Hill-base forest. In Hill-base forest, leaning trees are usually small, from 10–30 cm dbh, and these individuals presumably will not reach upper canopy levels. In this way, water flow may affect canopy height and structure as well as tree size-class distributions, with only scattered individuals remaining upright to achieve emergent height.

In the low canopy of Hill-base forest small treefall gaps may allow greater light penetration to the understory than do equal-sized gaps in Upland Forest. While small gaps in Upland Forest may only be regularly exploited by shade-tolerant species, small gaps in Hill-base forest may be occupied by light-demanding species, although not extremely shade-intolerant ones. Thus, for at least some light-demanding species, there are probably more usable light gaps for regeneration in Hill-base than in Upland Forest. This helps to explain both the high density of vines in this forest type, many of which are light-demanding, and the abundance of trees species such as *Trophis racemosa, Swietenia macrophylla, Sebastiana longicuspis, Simira salvadorensis* and *Spondias mombin*, which require high light intensity in at least some stage of regeneration.

Characteristic Species

Even in the least pronounced form of Hill-base forest, where overall species composition does not differ drastically from Upland Forest, species such as *Guarea glabra, Pouteria durlandii* and *Ampelocera hottlei*, which are only scattered in upland regions, are abundant. In the 'archetypical' Hill-base forest, species composition is strongly skewed toward species with higher moisture and/or light requirements than those of characteristic upland species. Included in this list of species which dominate Hill-base (and Sabal forest), and reach their abundance peaks in these forest types, are *Pouteria durlandii, Protium copal, Spondias mombin, Sabal mauritiiformis, Vatairea lundellii, Ampelocera hottlei, Guarea glabra, Tabebuia rosea, Licaria peckii, Trophis racemosa,* and *Trichilia moschata. Swietenia macrophylla*, while prominent here, reaches its abundance peak in lower-lying areas. Several species, such as *Ocotea* sp. and *Trichilia havanensis*, were encountered only in Hill-base forest, although they were never abundant.

Sabal Forest

Environmental factors and vegetation structure

A forest type (Fig. 20) that is closely associated with the Hill-base forest but which generally occurs farther away from the bottom of major hills is the Sabal Palm Forest, or Botanal (Lundell 1937). In some catenas, a zone of Sabal Forest is not distinguishable, for example, in elevated, hilly regions with only small valleys (100–300 m wide) connecting upland areas, or in areas of gradual transition from low, flat upland to lowland topography (Fig. 11). However, in most complete gradients from Upland to Scrub Swamp, this vegetation type is present, typically in the zone 100–400 m from a hill base.

The canopy was lower on average (17 m) than in Upland Standard or Hill-base forests (Fig. 12, Table 2), and considerably more broken in structure than even in Hill-base forest. As in Hill-base forest, heavily leaning trees and treefalls were frequent, presumably due to the unstable, frequently saturated soils. In addition to these influences on canopy irregularity, the tall, small-crowned *Sabal mauritiiformis* palms, which abound, often create small light gaps around their periphery. In this manner, areas receiving moderate to high light intensity at the forest floor are even more frequent in Sabal than in Hill-base Forest, rendering this forest type yet more hospitable to light-demanding species. Vine density can be low or high in this forest type and often varies dramatically over short distances; treefall history seems to be the major factor in this variation.

The soil underlying Sabal forest is similar texturally to that of Hill-base sites, although in soil pits the subsoil layer of decomposing limestone fragments was found to be at a depth greater than 70 cm. This last factor, combined with lower elevation, may result in poorer drainage of these soils during wet season inundations, which in turn may inhibit root growth. Aside from this difference, which may make Sabal forest less hospitable for some "upland species," Sabal forest appears to occupy soils very similar to those underlying Hill-base forest.

Characteristic species

This forest is similar in species composition to Hill-base Forest, but Sabal

Palms (*Sabal mauritiiformis*) dominate the upper canopy, forming a regular but incomplete cover, with a dicot sub-canopy and some scattered dicot emergents. Also, species such as *Guarea glabra, Vatairea lundellii, Trophis racemosa, Spondias mombin*, and *Pouteria durlandii*, which first become abundant in Hill-base forest (as one moves from upper to lower regions of the topographic gradient), provide a larger proportion of the stems, while many upland species become infrequent. The understory in Sabal Forest is distinctive for the abundance of *Costus* sp., *Psychotria* sp., *Alibertia edulis, Calyptranthes chytriculia,* and several species of branched grasses. Dry season moisture stress does not seem to be extreme in these regions, as evidenced by the occurrence of tree species that are typical of wetter climatic regions of Guatemala and Belize: *Pouteria sapota, Quararibea funebris, Ampelocera hottlei,* and *Guarea glabra.*

Transitional Forest

Environmental factors and vegetation structure

Moving down a typical gradient from upland areas into the low-lying, gently sloping drainage depressions, the canopy becomes consistently lower and the understory denser (Fig. 21). Between Sabal Forest and Scrub Swamp Forest is a zone of vegetation that is transitional, both in species composition and structure, between the broad-leaved mesophytic Upland and Hill-base/Sabal forest types and the Xerophytic Scrub Swamp. This may be equivalent to Lundell's (1937) Escobal. In terms of clay content, the soil in these areas is not significantly different from that of the Scrub Swamp, which occurs farther down the gradient on nearly pure clay soils. However the soil appears to have consistently higher organic content and is typically less compacted than Scrub Swamp soil. Although periods with standing water occur, there is less severe flooding in the Transitional Forest zone, and for a less extended period of time than farther down the gradient, as evidenced by the dark soil color under Transitional Forest compared to the light gray, heavily gleyed Scrub Swamp soils. Also by being closer to rocky uplands, the soil, although well over 70 cm deep, may be slightly shallower, with closer contact to decomposing rock below the surface, than are most Scrub Swamp soils. The above factors apparently result in less severe edaphic extremes than in Scrub Swamp soils, and may allow root contact with the mineral-rich decomposing limestone subsoil layer. However, in soil qualities, as in vegetation, this topographic region is intermediate between the mesic Hill-base/Sabal forests and xerophytic Scrub Swamp, and dry season edaphic moisture stress is no doubt a factor for plants occurring here.

The average height of emergent trees in the Transitional Forest was 19 m, average canopy height 14.5 m, and average lower canopy 11 m. The canopy in Transitional Forest was more open on average than in Upland Forest, although denser than in true Scrub Swamp (Fig. 12, Table 2). The understory is dense, due to abundant vines, shrubs, and tree saplings. However, trees frequently achieve diameters of 20–30 cm and occasionally larger, resulting in a more structurally diverse canopy and less dense understory than in Scrub Swamp (Figs. 13and 14). Canopy shading may still prevent regeneration of some particularly light-demanding species typical of the Scrub Swamp in the absence of treefall gaps or other disturbance; however, we have observed a full range of size classes of a number of relatively shade-intolerant species, such as *Matayba oppositifolia* and *Croton pyramidalis*, beneath intact canopy in Transitional Forest, indicating successful regeneration under such conditions. As in Hill-base forest and all other forest types of low-lying areas in Tikal, partially fallen and leaning trees are abundant. While the number of treefall gaps per sample was not significantly higher for Transitional than for Upland Forest types, the abundant small canopy gaps caused by leaning trees probably allow enough light penetration in this already low, sparse-canopied forest for germination of even highly light-demanding seedlings.

Characteristic species

A group of species reaches its peak abundance in Transitional Forest, including *Matayba oppositifolia*, *Terminalia amazonia*, and *Bursera simaruba*. The edaphic extremes of Transitional Forest, while not intolerable for most upland tree species, are probably suboptimal. A number of species that are most abundant in upland areas occur in very low densities in Transitional Forest. Such species include *Pouteria reticulata*, *P. amygdalina*, *P. campechiana*, *Blomia prisca*, and *Pseudolmedia oxyphyllaria*. A number of species that achieve their highest densities in Hill-base or Sabal Forest remain relatively abundant in Transitional Forest; *Trophis racemosa*, *Vatairea lundellii*, *Pouteria durlandii*, and *Simira salvadorensis* are conspicuous members of this group. Species that we consider Scrub Swamp specialists at Tikal, such as *Croton pyramidalis*, *Coccoloba acapulcensis*, *Coccoloba reflexiflora*, and *Metopium brownei*, first become abundant (when moving down-slope) in Transitional Forest, as light conditions become more favorable for them and edaphic conditions less favorable for their more upland-adapted competitors.

Tall and Low (Xerophytic) Scrub Swamp Forest

Environmental conditions and vegetation structure

In Tikal National Park there are three major lowland depressions or drainage systems, in addition to numerous smaller, related depressions (Fig. 1). In the wet season these depressions fill with water up to 1 m or more in depth, which may cover the ground in the lowest areas for months before gradual drainage and the onset of dry weather removes it. The three major depressions are drained by a network of seasonal streams or arroyos which eventually connect with perennial streams or large permanent swamp areas well outside the park boundaries. Soil in the central regions of these depressions is virtually pure, heavily gleyed and compact clay, which binds strongly to water molecules (Eyre 1964), suggesting that plants in Scrub Swamp experience extreme edaphic drought as these soils become desiccated and deeply fissured in the dry season.

Typical Scrub Swamp Forest is a thicket of stunted, gnarled trees of a uniform, low height, and corresponds to the forest types locally known as "bajo," including the particular type of bajo forest known as "Tintal" due to the predominance of tinto (*Haematoxylum campechianum*). As one moves from the periphery to the interior of the large basins where this forest type occurs, the vegetation increases in density and decreases in height, from taller, more open Scrub Swamp to a virtually impenetrable thicket of sapling-sized trees, vines, and sawsedge (*Scleria bracteata*). Despite the continuous nature of this variation, it is convenient to divide this forest into two categories, "tall" (Fig. 22) and "low" (Fig. 23), corresponding to the topographically higher (peripheral) and lower (central) regions of the depressions in which Scrub Swamp Forest occurs, and named so as to reflect the respective canopy heights of these two forest "types." Tall Scrub Swamp Forest typically occurs between 600 m and 1 km from the nearest upland relief, and Low Scrub Swamp Forest at distances greater than 800 m from such relief. There are a number of exceptions to this rule, as humps of higher ground or even rocky upland islands occur seemingly out of place within Scrub Swamp depressions. These formations may support Tall Scrub Swamp or even an unusual type of Transitional Forest, though the surrounding forest is Low Scrub Swamp. Between one drainage system and another, there is a high degree of variability in the relative locations of these forest types.

Sixteen plots totaling 0.61 ha were located in Low Scrub Swamp and 17 totaling 0.65 ha in Tall Scrub Swamp Forest. Duration of inundation increases from the peripheries to central portions of low-lying basins, and soil characters appear to vary in like fashion, with soils in central regions appearing higher in clay and lower in organic matter than those of peripheral areas. These patterns suggest that edaphic extremes are more pronounced for trees in Low than for those in Tall Scrub Swamp Forest.

Structural and floristic differences between Tall and Low Scrub Swamp Forest appear to be related to the differences in soil and drainage regime described above. The average emergent height in Tall Scrub Swamp Forest plots was 18 m, average modal canopy height 12.7 m, and average lowest canopy height 9 m, compared to 12 m, 10.1 m and 8.1 m respectively for Low Scrub Swamp. Vine density was slightly higher in Tall than in Low Scrub Swamp (Fig. 12, Table 2). Average canopy opening was significantly higher in Low Scrub Swamp, which is evidenced by the higher density of sedges in the understory (Fig. 12, Table 2). However, light availability does not seem to be a limiting factor for regeneration of trees in either of the Scrub Swamp forest types, where canopy opening averaged 2–3 times greater than in Upland forest types (Fig. 12). Stem density was higher on average in Low than in Tall Scrub Swamp forest, but basal area was higher in Tall Scrub Swamp (Figs. 13 and 14).

In Tall Scrub Swamp, light-demanding trees such as *Bucida* and *Swietenia* are often present as 16–20 m tall emergents over a uniform 9–12 m canopy. While these species also occur in the more severe Low Scrub Swamp, emergents of these and other species are much less frequent and lower in stature in the latter forest type.

Characteristic species

Tree species common to both types of Scrub Swamp include *Manilkara zapota, Croton pyramidalis, Croton reflexifolia, Ouratea nitida, Coccoloba reflexiflora, Coccoloba acapulcensis, Coccoloba cozumelensis, Swietenia macrophylla, Gliricidia sepium, Metopium brownei, Haematoxylum campechianum, Bucida buceras,* and *Amyris elemifera.* The following species occur commonly in Tall Scrub Swamp but are infrequent or absent from Low Scrub Swamp: *Vitex guameri, Bursera simaruba, Gymnanthes lucida, Matayba oppositifolia, Lonchocarpus castilloi, Guettarda combsii*, and *Terminalia amazonia*. Conversely, several species are infrequent in Tall Scrub Swamp, but are important components of Low Scrub Swamp, for example *Camareria latifolia, Erythroxylon guatemalensis, Rapanea guianensis*, and *Plumeria obtusa*. Several tree species that attain relatively large sizes (>20 cm dbh) in other topographic regions appear to occur only as stunted treelets in the Low Scrub Swamp (e.g. *Calophyllum brasiliense, Chrysophyllum mexicanum, Amyris elemifera, Ouratea lucens*). One of these species, *Ouratea lucens*, commonly fruits at a height of three meters in the Scrub Swamp.

Mesic Bajo (including Arroyo Forest) and True Swamp

Both of these forest "types" correspond to position 18 of our topographic position code. However, floristic and structural comparison of samples in this topographic range support recognition of two forest types.

Mesic Bajo (including Arroyo Forest)

Environmental conditions and vegetation structure

The larger lowland depression systems in Tikal generally are drained by one or more seasonal streams (arroyos). Along the margins of these waterways a distinct type of vegetation, Arroyo Forest (Fig. 24), occurs, apparently resulting from longer periods of inundation and soil saturation and shorter and less extreme periods of dry season edaphic drought than those experienced by the xerophytic Scrub Swamps occurring slightly higher on the topographic continuum. In the central, lowest-lying portion of one of these drainage systems we encountered an area of low swamp, below the Low Scrub Swamp forest, in an area where standing water was present even at the height of the dry season. We have termed this forest type "Mesic Bajo" (Fig. 25). It is likely that a similar type of permanent low swamp occurs in the other two major drainage basins in Tikal, although we did not intersect any such area in our sampling.

The vegetation occurring in these two zones (arroyos and permanent swamps) within the xerophytic Scrub Swamp-dominated depressions is similar in species composition and structure, and for the purposes of this study is considered under one forest type—Mesic Bajo Forest.

Mesic Bajo and Xerophytic Scrub Swamp differ more in structure than they do in species composition. While the average canopy heights for Mesic Bajo are virtually identical to those of the Tall Scrub Swamp, the average canopy opening is significantly less for Mesic Bajo than for Tall Scrub Swamp and drastically less than for Low Scrub Swamp (Table 2). In addition, the canopy in Mesic Bajo is much more irregular than in Scrub Swamp (Fig. 25); in areas without natural disturbance the canopy is high and quite dense, but adjacent to these patches of tall forest are areas consisting of a 14 m tall tangle of vines, bamboo, and saplings. Because canopy density is often high in Mesic Bajo, treefall gaps play a more important role in this forest type than in Xerophytic Scrub Swamp, and light, although available in high enough intensity for light-demanding tree species to dominate, is patchily distributed, in contrast to the universally high availability of light in the Scrub Swamp. Vine density is also higher in Mesic Bajo than in Xerophytic Scrub Swamp, contributing to canopy closure and presumably to tree mortality through crown-shading and increased susceptibility to toppling in the unstable soil conditions. Basal area was higher in Mesic Bajo than in neighboring Scrub Swamp forest, as trees here achieve greater size (Fig. 14). In contrast, sapling and treelet stem density is lower in Mesic Bajo, presumably due to shading by the dense canopy, combined with prolonged inundation.

Characteristic species:

As the Mesic Bajo is included within the Scrub Swamp spatial matrix, many of the tree species common in Scrub Swamp also occur here. The two most important are *Bucida buceras*, which often dominates tall, relatively open groves, which are interspersed with impenetrable bamboo tangles, and *Haematoxylum campechianum*, which forms almost pure stands (known as "tintales") in some areas with excessive inundation. Other Scrub Swamp specialists such as *Croton pyramidalis* occur in Mesic Bajo but are less common here than in Scrub Swamp. A number of species that are common in riparian forests in other areas of Petén and northern Belize, in Tikal were found only in Mesic Bajo and True Swamp, discussed below. Of these, *Pithecellobium belizensis, Lonchocarpus guatemalensis*, and *Casearia corymbosa* were particularly abundant. *Margaritaria nobilis* and *Amyris elemifera*, although occurring in Scrub Swamp forest in stunted treelet form, achieved their greatest densities and sizes in Mesic Bajo.

True Swamp

Environmental conditions and vegetation structure

Two forests classified as True Swamp were encountered at Tikal. Both were in relatively narrow valleys, 300–600 m wide, in low-lying areas with standing water in the dry season, but surrounded by upland topography, and at higher elevations than the large, Scrub Swamp-dominated depressions described above. Hill-base and Sabal forest were present in the transitional areas between the True Swamp and surrounding upland areas, but no Transitional or Scrub Swamp forest occurred adjacent to the swamp. While areas supporting True Swamp were edaphically similar to those supporting Mesic Bajo, and these forests shared important structural characters and species, they were sufficiently distinctive to warrant differentiation.

The two True Swamps were encountered during streamlined 1993 sampling, in which understory and most structural variables were not recorded. This precluded most quantitative structural comparisons of this with other forest types. Qualitatively, however, the True Swamp and Mesic Bajo seemed similar, both having high vine density, low stem density, and areas of tall, dense-canopied, open-understoried forest interspersed with low, dense vine tangles hardly meriting the term forest. As these two forest types are ecologically and structurally similar, they were combined for many of the analyses. The True Swamp is taller on average than Mesic Bajo, probably resulting in lower light intensity in a gap of any given size in this forest than in Mesic bajo. Hence there may be fewer suitable gaps in True Swamp for regeneration of bajo specialists than in Mesic Bajo.

Characteristic species

Many of the floristic differences between the Mesic Bajo and True Swamp appeared to be related to the forest matrix in which each occurs: Scrub Swamp forest versus upland/Sabal forest, respectively. The distance of the True Swamp from Scrub Swamp seed sources reduces the probability of colonization of True Swamp by many species that frequently occur in Mesic Bajo but are largely limited to Mesic Bajo and Scrub Swamp. Conversely, tree species that are abundant in Sabal or Hill-base forest and tolerant of prolonged inundation should have an advantage in dispersal to gaps in the neighboring True Swamp due to their proximity. *Trophis racemosa, Spondias mombin, Tabebuia rosea, Simira salvadorensis*, and *Sapium* are the more distinctive examples of Sabal Forest 'colonizers' of the True Swamp. These species also seem to be more successful in colonizing small gaps than are many more light demanding species typical of Scrub Swamp.

Common species shared by True Swamp and Mesic Bajo are *Lonchocarpus guatemalensis, Pithecellobium belizensis*, and *Casearia corymbosa*. In addition to these species, the following wet-tolerant species were found at Tikal only in True Swamp: *Inga edulis, Pachira aquatica*, and *Cassia grandis*. In some regions of these swamps the terrestrial bromeliad *Aechmea* sp. forms a dense ground cover and gives a distinctive appearance to the swamp.

Distribution Patterns of Individual Species

From the multivariate analyses presented above it is clear that a significant portion of tree species distribution patterns in Tikal can be explained by topographic position and associated microenvironmental conditions. The topographic/edaphic gradient in Tikal is not, however, simply a monotonic progression from dry upland sites to wet low-lying sites. Rather, conditions for plant life are affected not only by mean moisture availability, but also by seasonal extremes, including drought and standing water. Soil depth, texture, and resultant moisture holding and drainage characteristics, as well as pH and organic matter content, interact with both general position on the topographic sequence and with local site topography to produce a complex and non-linear environmental continuum.

To understand species-environment responses, it is therefore important to consider the distribution of each species along this entire environmental gradient, rather than simply peaks of abundance curves which are the principal currency of ordinations. This is particularly true for the numerous species displaying bimodal abundance curves. In addition, the abundance curves of canopy trees and saplings of a given species suggest the relative success in seedling survival to canopy stature at different points along the predominant environmental gradient. While it is unlikely that any two tree species have precisely the same response to this environmental gradient, species may be grouped into several general response patterns. Here we present graphs of adult and sapling abundance patterns for species representative of the major response types we were able to recognize. Memberships of 155 species in these ten response types are indicated in Appendix 1 under "Topographic Distribution Group."

Distribution patterns revealed three groups of species with abundance peaks in upland forest areas: (1) a group of species most common in the drier upper portions of the gradient (termed Xeric Upland species, Fig. 26); (2) species reaching maximum frequencies and densities in moister, lower-lying upland areas (Mesic Upland species, Fig. 27); and (3) a large group of species with relatively uniform abundance throughout the upland regions of the topographic gradient (Upland Generalists, Fig. 28). Species within these three groups were not restricted to upland regions of the gradient, but decreased in abundance with increased distance from upland areas and were virtually absent from the Scrub Swamp forests in the interiors of the lowland depressions.

A group of species showed an affinity for mesic topographic positions including wetter upland areas, true swamps, and particularly the moist areas at the bases of hills and up to 300 meters into lowland depressions (Mesic Forest species, Fig. 29). This group is interesting in that it included both shade-tolerant and light-demanding species that displayed virtually identical abundance patterns. Bimodal Xeric species (Fig. 30) showed virtually the opposite of Mesic forest species distributions, with peak abundances in the areas experiencing the most extreme xeric conditions—rocky upper slopes and the central regions of lowland depressions.

A large number of species appeared specialized for conditions existing in the lowland portions of the gradient. One group consisted of highly light-demanding species that were ubiquitous in Scrub Swamp forests but absent or significantly less frequent in more mesic lowland forests (Scrub Swamp Specialists, Fig. 31). Some of these species were also common in second growth forests. Transitional Forest Species (Fig. 32) displayed similar distribution to Scrub Swamp Specialists, but appeared susceptible to the most extreme drought conditions found in the Low Scrub Swamp Forest, and reached peak densities in Transitional or High Scrub Swamp Forest. Another group, (Swamp Obligates, Fig. 33) showed the reverse distribution pattern, occupying primarily those areas with seasonally waterlogged soils, but without the extreme drought of the Scrub Swamp areas. Finally, some species were uncommon in upland forest but occurred with uniformly high frequencies in lowland areas (Lowland Generalists, Fig. 34). A few species (Topographic Generalists, Fig. 35) were common throughout the topographic gradient.

Species Responses to Canopy Disturbance and Light Intensity

Ambient light levels in the forests of Tikal vary between regions of the topographic continuum, due to differences in canopy height, canopy cover, and evenness of the canopy's upper surface, and in the frequency of treefalls (Table 2, Fig. 12). Canopy height is an important determinant of the amount of light reaching the forest floor in canopy gaps, as a gap surrounded by tall-canopied forest will receive direct light for a lower percentage of the day than a similarly sized gap bordered by lower forest. Hence, the light environments within treefall gaps (and under other canopy openings) vary significantly with forest type along the dominant topographic gradient (Table 2), due simply to the pattern of decreasing average canopy height from upland to lowland portions of the gradient. This fact is well illustrated by comparison of light environments in human-made logging gaps in forest adjacent to Tikal. Light intensity was significantly higher in lowland forest logging gaps than in upland forest (ANOVA of total site factor, calculated from hemispherical photographs in 86 logging gaps, by forest type, p = 0.007), even though gap size did not differ significantly between forest types (Schulze et al. unpubl. data).

The density of intact forest canopy affects the light environment of seedlings and saplings occurring in undisturbed areas. In general, canopy cover decreased from upland to lowland portions of the topographic gradient, with two primary exceptions. In Dry Upland Forest on hilltops and upper slopes, the understory beneath intact canopy received significantly higher average light intensity (as calculated from hemispherical photographs; Fig. 36) than did Standard Upland understories (see Dry Upland Forest description above). Mesic Bajo typically is a mosaic of canopy gaps and patches of dense, vine-laden canopy. Beneath these patches of intact canopy, light intensities were typically only slightly higher than under Upland forests (est. total site factor from hemispherical photographs = 0.26, s.d. = 0.12 Mesic Bajo; range in undisturbed upland areas = 0.08–0.29), while in the intervening open areas light penetration was such that sedges were common as ground cover (Table 2). In the extreme case—Low Scrub Swamp—canopy cover was so sparse that light intensity was as high under intact canopy in this forest type as in logging gaps in Upland Forest (est. total site factor = 0.50, s.d. = 0.1 logging gaps; 0.45, s.d. = 0.08 Scrub Swamp), and treefalls in Low Scrub Swamp did not typically leave a discernible canopy gap. In some regions of the gradient, particularly Hill-base and Sabal forests, canopy cover can be locally quite dense, but overall canopy structure is broken, with numerous small openings created by processes other than treefall gaps (e.g. leaning trees, canopy palms, discontinuities in canopy cover). Canopy unevenness therefore results in higher understory light intensities in these areas, even in the absence of treefall gaps. Earlier we presented evidence that treefalls are more frequent in lowland forests than in upland (Table 2), resulting in more situations of high light intensity.

On top of the background variation in understory light environments among forest types, light levels within a given forest type or topographic range vary due to natural or anthropogenic disturbances and small-scale variation in canopy cover. Our multivariate analyses suggested that variation in light availability exerts a major influence on distribution of many tree species at Tikal (Figs. 9 and 10). Although the technique used to produce these ordinations (CCA) did not allow for significance testing of species associations with disturbance factors, plots of species centroids in ordination space indicated that for 16 species juvenile abundances were positively correlated with canopy opening, and 22 and 30 species showed associations between juvenile and adult occurrence, respectively, and natural canopy disturbance. To explicitly test the significance of these apparent associations with light and disturbance, we conducted a series of additional analyses, described under DATA ANALYSIS and reported below. We obtained large enough sample sizes ($n \geq 20$) for 63 tree species to include them in one or more of the nine analyses of associations of adults and juveniles with natural disturbance and understory light intensity. Results for all nine analyses are summarized in Table 4.

The most powerful technique for analysis of tree juvenile and treelet associations with light intensity and disturbance proved to be two-way ANOVA of species abundance with topographic position (8 values), natural disturbance, and degree of canopy opening (<10%, 10–20%, >20%) as categorical variables. Of the 56 species tested, 26 did not display significant associations with either natural disturbance or canopy opening: 12 of the 26 species (4 after Bonferroni) were significantly associated with forest type/topographic position, while ANOVA models were non-significant for the remaining 14 of 26 species. Thirty species had one or more effects of disturbance or canopy opening that were significant before Bonferroni correction (Table 4), and 15 species retained significant effects after Bonferroni adjustment. Nine species had significantly higher abundances in samples with high understory light intensity, with two additional species showing marginal associations with high light ($p \leq 0.05$, but n.s. under Bonferroni). Three species (*Haematoxylum campechianum*, *Ouratea lucens*, Myrtaceae sp1), showed significant positive associations with the interaction of forest type and canopy opening—i.e. they were most abundant in lowland sites with open canopies. Four species (*Nectandra coriacea*, *Gymnanthes lucida*, *Drypetes lateriflora*, *Laetia thamnia*) had highest abundances in sites with medium light intensity, although none of these models were significant under Bonferroni. *Cryosophila stauracantha* and *Piper psilorrachis* were significantly, and three other species marginally, associated with sites with dense canopy cover. The majority of species tested did not show any association with disturbance. Three species (*Lonchocarpus latifolius*, *Thevetia ahouai*, *Pithecellobium belizensis*) were significantly more abundant in disturbed than undisturbed plots, with seven species marginally associated with disturbance. One species was significantly, and one marginally, more abundant in undisturbed plots.

For Upland forest samples, we performed Chi-square analyses on data for 35 species to test associations of tree juveniles and treelets with disturbance and light intensity (Table 4). Of these, two species displayed significant (under Bonferroni) positive associations with disturbance (*Chamaedorea pacaya*, and *Piper sempervirens*, both treelets), while distribution of one species, *Gymnanthes lucida*, was negatively associated with disturbance. Fourteen of the remaining species displayed what we consider a convincing lack of correlation with natural disturbance ($p \geq 0.5$), suggesting the ability of seedlings to persist and recruit to sapling size classes in the absence of treefall gaps. Two species (*Piper psilorrachis*, *Pseudolmedia oxyphyllaria*) showed significant positive associations with low understory light intensity (≤10% canopy opening). In upland forest, no tree species showed significant associations with high light intensity (>10% canopy opening), but one such species association was significant prior to correction (*Eugenia* sp.), and another two displayed non-significant tendencies to occur under high light conditions (*Gymnanthes lucida*, *Pouteria durlandii*).

In transitional forest areas (Hill-base, Sabal, Transitional forests) we tested light and disturbance associations of 19 species using MRPP Chi-square tests

(Table 4). For one treelet species (*Piper* cf. *aduncum*) and one non-woody understory dominant (*Costus* sp.) associations with past canopy disturbance were significant, but no tree juveniles were positively associated with disturbance. One understory treelet, *Calyptranthes chytriculia*, was significantly associated with transitional forest areas that had not been subject to recent canopy disturbance. Eight species showed a convincing lack of relation between natural disturbance and juvenile abundances ($p \geq 0.5$). *Croton pyramidalis*, *Trichilia moschata*, and *Ouratea lucens* were significantly associated with sites under relatively open canopies (>20% opening), although they did not show an association with treefall gaps. *Gymnanthes lucida* and *Costus* sp. also displayed positive associations with high light intensity, but these were only significant prior to Bonferroni correction. *Piper psilorrachis* was significantly associated with low light levels, and 6 species showed a convincing lack of correlation with understory light levels ($p \geq 0.5$).

We were able to test sixteen species associations in lowland sites (Mesic Bajo, True Swamp, Tall and Low Scrub Swamp). Four species (*Xylosma* sp., *Haematoxylum campechianum*, *Croton pyramidalis*, *Coccoloba reflexiflora*) displayed significant associations with high understory light intensity (canopy opening >20%), while two species were significantly associated with low light conditions (*Trichilia moschata*, *Cryosophila stauracantha*; Table 4). Four species displayed a convincing lack of association with canopy opening in lowland forest. Interpretation of Chi-square tests of species associations with disturbance in lowland sites was complicated by the lack of influence of treefalls on canopy structure in many Scrub Swamp areas—canopy gaps were rarely recorded in plots from these forest types, even though treefall rates appeared to be equal to or higher than rates in other forests. Observed associations with disturbance for many species merely reflect associations with either Mesic Bajo and True Swamp (positive associations), or with Scrub Swamp (negative associations). An illustration of this confounding factor is the apparent association of the understory palm *Cryosophila stauracantha* with natural disturbance within these lowland sites. Any observer of this species at Tikal would conclude that it is shade-tolerant, and indeed our other Chi-square tests demonstrated that it is not positively associated with disturbance or high light intensity, and in fact displays an affinity for undisturbed, low light sites (Table 4). We do not, therefore place much confidence in results of disturbance correlations at lowland sites.

Adults of eight species were significantly more abundant in Upland forest plots with old treefall gaps than in undisturbed plots, with two more species displaying marginal associations with disturbance (Table 4). For one species, *Brosimum alicastrum*, distribution was significantly correlated with undisturbed forest, and two more species (*Pouteria reticulata*, *Cryosophila stauracantha*) displayed marginal associations with undisturbed forest. Fifteen species displayed a compelling lack of association with natural canopy disturbance (i.e. $p \geq 0.5$). In lowland forest (Hill-base through Mesic Bajo) one species, *Sebastiana longicuspis*, was significantly associated with undisturbed areas, with *Protium copal* and *Pouteria reticulata* marginally associated with undisturbed and disturbed areas, respectively. This last species was the most commonly encountered subcanopy or canopy tree species in the understory and is clearly shade-tolerant. Therefore we can only interpret this result as a statistical artifact.

Table 4. Results of chi-square and ANOVA testing of juvenile and adult tree associations with natural disturbance and canopy opening.

	Juveniles - stems <1m tall, <7.5cm dbh Chi-square						Trees >7.5 cm dbh Chi-square		Juveniles ANOVA
	Upland sites n=114		Transitional sites n=46		Lowland sites n=35		Upland n=114	Transitional n=46	Full gradient
Species	Canopy opening	Disturbance	Canopy opening	Disturbance	Canopy opening	Disturbance	Disturbance	Disturbance	Canopy opening / disturbance
Acacia cookii			0.482	0.847			0.659	0.556	
Amyris elemifera									0.001 H*
Ardisia densiflora									0.0003 H*
Ardisia paschalis	0.168	0.590	0.115 H	0.499					
Aspidosperma cruenta	0.393	0.393					0.702		
Aspidosperma megalocarpon	0.124 L	0.235					0.558		
Bactris sp.									0.0003 D*
Bamboo *					0.009 L*	0.283			
Blomia prisca	0.531	0.894					0.835		
Brosimum alicastrum	0.542	0.761					**0.001 U**	0.467	
Bursera simaruba							**0.0006 D**		
Calyptranthes chytraculia			0.656	**0.00005 U**					
Casearia bartlettii							0.276		
Cecropia peltata							**0.002 D**		
Chamaedorea pacaya	0.209	**0.00002 D**							0.023 D*
Chamaedorea sp2	0.737	0.386							
Chamaedorea sp1	0.921	0.336	0.802	0.896					
Coccoloba reflexifolia					**0.0001 H**	0.006 U*			**0.0002 H**
Costus sp. *			0.008 H*	**$0.2x10^{-5}$ D**					
Croton pyramidalis			**0.00004 H**	0.788	**$0.12x10^{-14}$ H**	0.057 U		0.715	**$0.16x10^{-4}$ H**
Cryosophila stauracantha	0.200	0.128 U	0.761	0.187	**0.004 L**	**$0.7x10^{-5}$ D**	0.023 U*	0.403	**$0.19x10^{-7}$ U&L**

Cupania belizensis	0.601	0.177	0.747	0.162			0.374		
Dendropanax arboreus							**0.0006 D**		
Drypetes lateriflora	0.415	0.503					0.636		0.005 M*
Eugenia sp.	0.029 H*	0.629							
Guettarda combsii							**0.0001 D**		
Gymnanthes lucida	0.111 H	**0.0002 U**	0.01 H*		0.394	0.738	**0.00004 D**		0.05 M*
Haematoxylum campechianum					**0.001 H**	0.0046 U*			**0.25 x10^{-5}H(F)**
Laetia thamnia							0.745		0.09 M
Lonchocarpus latifolius									**0.0002 H &D**
Malmea depressa	0.169	0.571					0.777		
Malpighia glabra	0.534	0.338							0.026 U*
Manilkara zapota	0.727	0.558			0.528	0.799	0.545		**0.2 x10^{-7} H**
Margaritaria nobilis									**0.16 x10^{-5} H**
Myrtaceae sp (bajo #1)					0.069 H	**0.4x10^{-4} U**			**0.00014 H**
Nectandra coriacea	0.939	0.883					0.013 D*		0.029 M*
Nectandra salicifolia							0.374		
OPPLV1 (Myrtaceae sp.)					0.052 H	0.261			**0.15 x10^{-5} H(F)**
Ouratea lucens			**0.0003 H**	0.332	0.875	0.045 D*			**0.001 H(F)**
Pimenta dioica	0.07 L	0.188	0.084 H	0.235			0.447	0.827	
Piper cf. aduncum	0.869	0.086 D	0.626	**0.001 D**					0.035 D*
Piper psilorrachis	**0.002 L**	0.842	**0.001 L**	0.564					**0.99 x10^{-15} L**
Piper sempervirens	0.056 L	**0.0002 D**							0.014 D & L*
Pithecellobium belizensis					0.743	**0.004 D**			**0.00078 D**
Pouteria amygdalina	0.555	0.840					0.378		
Pouteria campechiana	0.703	0.330					0.245		0.17 D
Pouteria durlandii	0.112 H	0.181	0.813	0.515	0.069 L	0.041 D*	0.520	0.520	

	Juveniles - stems <1m tall, <7.5cm dbh Chi-square						Trees >7.5 cm dbh Chi-square		Juveniles ANOVA
	Upland sites n=114		Transitional sites n=46		Lowland sites n=35		Upland n=114	Transitional n=46	Full gradient n=201
Species	Canopy opening	Disturbance	Canopy opening	Disturbance	Canopy opening	Disturbance	Disturbance	Disturbance	Canopy opening / disturbance
Pouteria reticulata	0.341	0.555	.084 H	0.648	0.080 L	0.046 D*	0.020 U*	0.005 D*	
Protium copal	0.567	0.152 U	0.263	0.849			0.694	0.041 U*	
Pseudolmedia oxyphyllaria	**0.004 L**	0.184					0.647	0.074 U	0.063 L
Phyllanthus nobilis									**0.33×10^{-5} H**
Sabal mauritiiformis	0.304	0.445	0.438	0.546			0.881	0.896	
Sebastiana longicuspis	0.227	0.517			0.887	**0.2×10^{-5} U**	**0.00008 D**	**0.0005 U**	0.07 L
Simira salvadorensis	0.233	0.118 D					0.727	0.712	0.012 D*
Spondias mombin							**0.003 D**		
Stemmadenia donnell-smithii							**0.004 D**		
Talisia olivaeformis	0.753	0.262					0.581		
Thevetia ahouai									**0.31×10^{-5} H&D**
Trichilia minutiflora	0.482	0.073 U	0.347	0.145			0.363	0.582	
Trichilia moschata	0.657	0.694	**0.004 H**	0.069 U	**0.0002 L**	0.213	0.061 D	0.587	
Trichilia pallida	0.401	0.629							
Wimmeria concolor	0.708	0.128 D					0.539		0.028 D*
Xylosma sp.					**0.7×10^{-6} H**	**0.0001 U**			**0.0003 H**

All p-values are reported for Chi-square tests. For ANOVA, p-values are reported for only those models that were significant or nearly significant. Values in bold indicate results that were significant following Bonferroni correction. Values followed by an * indicate results that were significant at p=0.05 prior to Bonferroni correction but not afterward. Letter codes indicate direction of association: D = + correlation with canopy disturbance; U = - correlation with canopy disturbance; L = associated with low light intensity (0-10% canopy opening); M = associated with moderate canopy opening (10-20%); H = associated with high light intensity (>20%); (F) = positively associated with the interaction of forest type and light intensity (i.e. most abundant in high-light, lowland forest).

The results of the above statistical analyses confirm the trends evidenced in the CCA ordinations of adults and juveniles with disturbance and canopy opening included as variables. Overall, 13 species displayed significant associations with canopy opening >20% (plus four marginal associations), and distributions of 13 species were significantly correlated with canopy disturbance (either juveniles or adults, with eight additional marginal associations). These numbers are only slightly lower than would be predicted from the CCA ordinations, and the discrepancy is due in part to the fact that several species showing associations in CCA were not included in Chi-square or ANOVA tests, due to small sample sizes.

Furthermore, these results demonstrate that species responses to light intensity and canopy disturbance vary within the tree community (Table 4). For some species, juveniles did not show a positive association with canopy opening or gap disturbance, but adult distribution was highly correlated with old disturbances, suggesting that these species were able to maintain seedling and sapling stocks under intact canopy, but required gaps for recruitment to pole and adult size classes.

A number of light-demanding species were significantly associated as adults with old treefall gaps in Upland forest within our sample, while juveniles were virtually absent from understory samples. This pattern suggests that such species require relatively large disturbances in order to colonize upland forest, but recent gaps (<5 years of age), where juveniles would be found, were much less abundant than older gaps (5–20^+ years) in our sample. It should be noted that for a number of long-lived, light-demanding species, such as *Pseudobombax ellipticum*, *Swietenia macrophylla*, and *Cedrela mexicana*, our limited ability to objectively record the presence of disturbance events older than ca. 20 years, restricted our ability to examine associations of adults with canopy disturbance. Size class distributions for these species were skewed towards diameters >45 cm; even assuming a very high growth rate of 2 cm per year, these individuals would be older than twenty years, and more likely they were closer to fifty years of age. Relatively small differences in canopy opening appeared to be significant for saplings of some species. For example *Gymnanthes lucida* seedlings and saplings were abundant under light, but intact canopy in dry upland forest, but were not common under the denser canopy of more mesic upland forest.

As noted above, in Scrub Swamp forests, treefall gaps do not significantly modify the understory light environment, and species reaching peak abundance in these forests showed no association with canopy disturbance, although both saplings and adults were positively associated with light intensity. In contrast, in upland areas and mesic lowland forests canopy disturbance does appear to be an important source of regeneration opportunities, with a number of tree species positively associated with treefall disturbances in juvenile (recent gaps) and/or adult classes (building phase forest). Hence, as in other tropical forest areas (Denslow 1987, Swaine et al. 1987), gap dynamics are important in determining local species composition, but only in some portions of the topographic gradient.

Knowing the manner in which light and edaphic conditions vary along the topographic gradient in Tikal, it is possible to infer the relative importance of edaphic factors and light availability in determining patterns of individual species occurrence, through comparison of juvenile and adult abundance peaks along the gradient. If a species is well represented by both juveniles and adults in Upland forest, and does not display a positive association with canopy disturbance, the logical assumption would be that light is not generally a limiting factor and that the species distribution pattern across the gradient is more likely influenced by edaphic conditions. A large number of species in our sample fit this model. Conversely, for species with juveniles and adults largely restricted to low-lying portions of the gradient (particularly Scrub Swamp), but with adults occasionally occupying upland areas, we infer that light availability is a more critical limiting factor in colonization and recruitment than are edaphic factors. Similarly, species entirely restricted to Scrub Swamp areas are probably light limited, as they are clearly able to tolerate extreme edaphic drought as well as inundation, and hence might be expected to occupy a greater range based solely on edaphic considerations.

The majority of tree species appear to fall in between the two extremes of species limited primarily by edaphic conditions and those limited chiefly by light availability. A number of species had juvenile abundance peaks in lowland forest even though adults were most common in upland forest. The majority of these species displayed positive associations with either canopy opening or disturbance in the analyses above. We hypothesize that there is a trade-off for these species between the optimal light regime and tolerable edaphic conditions. High intensity light environments are most common in Scrub Swamp regions of the continuum, yet these areas are also subject to the most severe edaphic extremes. Hence, while germination and early survival rates may be high for these species due to light availability, ultimately survival and recruitment to adult size appears to be quite low in Scrub Swamp. Few seedlings and saplings may establish in upland regions, but those that do so appear to have a much higher probability of survival here than in Scrub Swamp portions of the topographic gradient. For species with juvenile and adult abundance peaks in Hill-base through Transitional forests we can infer little, from distribution patterns alone, about the relative influence of light and edaphic conditions on survival and recruitment rates, as conditions in these areas are acceptable to both drought-sensitive and light-demanding species.

As mentioned above, numerous species were virtually absent from understory samples, with adults positively associated with past disturbance. In establishment and/or recruitment of seedlings these species likely are limited by light. In addition many of these species are also absent from the high-light environment of Scrub Swamp regions of the gradient, indicating that edaphic tolerances also play a role in determining their distribution patterns.

Using the results of the Chi-square and ANOVA analyses, as well as comparison of adult and juvenile distributions, we were able to recognize seven light/disturbance response patterns. The response types are presented in Fig. 37, ordered with respect to three variables: the association of adults with past canopy disturbance; the association of saplings with high understory light intensity; and the association of juveniles with treefall gaps. In Appendix 1, each of the species studied is assigned to one of these seven response types or guilds. For species with low sample sizes (indicated by an asterisk in Appendix 1) we based our classification on qualitative observations of light and disturbance associations during five years of field work in the region. Descriptions of light/disturbance response types (guilds) follow in order of increasing shade tolerance:

1. **Highly shade intolerant, non-gap species.**—This species group (Table 4, Appendix 1) is composed of species positively correlated with degrees of canopy opening of 20% or greater, but not correlated with intermediate (i.e. 10–20%) canopy opening or with disturbance history (treefall gaps). These species are poorly represented in Upland Forest and are most abundant in (often limited to) Scrub Swamp, Mesic Bajo and Transitional Forest, where treefall gaps are either insignificant modifiers of understory light environments, or are rendered suboptimal by edaphic factors for colonization by fast-growing pioneer species. Most of these species appear to be relatively slow growing, and probably do not compete well with pioneer species in the colonization of gaps in upland habitats.

2. **Large-gap colonizers.**—In this group (Table 4, Appendix 1), adults were positively correlated with evidence of older disturbance (five years or more of age), but saplings were too rare in samples to allow statistical tests. Most recent gaps recorded by our sampling were small or medium-sized, whereas the older disturbances that were detectable were primarily large ones. The observed association between adult trees of guild 2 members and large, old disturbance events, and the rarity of saplings in the prevalent small and medium-sized gaps, suggest that these species require large treefall gaps for successful regeneration. Indeed, several of the species in this group have been classed as pioneers in previous studies (e.g. Brokaw 1987; Popma and Bongers 1988; Whitmore 1989). The consistent absence of saplings, but occasional presence of seedlings, of this group in recent treefall gaps and the presence of larger saplings in older gaps, indicate that these species are regenerating in gaps from seed rather than from pre-established saplings.

3. **Gap generalists.**—This guild includes species with saplings (or adults in the case of treelets) positively associated with disturbance. These species show similar regeneration requirements to those of 'large-gap colonizers', but appear more able to colonize small and medium-sized treefall gaps, explaining the higher frequency of small individuals of these species in our sampling than of those in Guild 2. These species may colonize gaps in lowland forests as advance regeneration.

4. **Moderately light demanding species.**—This group includes species in which saplings are associated with relatively open (>10%) canopy, and adult trees, but not saplings, are associated with past disturbance. Species in this group do not appear to require treefall gaps for germination and establishment of saplings. However, moderate to high light intensity does seem to favor either the establishment or persistence of saplings. These light conditions can be found in the absence of treefalls or other disturbance, even beneath the relatively closed canopy of upland forest. Guild members *Gymnanthes lucida* and *Nectandra coriacea* are dominants in drier upland forests on upper slopes, where the canopy is typically uniform and thin; in such environs, saplings of these species were often abundant beneath the canopy, while adults were conspicuously linked to older canopy gaps. Other guild members such as *Trophis racemosa* and *Zuelania guidonia* occur commonly as saplings in the absence of treefall gaps in Hill-base and Sabal forests where a high frequency of leaning trees and relatively broken canopy combine to create numerous light patches smaller than those created by

treefall gaps. While gaps are not required for sapling establishment by members of this guild, gap occurrence appears to strongly favor growth from sapling to adult stature.

5. **Gap recruiters.**—This guild contains species in which sapling occurrence does not show a correlation with disturbance or canopy opening, but adult occurrence shows strong positive correlation with disturbance history. While only one species in our sampling significantly displayed this pattern, our field observations indicate that this is a common response type. Species in this group do not appear to require treefall gaps for germination and sapling establishment, but they do seem to require some canopy disturbance (at least in upland regions) in order to attain adult size. The main difference between the requirements of these species and those of members of Guild 7 (shade-tolerant species) is most likely that Guild 5 members require larger disturbances in order to reach adult stature. While we did not determine sapling survival rates, it is likely that members of Guild 5 have lower sapling survival rates under closed Upland forest canopies than do Guild 7 species. Saplings of Guild 5 species were less abundant on average than those of Guild 7 species in upland forests where light availability under intact canopies is generally low (Appendix 2).

6. **Semi-shade-tolerant species.**—Saplings of these species are positively correlated with relatively open canopy (>10% open) in upland and/or transitional regions of the topographic gradient, but uncorrelated with disturbance history. Some species in this group are abundant on upper slopes, where the canopy is typically uniform but thin, while others are more common in the hill-base and Sabal regions of the topographic gradient, where the canopy is typically more broken. While members of this guild did not show strong correlations with disturbance, it is likely that they successfully colonize gaps as advance regeneration. One guild member, *Nectandra salicifolia*, was among the more consistently dominant species in adult size classes in 12-year-old logging gaps in Upland Forest near Tikal (Schulze, unpubl. data), indicating that this species is well adapted to colonization of canopy gaps.

7. **Shade-tolerant species.**—Members of this guild show a convincing lack of correlation with canopy opening and disturbance, a significant negative correlation with disturbance (*Malpighia glabra*), or a significant negative association with degree of canopy opening (*Piper psilorrachis, Cryosophila stauracantha, Pseudolmedia oxyphyllaria, Calyptranthes chytriculia*). This group comprises shade-tolerant species. All members of the group can establish and maintain saplings under closed canopy, though they may not reach adult size there without some kind of opportunity for increased light. In contrast to members of more light-demanding guilds, these species probably can utilize small canopy openings such as those created by a fallen limb or uneven horizontal spacing of tree crowns, to reach adult sizes; they do not depend on treefalls. Not surprisingly, the species in this group account for an overwhelming majority of stems in a given patch of mature Upland Forest.

Ecological Groups

Up to this point we have shown that tree species composition varies predictably along the predominant topographic/edaphic gradient, and that more or less distinct distribution patterns can be identified for individual species. Natural disturbance, in the form of treefall gaps, and variation in vegetation structure, particularly canopy height and cover, play significant roles in determining species composition at any given point in space. Species-specific response patterns to light and disturbance regimes can also be identified. However, species with similar distribution patterns along the topographic gradient do not necessarily display the same responses to disturbance, and species with apparently similar light requirements often display different distribution patterns with respect to the topographic gradient. Hence, topographic/edaphic associations and light/disturbance response patterns must be considered simultaneously in order to create a meaningful grouping of tree species based on ecological characters.

By considering topographic distributions and disturbance/light response guilds jointly for each tree species we have been able to identify 19 ecological groups for trees at Tikal (Fig. 38). These groups are provisional; further research will likely show that even within a given "ecological group" species differ significantly in their tolerances to edaphic and light conditions. Moreover, a number of additional factors no doubt affect species distributions including: pathogens, processes and patterns of seed dispersal, seed predation and stochastic processes. In addition, edaphic and light tolerances are not clear cut and are probably reflections of interactions among numerous factors, both abiotic and biotic, which combine to confer reduced fitness and increased mortality on a species in a given portion of the topographic gradient. We were unable to classify many species due to small sample sizes. Despite these limitations, the following classification appears to be a useful translation of the patterns we have recorded in this sampling into ecologically meaningful species groups, and is more accurate than simple pioneer/climax species distinctions. In some cases where sample sizes were small, we have relied on understanding provided by qualitative observations over several years of field work, to aid in tentatively placing species into ecological groupings.

Figure 38 depicts the manner in which seven light/disturbance response guilds and 10 topographic distribution patterns combine to result in 19 ecological groupings of tree species at Tikal. Appendix 1 shows our tentative allocation of 155 tree species with regard to the three means of categorization.

We distinguish five groups of shade-tolerant tree species (groups 1–5, Fig. 38, Appendix 1). These species groups differ primarily in their success under edaphic extremes, especially in the ability to tolerate seasonal drought and soil saturation. The first three species groups appear to be favored by conditions in upland forest, with group 1 species favored by moderate conditions (Standard and Mesic Upland), group 2 species reaching highest densities in Dry Upland forest, and group 3 species able to exploit all upland areas with equal success. Group 4 species achieve peak abundances under mesic conditions, from mesic upland to Sabal lowland, and group 5 species show no significant topographic associations.

Eight species groups are classified as highly light-demanding (groups 12–19, Fig. 38, Appendix 1). These species differ in their ability to exploit gap disturbances to colonize upland forest areas and in their tolerance of drought and inundation. One extreme is exemplified by group 12 and 14 species, which successfully colonize gaps in upland forest, but appear to be highly susceptible to both flooding and seasonal drought. In contrast, group 17 species are highly tolerant of both extreme inundation and drought, but do not appear to compete successfully in gaps in Upland forest, and may even be at a competitive disadvantage in high-light, seasonally flooded, but not drought-impacted Swamp and Mesic Bajo. Group 18 and group 19 species also appear to have very low success in exploiting high-light situations in Upland forest and are thus largely restricted to lowlands, with group 19 species further restricted to mesic lowland forests (Mesic Bajo and True Swamp) by intolerance of drought. Species of groups 13–15 appear to be more successful in colonizing large gaps in Upland forest and particularly intermediate forests (Transitional, Sabal, Hill-base), but differ substantially in their edaphic tolerances (Fig. 38). Group 12 species are equivalent with pioneer species—they are adapted for high success in colonizing medium to large gaps in upland areas, but appear to be sensitive to extremes in both drought and inundation and are therefore uncommon in Transitional, Scrub Swamp, True Swamp and Mesic Bajo.

Moderately light-demanding species (light/disturbance guilds 4–6) can also be divided based on tolerance of environmental extremes. These species all show some capacity for seed germination and early survival under low or intermediate light conditions (canopy opening 10–20%). Species with intermediate shade tolerance appear to exploit areas with thin or broken canopies for recruitment of juveniles, and hence are present in treefall gaps as advanced regeneration in a manner similar to shade-tolerant species. These areas of intermediate light intensity are more common in some regions of the topographic continuum than others (e.g. hilltops, upper slopes, and Hill-base/Sabal forest), and distributions of these species appear partially determined by the availability of appropriate light conditions across the topographic gradient, and partially by the species' edaphic tolerances. Species with moderate shade-tolerance, high tolerance of inundation and low tolerance of drought make up group 7, and are found primarily in True Swamp and Mesic Bajo. At the other extreme are group 10 species, which are highly tolerant of excessive soil drainage and drought, but intolerant of inundation, and occur primarily in Dry Upland. Members of groups 11 and 8 are tolerant of both drought and inundation, but the former are better able to persist in the areas producing the most extreme edaphic stress (i.e. Low Scrub Swamp) than are group 8 species. Group 8 species are particularly abundant on hilltops and upper slopes, where the thin canopy appears to facilitate recruitment of seedlings to sapling size classes, allowing these species to exploit canopy openings as advanced regeneration to reach the canopy, and in Transitional and Tall Scrub Swamp forests, where treefall gaps do not appear to be necessary for recruitment during any stage of the life-cycle. Species in groups 6 and 9 show similar sensitivities to drought, with the former apparently better able to exploit small to large gaps in Upland forest from seedlings or saplings, and the latter more tolerant of inundation (evidenced by relatively high densities in True Swamp) and less successful in competing with advanced regeneration of shade-tolerant species and pioneers in upland forest gaps.

CONCLUSIONS

Tropical forests in the lowlands of Petén are at most 11,000 years old (Leyden 1984), and over much of the region age is probably 1,000 years or less. Hence, the current canopy trees might represent only the third or fourth generation since disturbance. The question of whether Petén forests have reach a steady-state equilibrium is a fascinating problem in the study of current forest dynamics. While it is still not possible to answer this question, our results may contribute to this discussion. That variation in forest structure and composition (i.e. forest types) along topographic/edaphic gradients is highly predictable, is indicative of some degree of stabilization. Throughout the topographic gradient, the dominant species in the canopy are also abundant in the understory, and appear to be regenerating successfully, although regeneration strategies vary considerably. Within a given forest type, many species do not display anything approaching a reverse-J diameter distribution; some species appear to regenerate successfully in treefall gaps and seem assured of representation in future generations, while others are so poorly represented by juveniles, even in the largest gap areas, that competitive exclusion is a plausible future scenario. However, even for the latter set of species, healthy populations in adjacent forest types would seem to preclude local extirpation of the species, and should provide sources for recolonization.

Judgment of whether the forests of Petén are in a steady-state will depend on the scale considered. In Tikal, it is relatively common to encounter patches of upland forest up to several hectares in size that are dominated by light-demanding emergent species, such as *Swietenia*, *Vitex*, *Pseudobombax*, and *Cedrela*. In these areas, the understory and subcanopy is dominated by the shade-tolerant species typical of upland forest, and clearly species composition will shift in the future. It has been hypothesized that such large assemblages of light-demanding emergents reflect large disturbances, such as hurricanes (Snook 1992). Given the absence of these species from small to medium gaps in upland forest, large disturbances do seem the best explanation for dense upland stands of emergents like *Swietenia*. Without the recurrence of a major disturbance event, *Swietenia* and similar species will likely decline through time in these upland areas. Nonetheless, in lower portions of the gradient, *Swietenia* is able to regenerate in the absence of major disturbances; *Swietenia* populations may expand and contract around lowland sources at intervals of several hundred years, and thus may be stable over large areas and long time periods. As discussed earlier, we believe that species associations with Maya ruins are more likely related to edaphic conditions than directly to activities of the ancient Maya. The evidence we have recorded at Tikal suggests that the vegetation is in some form of steady-state equilibrium, but not a static climax formation. This view does not discount the impact that land-use and forest clearing by the Maya may have had on the forests of Petén. In fact, human disturbance probably altered forest composition substantially, and we likely still observe the results today. At a regional scale, however, forest composition appears stable.

Our results suggest that topography (and related edaphic conditions), ambient light availability, and natural canopy disturbance all play major roles in determining patterns of tree species occurrence in Tikal. Most tree species showed strong abundance peaks in one or more parts of the topographic continuum, and many were rare in, or absent from, certain portions of the continuum. Not all species exhibited unimodal abundance patterns across the predominant environmental gradient; several showed two distinct abundance peaks in different portions of the continuum, suggesting that these positions were similar in at least some environmental characteristic. Responses of trees to the topographic continuum were as pronounced as were species associations with certain light and disturbance conditions. Indeed, we found cases in which incompatibility with local soil/environmental conditions appeared to prevent the occurrence of a species in spite of appropriate light conditions for regeneration.

Some workers have emphasized the role of specialization for different regeneration conditions in determining patterns within tropical tree communities (e.g. Denslow 1980; Pickett 1983; Whitmore 1985; Brandani 1988). Many studies have focused on treefall gaps as the primary source of variation in light availability and consequently in species composition. We find this approach oversimplified, not only in failing to recognize the importance of topographic/edaphic responses, but also with respect to the variety of light sources and tree responses to them. Levels of light availability in tropical forests often are intermediate between those of treefall gaps and continuous canopy, and light often reaches the understory by means of many small-scale sources (Chazdon 1988; Lieberman and Lieberman 1989; Clark et al. 1993). Moreover, relatively small differences in light intensity can have a significant impact on the establishment and survival of individual trees (Clark and Clark 1992; Kobe et al. 1995).

Our study provides additional evidence that light availability other than from major treefall gaps can be important to some tree species. We found that ambient light levels, in addition to being influenced by incidence and size of treefall gaps, varied across the topographic gradient, largely in concert with, and no doubt as a result of, canopy height and structural characteristics. In particular, many small gaps were provided by limb-falls, leaning trees, uneven canopy, and canopy discontinuities around the periphery of palm crowns. Small variations in light that did not depend on treefalls appeared to provide important recruitment opportunities for a number of species having intermediate levels of shade intolerance. Some highly light-demanding species did not appear to be adapted primarily for colonizing large treefall gaps but rather appeared to be associated mainly with areas of thinner canopy and overall higher levels of ambient light in the understory. Other species that relied on treefall gaps for regeneration in upland regions regenerated beneath the canopy in portions of the topographic continuum supporting thin-canopied forests. In lower, more open-canopied regions of the topographic continuum treefalls did not seem to significantly determine local species composition.

We suspect that greater diversity may exist in species regeneration strategies than has been commonly recognized (e.g. Kennedy and Swaine 1992; Lieberman et al. 1995). For example, some species that primarily colonize gaps as advanced regeneration (e.g. *Nectandra salicifolia*, *Sebastiana longicuspis*) rather than by seed as do pioneer species, seem to be adapted for more rapid growth in gaps than are most shade-tolerant species. Even within our shade-tolerant species groups, we have noted substantial variation in species responses to increased light availability.

We found that species guilds based on responses to topographic position and associated moisture and edaphic factors were recognizable, as were guilds based upon regeneration requirements with regard to light. However, neither of these methods of categorization was in itself adequate to describe observed patterns; in some cases two or more species reached abundance peaks in the same portions of the topographic gradient, but apparently for different reasons. Simultaneous consideration of species tolerances and optima with respect to both light and topographic/edaphic conditions leads to a better understanding of community composition than does either perspective by itself. This species categorization is based on specific hypotheses about relative growth and survival rates under varying light and edaphic conditions. These hypotheses should be tested experimentally; this would no doubt modify guild designations and increase our understanding of how these environmental factors structure tropical tree communities.

Physiological tolerance limits and optima with respect to topographically related environmental conditions only determine the broad boundaries within which a species can occur. The distribution patterns we recorded are almost certainly the result of a complex interaction of chance, species attributes, and many abiotic and biotic factors. In addition to those described above, such factors may include: soil and litter disturbance requirements for seedling establishment (cf. Putz 1983); variation in pathogen susceptibility both between species and between habitats for a single species (cf. Augsperger 1984b, c); seed dispersal methods and resultant seed shadows; seed predation (Janzen 1970); numerous stochastic factors (cf. Hubbell and Foster 1986a); and additional factors we have not mentioned.

Hubbell (1979) and Hubbell and Foster (1986a) have made a strong case against viewing niche partitioning as the primary factor allowing coexistence of so many tree species in tropical forest, and have shown that ecologically equivalent species may coexist for long periods without competitive exclusion, through the stochastic nature of regeneration. While we believe we have shown strong evidence of important levels of niche diversification among tree species at Tikal with respect to edaphic and light environments, we do not propose that this is the only, or even the dominant, mechanism permitting species coexistence there. Hubbell and Foster (1986a) further argued that high species diversity in tropical trees results in largely unpredictable species identity of neighboring individuals, rendering competitive niche divergence improbable. Unpredictability of neighbor identity amounts simply to diffuse competition; while such unpredictability may render unlikely fine-tuned divergence of species characteristics, it does not preclude specialization for some subset of the broad range of abiotic conditions existing at Tikal.

There is perhaps a need to refine the question of what mechanisms permit coexistence of so many tree species in tropical forests, to explicitly consider coexistence across obvious environmental gradients such as catenas, which contribute to beta diversity, versus coexistence within a more narrowly defined portion of the landscape (e.g. well-drained upland sites), amounting to alpha diversity. Presumably, much of the discussion to date surrounding the question of tropical tree species coexistence has implicitly considered coexistence in restricted, homogeneous areas, and hence dealt with alpha diversity. In that regard, the demonstration that many species respond strongly to a fairly pronounced topographic gradient at Tikal may perhaps be viewed as contributing little to the debate. However, on closer inspection, it becomes clear that specialization for some portion of the regionally available habitats may indeed have important outcomes for competitive and stochastic processes at the level of alpha diversity, as argued below.

The apparent fact that species are specialized to some degree with respect to soil moisture and perhaps other edaphic factors, renders the identity of neighbors more predictable than would otherwise be the case, such that a given species no doubt interacts more strongly with one subset of potential competitors than with others. The degree of diffuse or 'background' light penetration to the forest floor (i.e. not that caused by treefall gaps) is largely determined by structural characters that are strongly correlated with topographic position, and that presumably resulted from environmental conditions along the gradient. Hence, the light environment is in part an emergent property determined indirectly by topographic/edaphic factors. These two factors—apparent differences in species optima with respect to environmental factors, and predictable covariation of these factors (e.g. of diffuse light penetration and topographic/edaphic factors)—promote interaction among a certain set of species and admit more scope for niche divergence than generally has been recognized. Furthermore, the fact that most species have one or more abundance peaks somewhere along the gradient in effect may give them a refuge from which to send propagules to a broader range of the environmental gradient. In this manner upland regions may be colonized sporadically by species that are at a competitive disadvantage in those environmental conditions, but that maintain stable populations in neighboring lowland areas. A similar phenomenon appears to occur on a regional scale, as many species with very restricted ranges and low densities in Tikal, are much better represented in adjacent wetter forests in Belize and western Petén. Qualitative observation of forests in tropical Guatemala and Belize lead us to conclude that it is relatively common for 'rare' species in one locale to be substantially more abundant in another geographic region, with slightly different climatic or soil conditions. It is possible that regional 'source' populations in areas with optimal environmental conditions, provide a critical subsidy, in the form of genetic exchange and occasional seed input, for marginal populations of these species in Tikal.

Topographic gradients as pronounced as those in Tikal do not occur in all tropical areas. However, even in the relatively flat Amazon basin, regional and local variation in soil and moisture conditions can be substantial (Sombroek 1968, Tuomisto et al. 1995). Alpha diversity in many tropical areas is considerably higher than in Tikal, and in such areas there may be more reason to assign a portion of species richness to stochastic factors. However, in recognizing that niche divergence along light/disturbance axes is far from the only mode of divergence available to tropical tree species, it becomes clear that the potential for niche divergence is indeed large. While stochastic factors no doubt are important, they are played out upon an environmental stage which is more varied and influential than has generally been recognized.

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Appendix 1

Tree, treelet, and understory plant species codes and membership in light/disturbance, distribution, and ecological groupings

Abbreviation	Species	Light / Disturbance Response Group	Topographic Distribution Group	Ecological Group
acac 'sp	*Acacia* sp.	?	?	?
acaccook	*Acacia cookii*	4*	2	9
acacdoli	*Acacia dolichostachya*	?	?	?
acacglom	*Acacia glomerosa*	?	?	?
aegimons	*Aegiphila monstrosa*	2*	3	12
alibedul	*Alibertia edulis*	7*	2	4
allocomi	*Allophylus comina*	1*	8	18
alseyuca	*Alseis yucatanensis*	?	1	1 or 6
ampehott	*Ampelocera hottlei*	7*	2	4
amyrelim	*Amyris elemifera*	1	5	15
anno 'sp	*Annona* sp.	2*	1	12
ardidens	*Ardisia densiflora*	1	7	17
ardipasc	*Ardisia paschalis*	3*	6	16
aspicrue	*Aspidosperma cruenta*	7	1	1
aspimega	*Aspidosperma megalocarpon*	7	3	1
astrgrav	*Astronium graveolens*	4*	2	9
bactmajo	*Bactris major*	?	6	16
bernflam	*Bernoullia flammea*	2*	4	14
blompris	*Blomia prisca*	7	3	3
brosalic	*Brosimum alicastrum*	7	4	2
bucibuse	*Bucida buceras*	1*	8	18
burssima	*Bursera simaruba*	2	6	16
byrsbuci	*Byrsonima bucidaefolia*	1*	7	17
calobras	*Calophyllum brasiliense*	5*	10	11
calychyt	*Calyptranthes chytraculia*	7	9	7
camelati	*Cameraria latifolia*	1*	7	17
casebart	*Casearia bartlettii*	7	1	1
casecory	*Casearia corymbosa*	1*	9	19
casselip	*Cassipourea guianensis*	1*	2	13
cassgran	*Cassia grandis*	?	9	7
castelas	*Castilla elastica*	5*	2	9
cecrpelt	*Cecropia peltata*	2	3	12
cedrmexi	*Cedrela mexicana*	2*	3	12
ceibpent	*Ceiba pentandra*	2*	?	?
celttrin	*Celtis trinerva*	2*	4	14
cham 'sp1	*Chamaedorea* sp1	7	3	3
cham 'sp2	*Chamaedorea* sp2	7	1	1

Abbreviation	Species	Light / Disturbance Response Group	Topographic Distribution Group	Ecological Group
cham 'sp4	*Chamaedorea* sp4	7	9	7
champaca	*Chamaedorea pacaya*	3	3	12
chryicac	*Chrysobalanus icaco*	1*	7	17
chrymexi	*Chrysophyllum mexicanum*	1*	2	13
clus 'sp	*Clusia* sp.	hemiepiphyte	5	15
coccacap	*Coccoloba acapulcensis*	1	6	16
cocccozu	*Coccoloba cozumelensis*	1	7	17
coccrefl	*Coccoloba reflexiflora*	1	7	17
cordgera	*Cordia gerascanthus*	4*	1	6
cordseba	*Cordia sebastena*	1*	7	17
costus 'sp	*Costus* sp.	3	2	13
cousolig	*Coussapoa oligocephala*	hemiepiphyte	3	?
crotpyra	*Croton pyramidalis*	1	7	17
crotrefl	*Croton reflexifolia*	1	7	17
cryostau	*Cryosophila stauracantha*	7	1	1
cupabeli	*Cupania belizensis*	7	2	4
cymbpend	*Cymbopetalum penduliflorum*	2*	1	12
dendarbo	*Dendropanax arboreus*	2*	3	12
dioscamp	*Diospyros campechiana*	7	4	2
dryplate	*Drypetes laterifolia*	6	5	8
erytguat	*Erythroxylon guatemalensis*	1*	7	17
euge 'sp	*Eugenia* sp.	6	5	8
exotpani	*Exothea paniculata*	?	1	?
ficuglab	*Ficus glabra*	2*	2	13
forctrif	*Forchammeria trifoliata*	7	4	2
glirsepi	*Gliricidia sepium*	1*	7	17
guarglab	*Guarea glabra*	7*	2	4
gausmaya	*Gaussia maya*	7*	5	8
guetcomb	*Guettarda combsii*	2	7	17
gymnluci	*Gymnanthes lucida*	4	5	8
haemcamp	*Haematoxylum campechianum*	1	7	17
hamptril	*Hampea trilobata*	2*	7	17
hirtamer	*Hirtella americana*	?	1	6?
ingaedul	*Inga edulis*	?	9	19
jacq 'sp	*Jacquinia* sp.	1*	6	16
krugferr	*Krugiodendron ferreum*	?	5	8
laettham	*Laetia thamnia*	6	5	8
licapeck	*Licaria peckii*	4*	6	16

Abbreviation	Species	Light / Disturbance Response Group	Topographic Distribution Group	Ecological Group
lonccast	*Lonchocarpus castilloi*	2	6	16
loncguat	*Lonchocarpus guatemalensis*	?	9	19
lonclati	*Lonchocarpus latifolius*	3	6	16
loncrugo	*Lonchocarpus rugosus*	1	7	17
malmdepr	*Malmea depressa*	7	4	2
malpglab	*Malpighia glabra*	7	3	3
manizapo	*Manilkara zapota*	7	10	5
margnobi	*Margaritaria nobilis*	1	8	18
mastfoet	*Mastichodendron foetidesimum*	7*	3	3
mataoppo	*Matayba oppositifolia*	1*	6	16
metobrow	*Metopium brownei*	2*	5	15
myriceri	*Myrica cerifera*	1*	7	17
myrt 'sp	*Myrtaceae* sp. *(pimim)*	1	7	17
myrt 'sp	*Myrtaceae* sp.	?	?	?
nectcori	*Nectandra coriacea*	4	4	10
nectsali	*Nectandra salicifolia*	6*	1	6
ocot 'sp	*Ocotea* sp.	6*	2	9
opplv1	*OPPLV1* (Myrtaceae sp)	1	7	17
orbicohu	*Orbignya cohune*	7*	11	4
oreo 'sp	*Oreopanax* sp.	?	?	?
oureluce	*Ouratea lucens*	1	6	16
pachaqua	*Pachira aquatica*	1*	9	19
phylnobi	*Phyllanthus nobilis*	1	7	17
pimedioi	*Pimenta dioica*	7	3	3
pipe 'ad	*Piper* cf. *aduncum*	3	2	13
pipe 'ps	*Piper psilorrachis*	7	4	2
pipesemp	*Piper sempervirens*	3	3	12
pithbeli	*Pithecellobium belizensis*	3	9	19
plumobtu	*Plumeria obtusa*	1*	7	17
poutamyg	*Pouteria amygdalina*	7	1	1
poutcamp	*Pouteria campechiana*	6-7*	4	2
poutdurl	*Pouteria durlandii*	7	2	4
poutreti	*Pouteria reticulata*	7	3	3
poutsapo	*Pouteria sapota*	7*	2	4
protcopa	*Protium copal*	6*	2	9
pseuelip	*Pseudobombax elliptica*	2*	5	15
pseuoxyp	*Pseudolmedia oxyphyllaria*	7	1	1
psyc 'sp	*Psychotria* sp.	7	2	4

Abbreviation	Species	Light / Disturbance Response Group	Topographic Distribution Group	Ecological Group
quarfune	*Quararibea funebris*	7*	2	4
quinschi	*Quiina schippii*	?	?	?
rapaguia	*Rapanea guianensis*	1*	7	17
rehepenn	*Rehdera penninervia*	2*	2	13
sabamaur	*Sabal mauritiiformis*	7	2	4
sapiniti	*Sapium nitidum*	1*	9	19
sebalong	*Sebastiana longicuspis*	5	1	6
simaglau	*Simarouba glauca*	5*	2	9
simisalv	*Simira salvadorensis*	3	2	13
sponmomb	*Spondias mombin*	2	2	13
stemdonn	*Stemmadenia donnell-smithii*	2	1	12
swarcube	*Swartzia cubensis*	5*	3	6
swiemacr	*Swietenia macrophylla*	2*	8	18
tabe 'sp	*Tabebuia* sp.	6*	2	9
taliflor	*Talisia floresii*	?	5	8
talioliv	*Talisia olivaeformis*	7	4	2
termamaz	*Terminalia amazonia*	2*	6	16
terntepa	*Ternstroemia tepazapote*	?	?	?
thevahou	*Thevetia ahouai*	3	6	16
thoupauc	*Thouinia paucidentata*	4*	4	10
trichava	*Trichilia havanensis*	1*	3	12
tricminu	*Trichilia minutiflora*	7	4	2
tricmosc	*Trichilia moschata*	6*	10	11
tricpall	*Trichilia pallida*	7	3	3
troprace	*Trophis racemosa*	5*	2	9
vatalund	*Vatairea lundellii*	6*	2	9
viteguam	*Vitex guameri*	2*	6	16
wimmconc	*Wimmeria concolor*	3	3	6
xylo 'sp	*Xylosma* sp.	1	7	17
xylofrut	*Xylopia frutescens*	?	?	?
zantcari	*Zanthoxylum caribeum*	?	9	19
zantproc	*Zanthoxylum procerum*	5*	1	6
zuelguid	*Zuelania guidonia*	4*	2	9

* = Assignment to light/disturbance response type was based on qualitative observations rather than statistical tests due to small sample size for that species.

Numbers refer to patterns described in text. Names of light/disturbance response groups appear in Figure 37, those of topographic distribution groups in Figures 26-35, ecological groups described in Figure 38.

Appendix 2

Tree species abundances by forest type. Values given are mean number of individuals per 0.041 ha plot for trees ≥ 7.5 cm dbh, and number per 1.7 x 20 m belt transect for juveniles. Means and std errors are based on 294 sample plots; ‘n’ gives the number of individuals detected overall.

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
Anacardiaceae	*Astronium graveolens*	23	0.03	*0.03*	0.05	*0.04*	0.00	*0.00*	0.14	*0.05*
	juveniles	7	0.07	*0.05*	0.00	*0.00*	0.04	*0.04*	0.05	*0.04*
	Metopium brownei	54	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	10	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Spondias mombin	74	0.03	*0.03*	0.05	*0.04*	0.16	*0.08*	0.14	*0.05*
	juveniles	2	0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*
Annonaceae	*Annona* sp.	11	0.00	*0.00*	0.05	*0.04*	0.10	*0.05*	0.11	*0.05*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Cymbopetalum penduliflorum	8	0.00	*0.00*	0.00	*0.00*	0.13	*0.09*	0.05	*0.03*
	juveniles	1	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
	Malmea depressa	45	0.53	*0.17*	0.32	*0.13*	0.03	*0.03*	0.19	*0.07*
	juveniles	32	0.15	*0.07*	0.24	*0.10*	0.13	*0.07*	0.38	*0.12*
	Xylopia frutescens	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Apocynaceae	*Aspidosperma cruenta*	320	0.35	*0.14*	0.73	*0.27*	1.19	*0.18*	2.09	*0.22*
	juveniles	48	0.11	*0.06*	0.06	*0.06*	0.30	*0.11*	0.38	*0.10*
	Aspidosperma megalocarpon	66	0.21	*0.07*	0.14	*0.10*	0.13	*0.06*	0.26	*0.08*
	juveniles	24	0.19	*0.07*	0.35	*0.18*	0.30	*0.13*	0.11	*0.05*
	Cameraria latifolia	20	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	7	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Plumeria obtusa	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Stemmadenia donnell-smithii	39	0.09	*0.05*	0.14	*0.07*	0.06	*0.04*	0.18	*0.07*
	juveniles	5	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Thevetia ahouai[1]	26	0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.05	*0.04*
Arecaceae	*Bactris major*[1]	24	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
(Palmae)	*Chamaedorea pacaya*[1]	31	0.19	*0.18*	0.00	*0.00*	0.00	*0.00*	0.11	*0.08*
	Chamaedorea sp1[1]	330	2.33	*0.52*	2.88	*0.44*	1.57	*0.38*	3.05	*0.50*
	Chamaedorea sp2[1]	12	0.04	*0.04*	0.06	*0.06*	0.09	*0.06*	0.14	*0.07*
	Chamaedorea sp4[1]	30	0.26	*0.16*	0.24	*0.16*	0.17	*0.10*	0.19	*0.14*
	Cryosophila stauracantha	4223	6.3	*1.0*	14.6	*1.9*	17.7	*1.5*	20.3	*1.1*
	juveniles	1022	5.22	*0.77*	5.71	*0.85*	6.91	*0.64*	7.00	*0.55*
	Gaussia maya	16	0.06	*0.04*	0.23	*0.16*	0.10	*0.05*	0.09	*0.04*
	juveniles	3	0.04	*0.04*	0.06	*0.06*	0.04	*0.04*	0.00	*0.00*

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*
0.18	*0.10*	0.12	*0.06*	0.22	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	1.00	*0.29*	2.12	*0.51*	0.05	*0.04*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.08	*0.08*	0.64	*0.19*	0.00	*0.00*
0.50	*0.17*	0.47	*0.12*	0.26	*0.13*	0.00	*0.00*	0.00	*0.00*	0.50	*0.18*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.05*	0.04	*0.04*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.20	*0.12*	0.25	*0.13*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.91	*0.30*	0.68	*0.16*	2.52	*0.41*	1.50	*0.46*	0.24	*0.23*	0.05	*0.04*
0.40	*0.16*	0.13	*0.09*	0.30	*0.14*	0.75	*0.28*	0.07	*0.07*	0.00	*0.00*
0.32	*0.13*	0.26	*0.09*	0.30	*0.13*	0.06	*0.06*	0.00	*0.00*	0.32	*0.13*
0.07	*0.06*	0.00	*0.00*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	1.18	*0.74*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.50	*0.33*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.43	*0.19*	0.00	*0.00*
0.18	*0.08*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.20	*0.10*	0.47	*0.16*	0.20	*0.12*	0.58	*0.19*	0.14	*0.09*	0.20	*0.13*
0.00	*0.00*	0.40	*0.26*	0.40	*0.15*	1.00	*0.37*	0.00	*0.00*	0.20	*0.19*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
1.27	*0.32*	1.20	*0.54*	0.30	*0.14*	0.42	*0.19*	0.00	*0.00*	0.20	*0.13*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.70	*0.57*
16.32	*1.82*	28.15	*1.96*	14.48	*1.34*	9.75	*2.16*	0.53	*0.32*	3.45	*0.83*
6.13	*1.15*	4.07	*0.75*	3.30	*0.81*	2.67	*0.71*	0.07	*0.07*	3.50	*1.09*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	Orbignya cohune	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	21	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Sabal mauritiiformis	777	0.35	*0.12*	0.86	*0.26*	1.10	*0.28*	2.14	*0.31*
	juveniles	128	0.48	*0.20*	0.41	*0.12*	0.30	*0.11*	0.62	*0.14*
Araliaceae	*Dendropanax arboreus*	25	0.12	*0.06*	0.00	*0.00*	0.19	*0.07*	0.19	*0.09*
	juveniles	2	0.00	*0.00*	0.06	*0.06*	0.04	*0.04*	0.00	*0.00*
	Oreopanax sp.	2	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Bignoniaceae	*Tabebuia* sp.	17	0.03	*0.03*	0.00	*0.00*	0.03	*0.03*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
Bombacaceae	*Bernoullia flammea*	3	0.00	*0.00*	0.05	*0.04*	0.00	*0.00*	0.04	*0.03*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ceiba pentandra	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pachira aquatica	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pseudobombax elliptica	6	0.03	*0.03*	0.09	*0.09*	0.00	*0.00*	0.02	*0.02*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Quararibea funebris	9	0.00	*0.00*	0.00	*0.00*	0.06	*0.04*	0.04	*0.02*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*
Boraginaceae	*Cordia gerascanthus*	13	0.00	*0.00*	0.05	*0.04*	0.03	*0.03*	0.16	*0.05*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Cordia sebastena	2	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Burseraceae	*Bursera simaruba*	58	0.06	*0.04*	0.09	*0.06*	0.06	*0.04*	0.14	*0.05*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Protium copal	168	0.38	*0.11*	0.59	*0.15*	0.55	*0.14*	0.49	*0.09*
	juveniles	47	0.26	*0.08*	0.12	*0.08*	0.13	*0.07*	0.30	*0.08*
Capparidaceae	*Forchammeria trifoliata* [1]	9	0.19	*0.07*	0.00	*0.00*	0.00	*0.00*	0.08	*0.04*
Celastraceae	*Wimmeria concolor*	150	0.62	*0.14*	0.95	*0.20*	1.06	*0.25*	1.12	*0.18*
	juveniles	21	0.11	*0.06*	0.12	*0.08*	0.22	*0.11*	0.24	*0.10*
Chrysobalanaceae	*Chrysobalanus icaco*	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Hirtella americana	18	0.03	*0.03*	0.14	*0.07*	0.10	*0.05*	0.16	*0.05*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.05	*0.04*
Clusiaceae	*Calophyllum brasiliense*	67	0.00	*0.00*	0.23	*0.13*	0.10	*0.10*	0.16	*0.05*
	juveniles	16	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*

Hillbase		**Sabal**		**Transitional**		**Tall Scrub Swamp**		**Low Scrub Swamp**		**Mesic bajo/ Swamp**	
avg.	***s.e.***	**avg..**	***s.e.***	**avg.**	***s.e.***	**avg.**	***s.e.***	**avg..**	***s.e.***	**avg.**	***s.e.***
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
4.50	*0.83*	10.03	*0.84*	3.52	*0.56*	0.81	*0.30*	0.12	*0.11*	1.36	*0.42*
1.47	*0.42*	1.20	*0.25*	0.90	*0.28*	0.58	*0.26*	0.00	*0.00*	0.90	*0.36*
0.09	*0.06*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.21	*0.07*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.27	*0.09*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.18	*0.18*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.14	*0.10*	0.06	*0.04*	0.30	*0.13*	0.69	*0.28*	0.24	*0.10*	0.14	*0.10*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.50	*0.20*	1.35	*0.31*	1.09	*0.28*	0.25	*0.19*	0.00	*0.00*	0.18	*0.18*
0.13	*0.09*	0.67	*0.24*	0.40	*0.15*	0.17	*0.11*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.03	*0.03*	0.26	*0.15*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.02*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.09	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.21	*0.08*	0.48	*0.14*	1.06	*0.37*	0.29	*0.16*	0.36	*0.16*
0.07	*0.06*	0.07	*0.06*	0.20	*0.12*	0.92	*0.45*	0.00	*0.00*	0.00	*0.00*

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	Clusia sp.	21	0.12	*0.06*	0.05	*0.04*	0.00	*0.00*	0.09	*0.06*
	juveniles	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Combretaceae	*Bucida buceras*	55	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	2	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Terminalia amazonia	36	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*	0.04	*0.02*
	juveniles	5	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Ebenaceae	*Diospyros campechiana*	6	0.09	*0.05*	0.00	*0.00*	0.03	*0.03*	0.00	*0.00*
	juveniles	2	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.03	*0.03*
Erythroxylaceae	*Erythroxylon guatemalensis*	7	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Euphorbiaceae	*Croton pyramidalis*	338	0.00	*0.00*	0.05	*0.04*	0.03	*0.03*	0.00	*0.00*
	juveniles	308	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
	Croton reflexifolia	19	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	10	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Drypetes lateriflora	51	0.76	*0.21*	0.18	*0.08*	0.06	*0.04*	0.14	*0.05*
	juveniles	17	0.33	*0.12*	0.06	*0.06*	0.13	*0.07*	0.08	*0.04*
	Gymnanthes lucida	157	1.03	*0.56*	0.14	*0.13*	0.00	*0.00*	0.02	*0.02*
	juveniles	69	1.11	*0.60*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Margaritaria nobilis	35	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Phyllanthus nobilis	35	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.04	*0.02*
	juveniles	10	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Sapium nitidum	5	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Sebastiana longicuspis	250	0.12	*0.06*	0.68	*0.29*	0.77	*0.42*	1.79	*0.46*
	juveniles	133	0.04	*0.04*	0.47	*0.35*	0.04	*0.04*	0.22	*0.08*
Fabaceae	*Cassia grandis*	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
(Caesalpinioideae)	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Haematoxylum campechianum	199	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	33	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Swartzia cubensis	12	0.03	*0.03*	0.00	*0.00*	0.13	*0.06*	0.05	*0.03*
	juveniles	10	0.00	*0.00*	0.06	*0.06*	0.04	*0.04*	0.11	*0.05*
(Papilionoideae)	*Gliricidia sepium*	23	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Lonchocarpus castilloi	29	0.06	*0.04*	0.00	*0.00*	0.10	*0.05*	0.07	*0.03*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Lonchocarpus guatemalensis	17	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*
0.00	0.00	0.00	0.00	0.13	0.07	0.19	0.13	0.29	0.18	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.16	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.37	1.00	0.31	1.23	0.40
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.09	0.00	0.00
0.00	0.00	0.24	0.13	0.52	0.16	0.69	0.19	0.12	0.08	0.00	0.00
0.00	0.00	0.00	0.00	0.10	0.09	0.33	0.19	0.00	0.00	0.00	0.00
0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.35	0.14	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.09	0.10	0.09
0.14	0.13	0.09	0.06	1.70	0.40	6.50	1.14	9.41	0.92	1.18	0.33
0.27	0.20	0.07	0.06	2.80	1.37	6.50	2.23	13.00	2.39	1.00	0.65
0.00	0.00	0.00	0.00	0.17	0.12	0.38	0.25	0.47	0.28	0.05	0.04
0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.29	0.10	0.00	0.00
0.00	0.00	0.03	0.03	0.04	0.04	0.19	0.13	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.09	0.09	0.00	0.00	0.39	0.30	6.31	1.57	0.29	0.23	0.05	0.04
0.07	0.06	0.00	0.00	0.90	0.72	1.83	0.59	0.50	0.35	0.00	0.00
0.00	0.00	0.00	0.00	0.04	0.04	0.25	0.14	0.06	0.06	1.32	0.63
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.93	0.84	5.40	3.58
0.00	0.00	0.03	0.03	0.04	0.04	0.75	0.21	0.65	0.20	0.32	0.19
0.00	0.00	0.07	0.06	0.00	0.00	0.08	0.08	0.50	0.17	0.10	0.09
0.00	0.00	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.10
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.36	0.16	0.65	0.23	1.39	0.52	0.00	0.00	0.12	0.11	1.55	0.68
0.13	0.13	0.07	0.06	0.20	0.12	0.08	0.08	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.18
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.00	0.26	0.15	1.94	0.49	6.59	0.87	2.27	1.72
0.00	0.00	0.00	0.00	0.10	0.09	0.17	0.11	2.07	0.36	0.10	0.09
0.00	0.00	0.03	0.03	0.09	0.06	0.00	0.00	0.00	0.00	0.05	0.04
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.09
0.00	0.00	0.00	0.00	0.09	0.09	0.31	0.19	0.82	0.30	0.05	0.04
0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.11	0.07	0.07	0.00	0.00
0.00	0.00	0.09	0.05	0.35	0.15	0.19	0.10	0.12	0.11	0.09	0.06
0.07	0.06	0.20	0.14	0.20	0.12	0.50	0.34	0.00	0.00	0.60	0.29
0.05	0.04	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.40

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	juveniles	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Lonchocarpus latifolius	57	0.00	*0.00*	0.05	*0.04*	0.03	*0.03*	0.02	*0.02*
	juveniles	18	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Lonchocarpus rugosus	2	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Platymiscium yucatanum	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Vatairea lundellii	21	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*	0.05	*0.03*
	juveniles	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
(Mimosoideae)	*Acacia cookii*	118	0.24	*0.08*	0.36	*0.15*	0.42	*0.13*	0.42	*0.11*
	juveniles	43	0.11	*0.06*	0.18	*0.09*	0.17	*0.10*	0.11	*0.05*
	Acacia dolichostachya	8	0.03	*0.03*	0.05	*0.04*	0.00	*0.00*	0.05	*0.03*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Acacia glomerosa	3	0.03	*0.03*	0.05	*0.04*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Acacia sp.	34	0.03	*0.03*	0.14	*0.07*	0.00	*0.00*	0.05	*0.03*
	juveniles	6	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
	Inga edulis	20	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pithecellobium c.f. *pachypus*	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pithecellobium belizensis	80	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	28	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Flacourtiaceae	*Casearia bartlettii*	43	0.09	*0.06*	0.09	*0.06*	0.23	*0.11*	0.49	*0.11*
	juveniles	7	0.07	*0.05*	0.00	*0.00*	0.09	*0.06*	0.08	*0.04*
	Casearia corymbosa	15	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Laetia thamnia	41	0.21	*0.09*	0.18	*0.10*	0.29	*0.14*	0.18	*0.06*
	juveniles	21	0.07	*0.05*	0.00	*0.00*	0.04	*0.04*	0.11	*0.05*
	Xylosma sp.	17	0.03	*0.03*	0.00	*0.00*	0.03	*0.03*	0.04	*0.02*
	juveniles	59	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Zuelania guidonia	16	0.00	*0.00*	0.05	*0.04*	0.03	*0.03*	0.07	*0.03*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Lauraceae	*Licaria peckii*	49	0.00	*0.00*	0.00	*0.00*	0.13	*0.08*	0.19	*0.06*
	juveniles	17	0.00	*0.00*	0.06	*0.06*	0.04	*0.04*	0.19	*0.06*
	Nectandra coriacea	61	0.94	*0.29*	0.14	*0.10*	0.32	*0.24*	0.07	*0.03*
	juveniles	129	2.67	*0.67*	0.88	*0.31*	0.65	*0.29*	0.22	*0.09*

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
0.00	*0.00*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.50	*0.15*	0.22	*0.12*	0.69	*0.28*	0.00	*0.00*	0.77	*0.32*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.60	*0.38*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.09	*0.06*
0.00	*0.00*	0.00	*0.00*	0.20	*0.12*	0.00	*0.00*	0.50	*0.24*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.18	*0.10*	0.12	*0.06*	0.17	*0.08*	0.00	*0.00*	0.00	*0.00*	0.23	*0.11*
0.07	*0.06*	0.00	*0.00*	0.20	*0.18*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
0.55	*0.20*	0.85	*0.19*	0.39	*0.15*	0.31	*0.19*	0.00	*0.00*	0.27	*0.13*
0.20	*0.10*	0.53	*0.34*	0.60	*0.20*	0.50	*0.23*	0.29	*0.21*	0.10	*0.09*
0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.12	*0.06*	0.04	*0.04*	0.31	*0.12*	0.47	*0.24*	0.32	*0.15*
0.07	*0.06*	0.20	*0.14*	0.00	*0.00*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.91	*0.53*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.09	*0.06*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.08	*0.08*	0.07	*0.07*	0.20	*0.13*
0.14	*0.10*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.12	*0.11*	3.41	*0.87*
0.53	*0.40*	0.00	*0.00*	0.10	*0.09*	0.42	*0.42*	0.00	*0.00*	1.40	*0.57*
0.09	*0.06*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.59	*0.34*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.30	*0.14*
0.05	*0.04*	0.03	*0.03*	0.17	*0.08*	0.13	*0.12*	0.06	*0.06*	0.00	*0.00*
0.07	*0.06*	0.07	*0.06*	0.20	*0.12*	0.25	*0.18*	0.36	*0.22*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.13	*0.09*	0.19	*0.10*	0.12	*0.08*	0.05	*0.04*
0.27	*0.20*	0.00	*0.00*	0.10	*0.09*	0.50	*0.26*	3.36	*0.69*	0.00	*0.00*
0.09	*0.06*	0.12	*0.06*	0.09	*0.09*	0.00	*0.00*	0.06	*0.06*	0.05	*0.04*
0.13	*0.09*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.09*	0.18	*0.08*	0.87	*0.33*	0.06	*0.06*	0.00	*0.00*	0.14	*0.07*
0.00	*0.00*	0.20	*0.14*	0.20	*0.12*	0.08	*0.08*	0.00	*0.00*	0.10	*0.09*
0.00	*0.00*	0.03	*0.03*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.20	*0.12*	1.08	*0.74*	0.00	*0.00*	0.00	*0.00*

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	**Species**	**n**	**avg.**	*s.e.*	**avg..**	*s.e.*	**avg.**	*s.e.*	**avg.**	*s.e.*
	Nectandra salicifolia	17	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
	juveniles	41	0.00	*0.00*	0.18	*0.12*	0.13	*0.06*	0.26	*0.12*
	Ocotea sp.	8	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Malphigiaceae	*Byrsonima bucidaefolia*	23	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	7	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Malpighia glabra	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*
	juveniles	26	0.33	*0.16*	0.12	*0.08*	0.22	*0.09*	0.08	*0.04*
Malvaceae	*Hampea trilobata*	12	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	12	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Meliaceae	*Cedrela mexicana*	12	0.06	*0.04*	0.05	*0.04*	0.06	*0.04*	0.02	*0.02*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Guarea glabra	34	0.03	*0.03*	0.05	*0.04*	0.13	*0.06*	0.05	*0.03*
	juveniles	9	0.04	*0.04*	0.06	*0.06*	0.00	*0.00*	0.03	*0.03*
	Swietenia macrophylla	47	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.03*
	juveniles	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
	Trichilia havanensis	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*
	Trichilia minutiflora	275	2.24	*0.39*	1.91	*0.56*	0.77	*0.19*	0.98	*0.17*
	juveniles	166	1.52	*0.37*	1.12	*0.30*	1.43	*0.40*	0.97	*0.24*
	Trichilia moschata	239	1.74	*0.48*	0.86	*0.53*	0.77	*0.40*	0.53	*0.15*
	juveniles	117	0.74	*0.48*	0.06	*0.06*	0.35	*0.16*	0.41	*0.13*
	Trichilia pallida	2	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*
	juveniles	42	0.19	*0.09*	0.59	*0.19*	0.35	*0.12*	0.35	*0.09*
Moraceae	*Brosimum alicastrum*	366	3.50	*0.47*	2.32	*0.28*	1.16	*0.23*	0.82	*0.13*
	juveniles	30	0.30	*0.11*	0.06	*0.06*	0.22	*0.11*	0.22	*0.09*
	Castilla elastica	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Cecropia peltata	32	0.09	*0.06*	0.09	*0.06*	0.13	*0.08*	0.12	*0.06*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Coussapoa oligocephala	17	0.12	*0.07*	0.09	*0.09*	0.06	*0.04*	0.04	*0.02*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ficus glabra	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ficus salicifolia	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ficus sp (free standing)	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*
0.40	*0.32*	0.33	*0.20*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.14	*0.07*	0.12	*0.07*	0.13	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.32	*0.15*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.07	*0.06*	0.20	*0.14*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.38	*0.17*	1.00	*0.29*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.17	*0.17*	0.36	*0.16*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.20	*0.13*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.50	*0.20*	0.12	*0.08*	0.05	*0.04*
0.07	*0.06*	0.00	*0.00*	0.10	*0.09*	0.33	*0.14*	0.43	*0.19*	0.00	*0.00*
0.05	*0.04*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.55	*0.17*	0.18	*0.07*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.14	*0.10*
0.07	*0.06*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.18	*0.07*	0.52	*0.15*	0.19	*0.10*	0.47	*0.17*	0.50	*0.24*
0.07	*0.06*	0.00	*0.00*	0.10	*0.09*	0.00	*0.00*	0.14	*0.09*	0.10	*0.09*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
1.27	*0.40*	0.44	*0.19*	0.26	*0.11*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
1.13	*0.41*	0.20	*0.10*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.40	*0.29*
1.23	*0.34*	0.38	*0.14*	0.48	*0.35*	0.00	*0.00*	0.00	*0.00*	2.14	*0.89*
1.40	*0.59*	0.67	*0.28*	1.10	*0.90*	0.00	*0.00*	0.00	*0.00*	2.10	*1.06*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.13	*0.09*	0.27	*0.15*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
1.41	*0.33*	1.44	*0.25*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.23	*0.16*
0.13	*0.09*	0.13	*0.09*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.06	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.06	*0.04*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.18	*0.12*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.12	*0.06*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.05*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.00	*0.00*	0.00	*0.00*	0.13	*0.08*	0.00	*0.00*	0.05	*0.04*

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ficus sp (strangler)	17	0.06	*0.04*	0.00	*0.00*	0.06	*0.04*	0.04	*0.02*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pseudolmedia oxyphyllaria	360	0.71	*0.19*	0.95	*0.30*	1.81	*0.36*	3.42	*0.48*
	juveniles	88	0.22	*0.10*	0.88	*0.63*	0.52	*0.21*	1.03	*0.27*
	Trophis racemosa	37	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.03*
	juveniles	8	0.04	*0.04*	0.00	*0.00*	0.04	*0.04*	0.03	*0.03*
Myricaceae	*Myrica cerifera*	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Myrsinaceae	*Ardisia densiflora*	8	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*
	juveniles	11	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Ardisia paschalis [1]	52	0.22	*0.15*	0.06	*0.06*	0.52	*0.25*	0.27	*0.11*
	Rapanea guianensis	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	7	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Myrtaceae	*Calyptranthes chytraculia*	28	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	53	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Calyptranthes sp.	13	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	15	0.11	*0.11*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
	Eugenia sp.	19	0.15	*0.06*	0.00	*0.00*	0.00	*0.00*	0.09	*0.05*
	juveniles	45	0.78	*0.25*	0.24	*0.13*	0.04	*0.04*	0.16	*0.07*
	Myrtaceae sp.	131	0.26	*0.08*	0.00	*0.00*	0.22	*0.11*	0.22	*0.08*
	juveniles	25	0.03	*0.03*	0.00	*0.00*	0.03	*0.03*	0.02	*0.02*
	Myrtaceae sp. (pimim)	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	77	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	OPPLV1	50	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	56	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pimenta dioica	110	0.59	*0.13*	0.64	*0.21*	0.32	*0.12*	0.40	*0.11*
	juveniles	100	0.48	*0.15*	0.35	*0.18*	0.52	*0.17*	0.62	*0.15*
Ochnaceae	*Ouratea lucens*	21	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.19	*0.06*
	juveniles	142	0.00	*0.00*	0.06	*0.06*	0.09	*0.06*	0.11	*0.06*
Piperaceae	*Piper* cf. *aduncum* [1]	70	0.15	*0.15*	0.06	*0.06*	0.09	*0.06*	0.51	*0.15*
	Piper psilorrachis [1]	911	11.07	*1.45*	8.59	*1.23*	5.61	*0.70*	4.92	*0.59*
	Piper sempervirens [1]	45	0.11	*0.06*	0.88	*0.74*	0.04	*0.04*	0.19	*0.11*
Polygonaceae	*Coccoloba acapulcensis*	48	0.06	*0.04*	0.00	*0.00*	0.00	*0.00*	0.02	*0.02*
	juveniles	15	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Coccoloba cozumelensis	9	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.05*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.23	*0.13*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.95	*0.32*	0.18	*0.12*	1.48	*0.52*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.93	*0.64*	0.00	*0.00*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.23	*0.11*	0.50	*0.15*	0.13	*0.07*	0.00	*0.00*	0.06	*0.06*	0.32	*0.15*
0.07	*0.06*	0.07	*0.06*	0.10	*0.09*	0.08	*0.08*	0.00	*0.00*	0.10	*0.09*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.19	*0.13*	0.24	*0.13*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.17	*0.11*	0.64	*0.28*	0.00	*0.00*
0.40	*0.16*	0.27	*0.26*	0.80	*0.30*	0.17	*0.11*	0.21	*0.21*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.24	*0.10*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.17	*0.11*	0.36	*0.19*	0.00	*0.00*
0.00	*0.00*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	1.09	*0.56*
0.13	*0.09*	2.67	*1.08*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	1.10	*0.74*
0.00	*0.00*	0.35	*0.23*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.00	*0.00*	0.10	*0.09*	0.33	*0.19*	0.00	*0.00*	0.50	*0.47*
0.00	*0.00*	0.09	*0.06*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.14	*0.13*
0.07	*0.06*	0.07	*0.06*	0.20	*0.12*	0.25	*0.13*	0.00	*0.00*	0.20	*0.13*
0.53	*0.21*	0.20	*0.10*	1.10	*0.44*	2.00	*0.71*	3.93	*1.40*	0.40	*0.21*
0.05	*0.04*	0.12	*0.09*	0.26	*0.13*	0.19	*0.10*	0.47	*0.17*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.10	*0.09*	2.25	*2.25*	3.36	*1.42*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.09	*0.09*	0.63	*0.23*	1.76	*0.42*	0.36	*0.16*
0.00	*0.00*	0.00	*0.00*	0.20	*0.18*	1.08	*0.38*	2.57	*0.60*	0.50	*0.29*
0.23	*0.11*	0.47	*0.16*	0.43	*0.15*	0.19	*0.10*	0.00	*0.00*	0.05	*0.04*
0.80	*0.27*	0.60	*0.21*	0.50	*0.28*	1.42	*0.47*	0.00	*0.00*	0.00	*0.00*
0.09	*0.06*	0.03	*0.03*	0.26	*0.15*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.27	*0.18*	0.87	*0.28*	2.50	*0.99*	3.83	*0.78*	1.50	*0.30*	2.50	*1.02*
0.60	*0.32*	1.73	*1.09*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
2.47	*0.64*	0.53	*0.28*	0.20	*0.12*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.53	*0.23*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.06	*0.04*	0.70	*0.28*	0.94	*0.42*	0.47	*0.25*	0.14	*0.10*
0.00	*0.00*	0.07	*0.06*	0.60	*0.28*	0.25	*0.18*	0.00	*0.00*	0.50	*0.16*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.25	*0.14*	0.29	*0.23*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.20	*0.12*	0.83	*0.42*	3.71	*0.89*	0.20	*0.13*

			Dry Upland		Upland Stand.		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	Coccoloba reflexiflora	144	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	66	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Quinaceae	*Quiina schippii*	5	0.00	*0.00*	0.05	*0.04*	0.00	*0.00*	0.02	*0.02*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Rhamnaceae	*Krugiodendron ferreum*	2	0.06	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Rhizophoraceae	*Cassipourea guianensis*	22	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Rubiaceae	*Alibertia edulis* [1]	16	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Alseis yucatanensis	19	0.00	*0.00*	0.00	*0.00*	0.35	*0.19*	0.09	*0.04*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
	Guettarda combsii	40	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*	0.04	*0.02*
	juveniles	4	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Rubiaceae sp (ruins)	3	0.09	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	6	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
	Rubiaceae sp.	38	0.03	*0.03*	0.05	*0.04*	0.19	*0.10*	0.16	*0.06*
	juveniles	123	0.11	*0.06*	0.12	*0.08*	0.17	*0.08*	0.24	*0.10*
	Simira salvadorensis	94	0.12	*0.08*	0.18	*0.08*	0.16	*0.07*	0.09	*0.06*
	juveniles	46	0.11	*0.06*	0.12	*0.08*	0.30	*0.18*	0.16	*0.06*
Rutaceae	*Amyris elemifera*	16	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	35	0.41	*0.12*	0.24	*0.13*	0.00	*0.00*	0.05	*0.04*
	Zanthoxylum caribaeum	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Zanthoxylum procerum	22	0.09	*0.06*	0.00	*0.00*	0.10	*0.07*	0.21	*0.08*
	juveniles	9	0.11	*0.06*	0.06	*0.06*	0.00	*0.00*	0.05	*0.04*
Sapindaceae	*Allophyllus comina*	7	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	3	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Blomia prisca	274	1.76	*0.42*	1.50	*0.29*	1.39	*0.31*	1.86	*0.33*
	juveniles	30	0.19	*0.07*	0.35	*0.14*	0.35	*0.12*	0.16	*0.06*
	Cupania belizensis	57	0.03	*0.03*	0.23	*0.13*	0.16	*0.08*	0.28	*0.06*
	juveniles	63	0.15	*0.09*	0.59	*0.32*	0.39	*0.15*	0.38	*0.10*
	Exothea paniculata	10	0.09	*0.05*	0.00	*0.00*	0.06	*0.04*	0.07	*0.03*
	juveniles	13	0.07	*0.07*	0.18	*0.09*	0.00	*0.00*	0.19	*0.11*
	Matayba oppositifolia	70	0.00	*0.00*	0.05	*0.04*	0.06	*0.04*	0.18	*0.08*
	juveniles	21	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.05	*0.04*
	Talisia floresii	16	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

Hillbase		**Sabal**		**Transitional**		**Tall Scrub Swamp**		**Low Scrub Swamp**		**Mesic bajo/ Swamp**	
avg.	***s.e.***	**avg..**	***s.e.***	**avg.**	***s.e.***	**avg.**	***s.e.***	**avg..**	***s.e.***	**avg.**	***s.e.***
0.00	*0.00*	0.03	*0.03*	0.48	*0.17*	1.56	*0.34*	6.06	*1.00*	0.18	*0.10*
0.00	*0.00*	0.00	*0.00*	0.09	*0.02*	0.63	*0.04*	3.06	*1.20*	0.09	*0.02*
0.05	*0.04*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.47	*0.17*	0.13	*0.09*	0.13	*0.12*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.07	*0.06*	0.93	*0.59*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.10	*0.09*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.30	*0.10*	0.25	*0.11*	0.53	*0.25*	0.00	*0.00*
0.00	*0.00*	0.07	*0.06*	0.20	*0.12*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.33	*0.26*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.18	*0.08*	0.29	*0.11*	0.09	*0.06*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.33	*0.26*	1.60	*1.08*	1.10	*0.55*	1.50	*0.53*	0.79	*0.32*	3.30	*1.23*
0.36	*0.14*	0.82	*0.15*	0.48	*0.17*	0.31	*0.19*	0.06	*0.06*	0.82	*0.27*
0.20	*0.14*	0.27	*0.11*	0.60	*0.24*	0.67	*0.31*	0.00	*0.00*	0.50	*0.29*
0.09	*0.09*	0.06	*0.04*	0.04	*0.04*	0.31	*0.19*	0.00	*0.00*	0.23	*0.13*
0.20	*0.14*	0.00	*0.00*	0.10	*0.09*	0.00	*0.00*	0.86	*0.28*	0.20	*0.13*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.20	*0.12*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.00	*0.00*	0.04	*0.04*	0.06	*0.06*	0.00	*0.00*	0.14	*0.13*
0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.17	*0.11*	0.00	*0.00*	0.00	*0.00*
0.50	*0.17*	0.18	*0.08*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.20	*0.10*	0.07	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.55	*0.17*	0.24	*0.10*	0.13	*0.07*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.20	*0.10*	0.93	*0.39*	0.50	*0.15*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.09	*0.06*	1.22	*0.46*	1.50	*0.51*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.20	*0.10*	0.20	*0.12*	1.08	*0.56*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.05*	0.17	*0.12*	0.13	*0.08*	0.35	*0.17*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.07	*0.07*	0.00	*0.00*

			Dry Upland		Upland Stand		Mesic1 Upland		Mesic2 Upland	
Family	Species	n	avg.	*s.e.*	avg..	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
	Talisia olivaeformis	45	0.47	*0.14*	0.45	*0.15*	0.19	*0.10*	0.05	*0.03*
	juveniles	30	0.30	*0.13*	0.24	*0.10*	0.17	*0.10*	0.16	*0.08*
	Thouinia paucidentata	16	0.35	*0.12*	0.09	*0.06*	0.00	*0.00*	0.02	*0.02*
	juveniles	2	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
Sapotaceae	*Chrysophyllum mexicanum*	7	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Manilkara zapota	229	1.29	*0.27*	0.59	*0.14*	1.13	*0.27*	0.63	*0.13*
	juveniles	82	0.22	*0.10*	0.29	*0.14*	0.17	*0.08*	0.27	*0.08*
	Mastichodendron	12	0.09	*0.05*	0.14	*0.07*	0.06	*0.04*	0.02	*0.02*
	juveniles (*foetidesimum*)	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Pouteria amygdalina	173	0.21	*0.08*	0.68	*0.23*	1.10	*0.23*	1.56	*0.18*
	juveniles	69	0.37	*0.14*	0.47	*0.15*	1.00	*0.25*	0.57	*0.15*
	Pouteria campechiana	100	0.74	*0.13*	0.73	*0.17*	0.61	*0.17*	0.49	*0.09*
	juveniles	26	0.11	*0.08*	0.06	*0.06*	0.30	*0.11*	0.19	*0.06*
	Pouteria durlandii	257	0.09	*0.05*	0.18	*0.14*	0.61	*0.25*	0.70	*0.12*
	juveniles	84	0.11	*0.08*	0.12	*0.08*	0.17	*0.08*	0.32	*0.14*
	Pouteria reticulata	955	4.76	*0.52*	5.09	*0.61*	4.71	*0.56*	3.98	*0.35*
	juveniles	425	3.44	*0.58*	3.65	*0.68*	2.48	*0.51*	1.97	*0.24*
	Pouteria sapota	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Simaroubaceae	*Simarouba glauca*	12	0.03	*0.03*	0.05	*0.04*	0.06	*0.04*	0.07	*0.03*
	juveniles	10	0.07	*0.07*	0.12	*0.08*	0.00	*0.00*	0.05	*0.04*
Solanaceae	*Cestrum racemosum*	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Theophrastaceae	*Jacquinia* sp	3	0.00	*0.00*	0.05	*0.04*	0.00	*0.00*	0.02	*0.02*
	juveniles	11	0.11	*0.08*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
Ulmaceae	*Ampelocera hottlei*	13	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*	0.02	*0.02*
	juveniles	11	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.14	*0.06*
	Celtis trinerva	13	0.21	*0.09*	0.09	*0.06*	0.06	*0.04*	0.04	*0.02*
	juveniles	2	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.03	*0.03*
Verbenaceae	*Aegiphila monstrosa*	12	0.00	*0.00*	0.05	*0.04*	0.10	*0.07*	0.00	*0.00*
	juveniles	1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
	Rehdera penninervia	12	0.00	*0.00*	0.00	*0.00*	0.06	*0.04*	0.07	*0.04*
	juveniles	7	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.08	*0.04*
	Vitex guameri	27	0.03	*0.03*	0.05	*0.04*	0.13	*0.06*	0.05	*0.03*
	juveniles	0	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

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[1] = treelet or shrub species - no individuals > 7.5 cm dbh

Hillbase		Sabal		Transitional		Tall Scrub Swamp		Low Scrub Swamp		Mesic bajo/ Swamp	
avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*	avg.	*s.e.*
0.00	*0.00*	0.18	*0.10*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.05	*0.04*
0.00	*0.00*	0.13	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.15	*0.07*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.07	*0.07*	0.00	*0.00*
0.09	*0.06*	0.32	*0.18*	0.83	*0.24*	1.63	*0.29*	1.59	*0.34*	0.36	*0.14*
0.13	*0.13*	0.07	*0.06*	1.00	*0.52*	1.42	*0.40*	1.50	*0.28*	0.60	*0.29*
0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.32	*0.20*	0.12	*0.07*	0.43	*0.21*	0.19	*0.18*	0.00	*0.00*	0.00	*0.00*
0.33	*0.18*	0.07	*0.06*	0.10	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.27	*0.15*	0.03	*0.03*	0.13	*0.09*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.07	*0.06*	0.20	*0.10*	0.30	*0.14*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
1.91	*0.52*	2.62	*0.35*	2.00	*0.56*	0.00	*0.00*	0.00	*0.00*	0.23	*0.16*
0.93	*0.24*	1.00	*0.35*	1.10	*0.72*	1.08	*0.31*	0.00	*0.00*	0.50	*0.38*
4.05	*0.91*	2.15	*0.46*	3.65	*0.68*	1.00	*0.46*	0.00	*0.00*	0.32	*0.19*
3.13	*0.54*	1.60	*0.45*	1.90	*0.44*	1.67	*0.45*	0.00	*0.00*	0.90	*0.33*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.09	*0.06*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.20	*0.12*	0.00	*0.00*	0.14	*0.14*	0.00	*0.00*
0.05	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.06	*0.06*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.17	*0.11*	0.36	*0.16*	0.10	*0.09*
0.18	*0.12*	0.12	*0.06*	0.04	*0.04*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.20	*0.14*	0.00	*0.00*	0.20	*0.12*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.03	*0.03*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*
0.00	*0.00*	0.09	*0.05*	0.04	*0.04*	0.06	*0.06*	0.00	*0.00*	0.05	*0.04*
0.07	*0.06*	0.00	*0.00*	0.10	*0.09*	0.08	*0.08*	0.00	*0.00*	0.00	*0.00*
0.05	*0.04*	0.09	*0.05*	0.35	*0.12*	0.31	*0.15*	0.06	*0.06*	0.00	*0.00*
0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*

Figure 1. An illustration of the predominant influence of topographic position on forest structure at Tikal, Guatemala; tall, upland forest on a slight ridge extending into a low-lying basin dominated by Low Scrub Swamp Forest

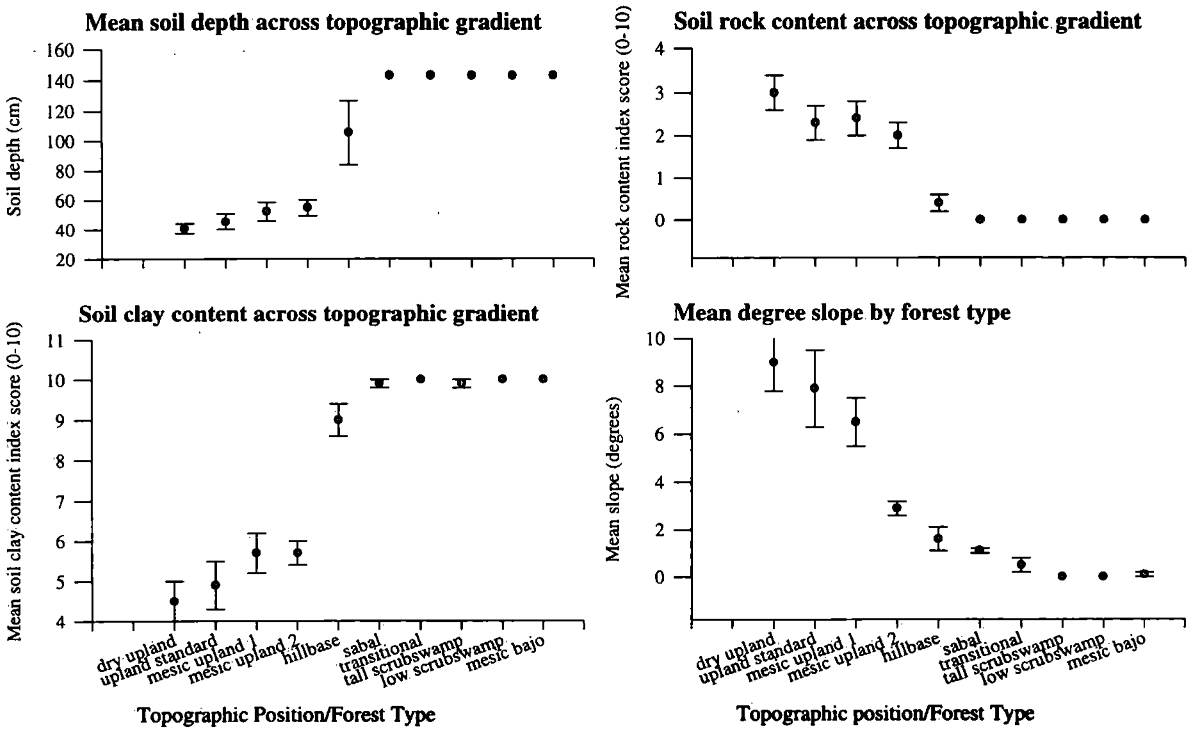


Figure 2. Variation in physical characteristics across the dominant topographic gradient, Tikal, Guatemala. Values are presented as means per forest type (= topographic position), ± 1 standard error.

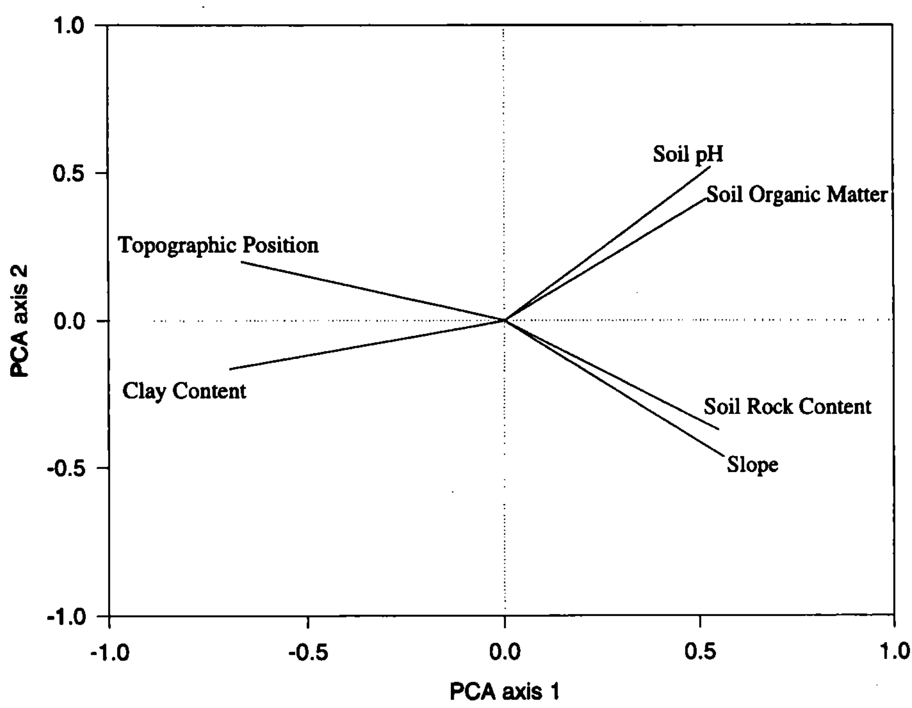


Figure 3. Ordination of six environmental characteristics along first two axes of a Principal Components Analysis; data from vegetation sample plots, Tikal, Guatemala. The first axis (eigenvalue = 3.62) explained 60.3 % of the variance and the second axis (eigenvlaue = 0.84) explained 14.0 % of the variance. Topographic Position takes values from 1 (hilltop) to 18 (low-lying areas with standing water in dry season); Soil Rock Content, based on visual assessment of soil samples, ranges from 0-10; Slope is measured substrate angle; remaining variables are from laboratory soil analyses.

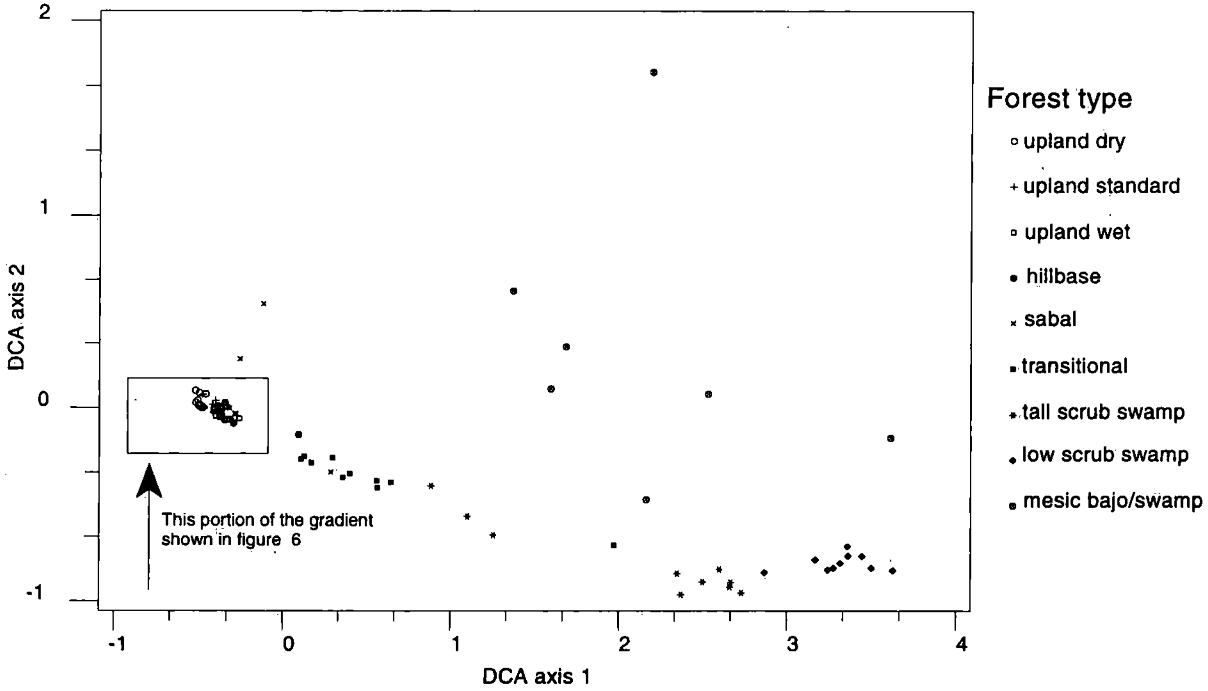

2
1
0
-1
DCA axis 2
-1
0
1
2
3
4
DCA axis 1
This portion of the gradient shown in figure 6
Forest type
○ upland dry
+ upland standard
□ upland wet
● hillbase
× sabal
■ transitional
* tall scrub swamp
◆ low scrub swamp
● mesic bajo/swamp

Figure 4. Position of sample plots at Tikal, Guatemala along first two axes of a Detrended Correspondence Analysis (283 active samples, 98 active species) of mature tree (> 7.5 cm d.b.h.) data. Samples are coded according to forest classes identified mainly on the basis of topographic and edaphic conditions; forest codes are as in Table 1. Not all samples are visible in plot due to high degree of overlap in ordination space. Upland sites on the left of the plot are detailed in Fig. 6.

Ordination diagnostics	Ordination Axes				
	1	2	3	4	Total inertia
Eigenvalues	0.756	0.645	0.382	0.258	7.483
Cumulative % of variance in species data accounted for	10.1	18.7	23.8	27.3	

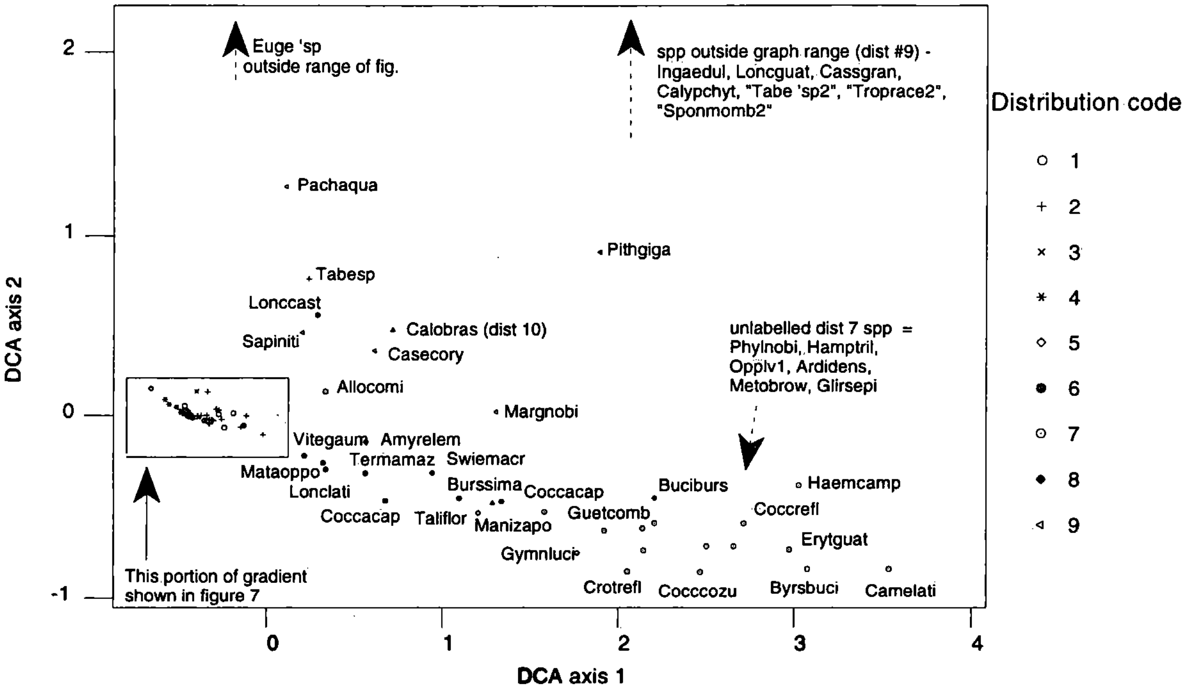


Figure 5. Positions of tree species centroids along first two axes of a Detrended Correspondence Analysis (283 active samples, 98 active species) of mature tree (> 7.5 cm d.b.h.) data. Species are coded by distribution type as identified through examination of individual species distributions along a topographic/edaphic gradient (refer to topographic distribution groups in Appendix 1 and section on species distribution patterns). Not all species are labelled due to high degree of overlap in ordination space. Full species names corresponding to abbreviations are given in Appendix 1. Upland sites on the left of the plot are detailed in Fig. 7.

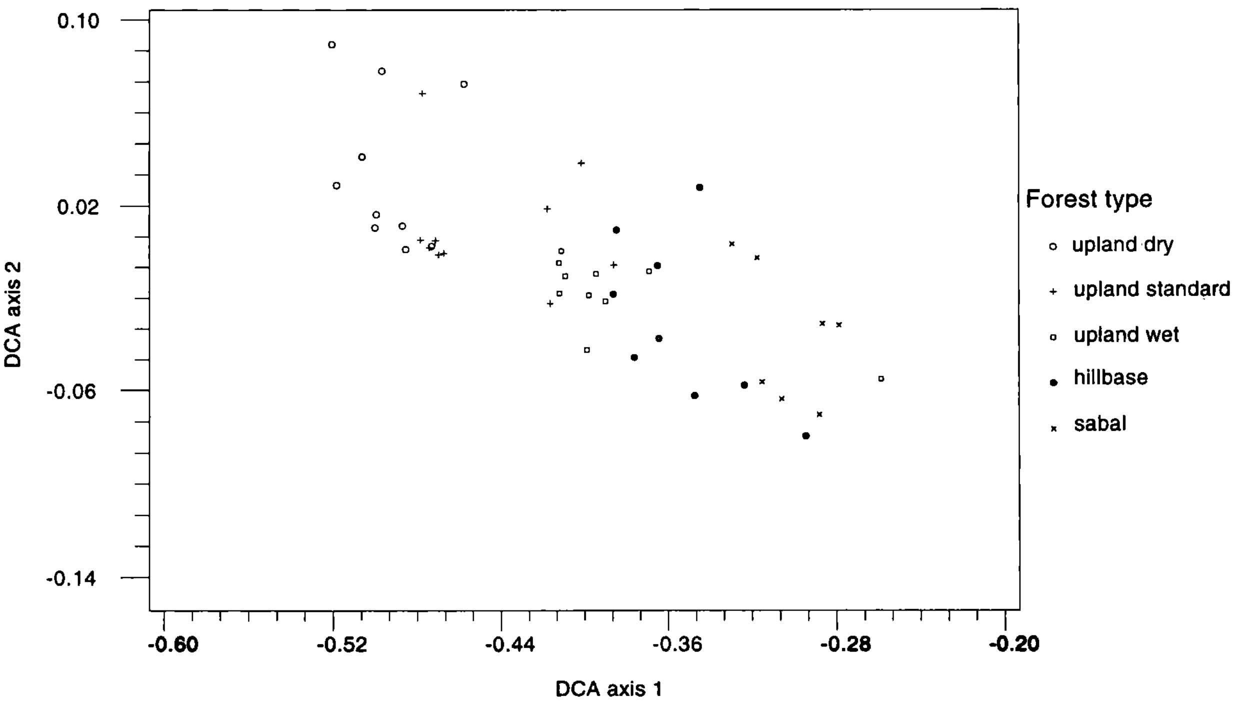


Figure 6. Positions of upland samples along first two axes of a Detrended Correspondence Analysis of mature tree (> 7.5 cm d.b.h.) data. Plots are coded according to forest type as in Fig. 4. Not all samples are visible in figure due to overlap in ordination space.

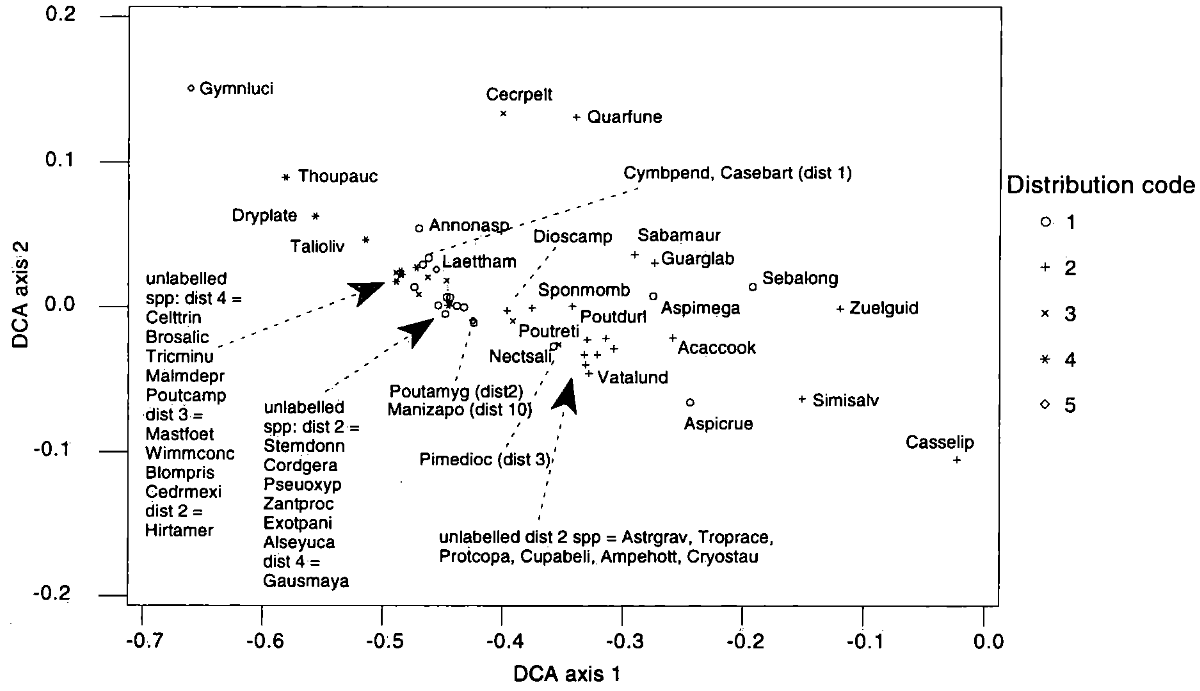


Figure 7. Species centroids for tree species with abundance peaks in upland areas; ordination space defined by first two axes of a Detrended Correspondence Analysis of mature tree (> 7.5 cm d.b.h.) data. Species centroids are coded by distribution type as in Fig. 5 and Appendix 1; species names corresponding to abbreviations are given in Appendix 1.

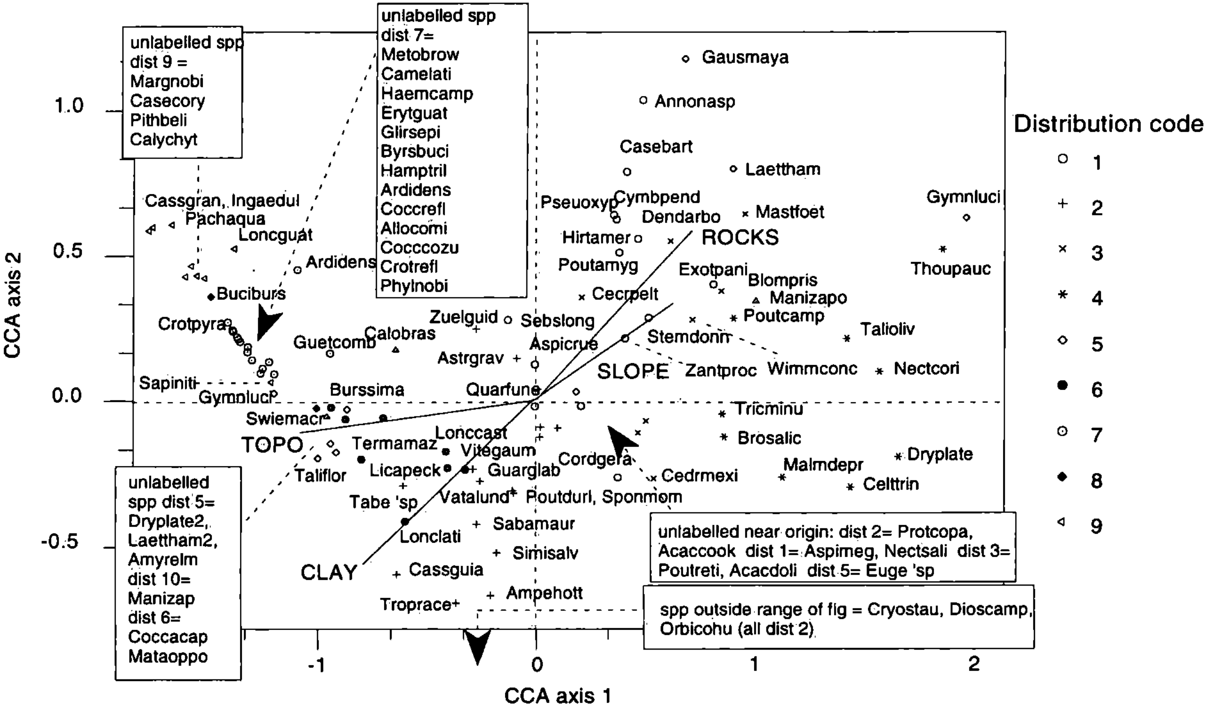

unlabelled spp dist 9 = Margnobi Casecory Pithbeli Calychyt
unlabelled spp dist 7= Metobrow Camelati Haemcamp Erytguat Glirsepi Byrsbuci Hamptril Ardidens Coccrefl Allocomi Cocccozu Crotrefl Phylnobi
unlabelled spp dist 5= Dryplate2, Laettham2, Amyrelm dist 10= Manizap dist 6= Coccacap Mataoppo
unlabelled near origin: dist 2= Protcopa, Acaccook dist 1= Aspimeg, Nectsali dist 3= Poutreti, Acacdoli dist 5= Euge 'sp
spp outside range of fig = Cryostau, Dioscamp, Orbicohu (all dist 2)
Distribution code
○ 1
+ 2
× 3
* 4
◇ 5
● 6
⊙ 7
◆ 8
◁ 9
CCA axis 2
1.0
0.5
0.0
-0.5
CCA axis 1
-1
0
1
2
ROCKS
SLOPE
TOPO
CLAY
Gausmaya
Annonasp
Casebart
Laettham
Gymnluci
Pseuoxyp
Cymbpend
Dendarbo
Mastfoet
Hirtamer
Poutamyg
Exotpani
Blompris
Manizapo
Thoupauc
Cecrpelt
Poutcamp
Talioliv
Stemdonn
Zantproc
Wimmconc
Nectcori
Cassgran, Ingaedul
Pachaqua
Loncguat
Ardidens
Buciburs
Crotpyra
Guetcomb
Calobras
Zuelguid
Sebslong
Aspicrue
Astrgrav
Sapiniti
Gymnlucr
Burssima
Quarfune
Swiemacr
Tricminu
Brosalic
Dryplate
Malmdepr
Celttrin
Lonccast
Termamaz
Vitegaum
Cordgera
Cedrmexi
Licapeck
Guarglab
Taliflor
Vatalund
Poutdurl, Sponmom
Tabe 'sp
Sabamaur
Lonclati
Simisalv
Cassguia
Ampehott
Troprace

Figure 8. Positions of tree species centroids along first two axes of a Canonical Correspondence Analysis (283 active samples, 98 active species) of mature tree (> 7.5 cm d.b.h.) data, incorporating four environmental variables: topographic position, slope, soil clay content and soil rockiness. Lines indicate relation of environmental variables with first two canonical axes. Species are coded according to distribution classes identified through examination of individual species distributions along the predominant topographic gradient. Distribution codes and full species names are given in Appendix 1. Complete lists of species corresponding to each distribution code are presented in Figs. 26-35.

	Ordination Axes				Total
Ordination diagnostics	1	2	3	4	inertia
Eigenvalues	0.425	0.068	0.020	0.012	7.483
Species-environment correlations	0.827	0.533	0.372	0.314	
Cum. % variance of species data accounted for	5.7	6.6	6.9	7.0	
Cumulative % of spp-environment relation	81.0	93.9	97.8	100.0	
Sum of all unconstrained eigenvalues (after fitting covariables)					7.483
Sum of all canonical eigenvalues (after fitting covariables)					0.525

Monte Carlo test of significance of environmental variables (99 permutations under full model):

(1) topographic position: $F = 16.79$; $p = 0.01$; (2) soil clay content: $F = 2.3$; $p = 0.01$; soil rock content and slope n.s. after fitting of topographic position and clay content.

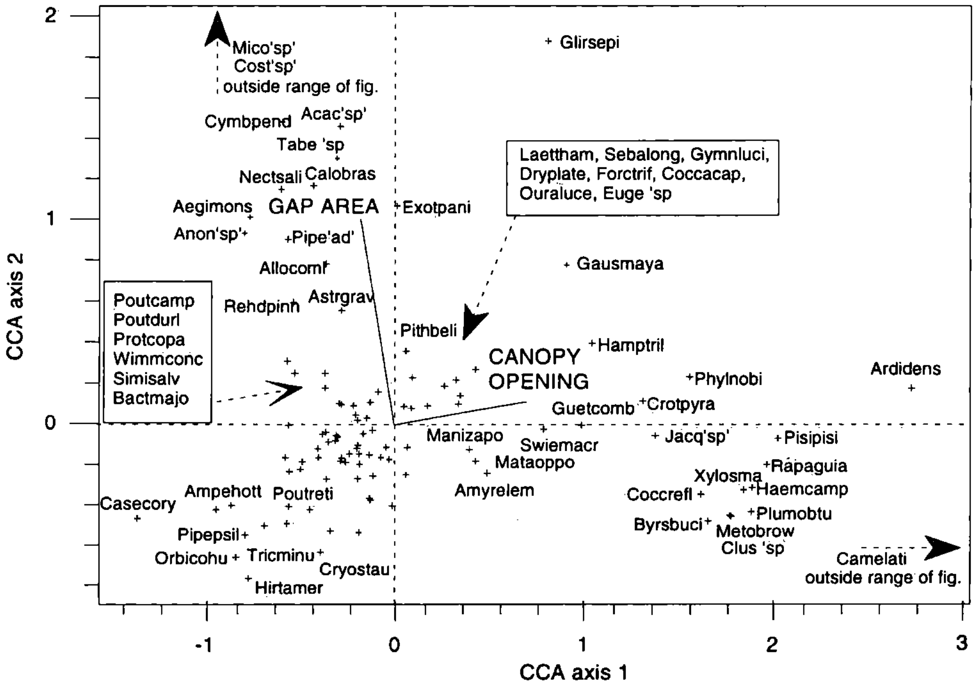

Mico'sp'
Cost'sp'
outside range of fig.
Glirsepi
Cymbpend
Acac'sp'
Tabe 'sp
Nectsali
Calobras
Laettham, Sebalong, Gymnluci, Dryplate, Forctrif, Coccacap, Ouraluce, Euge 'sp
Aegimons
GAP AREA
Exotpani
Anon'sp'
Pipe'ad'
Gausmaya
Allocomf
Poutcamp
Poutdurl
Protcopa
Wimmconc
Simisalv
Bactmajo
Rehdpinh
Astrgrav
Pithbeli
CANOPY OPENING
Hamptril
Phylnobi
Ardidens
Guetcomb
Crotpyra
Manizapo
Swiemacr
Jacq'sp'
Pisipisi
Mataoppo
Rapaguia
Xylosma
Haemcamp
Casecory
Ampehott
Poutreti
Amyrelem
Coccrefl
Plumobtu
Byrsbuci
Metobrow
Pipepsil
Clus 'sp
Orbicohu
Tricminu
Camelati
outside range of fig.
Cryostau
Hirtamer
2
1
0
-1
0
1
2
3
CCA axis 2
CCA axis 1

Figure 9. Position of species centroids along first two axes of a Canonical Correspondence Analysis of data on tree juveniles and understory treelets (< 7.5 cm d.b.h.; 196 active samples, 126 active species) with percent canopy opening and percentage of plot area in gap or building phase included as environmental variables. Effects of topography, slope, and soil clay and rock content were removed by incorporating these as covariables in the analysis. Lines indicate relation of environmental variables with first two canonical axes. Unlabelled species at center of plot showed low correlations between juvenile occurrence and both light availability and canopy disturbance; unlabelled species are as follows (see Appendix 1 for full names): *Sabamaur, Poutamyg, Ardipasc, Malmdepr, Zantproc, Cupabeli, Casebart, Aspicrue, Aspimega, Stemdonn, Simaglau, Blompris, Talioliv, Qaurfune, Swarcube, Bucibuce, Termamaz, Dioscamp, Erytguat, Lonccast, Lonclati, Alibedul, Pseuoxyp, Pimedioi, Calychyt, Acaccook, Tricpall, Tricmosc, Licapeck, Vatalund, Troprace, Brosalic, Zuelguid, Sponmomb.*

Ordination diagnostics	Ordination Axes 1	2	3	4	Total inertia
Eigenvalues	0.238	0.040	0.260	0.213	4.750
Species-environment correlations	0.776	0.511	0.000	0.000	
Cum. % variance in species data accounted for	5.6	6.5	12.6	17.6	
Cum. % of spp-environment relation	85.6	100.0	0.0	0.0	
Sum of all unconstrained eigenvalues (after fitting covariables)					4.271
Sum of all canonical eigenvalues (after fitting covariables)					0.278

Monte Carlo test summaries (99 permutations under full model):
Test of significance of first canonical axis: eigenvalue = 0.24; $F = 11.13$; $p = 0.01$.
Overall test: Trace = 0.28; $F = 6.57$, $p = 0.01$.
Test of significance of environmental variables: (1) canopy opening: $F = 10.88$; $p = 0.01$; (2) gap area: $F = 2.19$; $p = 0.03$.

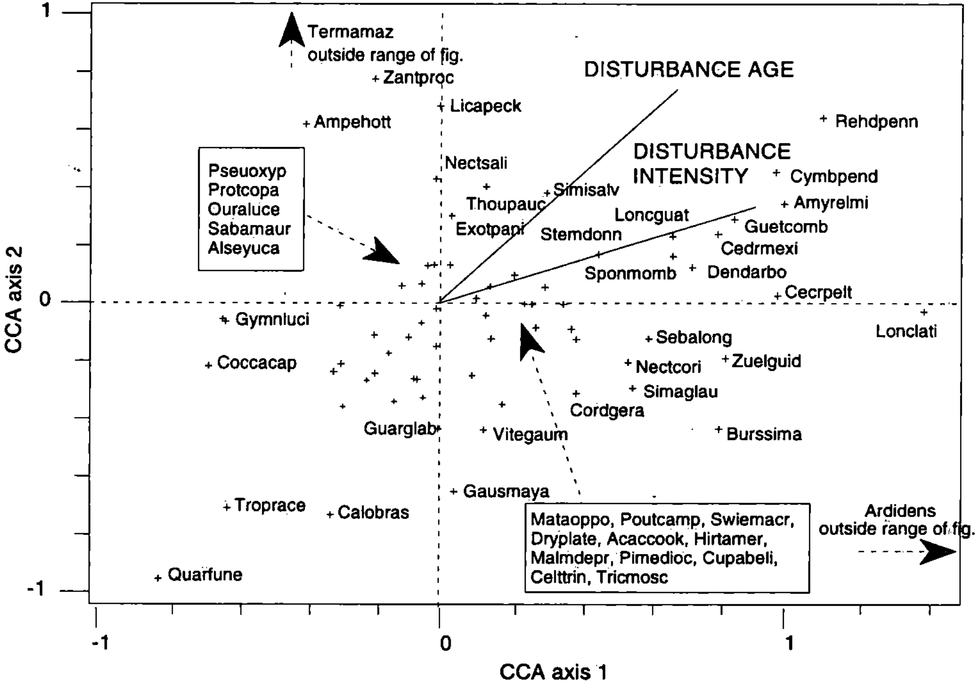

Termamaz
outside range of fig.
Zantproc
Licapeck
Ampehott
DISTURBANCE AGE
Rehdpenn
Pseuoxyp
Protcopa
Ouraluce
Sabamaur
Alseyuca
Nectsali
DISTURBANCE
INTENSITY
Cymbpend
Simisalv
Amyrelmi
Thoupauc
Loncguat
Guetcomb
Exotpapi
Stemdonn
Cedrmexi
Sponmomb
Dendarbo
Cecrpelt
Gymnluci
Lonclati
Sebalong
Coccacap
Nectcori
Zuelguid
Simaglau
Cordgera
Guarglab
Vitegaum
Burssima
Gausmaya
Troprace
Calobras
Mataoppo, Poutcamp, Swiemacr,
Dryplate, Acaccook, Hirtamer,
Malmdepr, Pimedioc, Cupabeli,
Celttrin, Tricmosc
Ardidens
outside range of fig.
Quarfune
1
0
-1
CCA axis 2
-1
0
1
CCA axis 1

Figure 10. Positions of tree species centroids along first two axes of a Canonical Correspondence Analysis of mature tree (> 7.5 cm d.b.h.) data from upland sites (149 active samples, 62 active species) with natural treefall canopy disturbance intensity and disturbance age as environmental variables. Effects of topography, soil clay and rock content and substrate slope were removed by incorporating these as covariables in the analysis. Lines indicate relation of environmental variables with first two canonical axes. Unlabelled species at center of plot showed low correlation with canopy disturbance, and are as follows (see Appendix 1 for full names): *Poutreti, Poutamyg, Poutdurl, Manizapo, Mastfoet, Astrgrav, Casebart, Aspicrue, Aspimega, Swarcube, Wimmconc, Laettham, Lonccast, Vatalund, Tricminu, Acacdoli, Brosalic, Talioliv, Blompris, Vitegaum, Cryostau.*

Ordination diagnostics	Ordination Axes				Total
Eigenvalues	1	2	3	4	inertia
Species-environment correlations	0.041	0.025	0.308	0.189	2.839
Cum. % variance of species data accounted for	0.593	0.603	0.000	0.000	
Cum. % of spp-environment relation	1.6	2.6	14.5	21.8	
Sum of all unconstrained eigenvalues (after fitting covariables)	62.0	100.0	0.0	0.0	
Sum of all canonical eigenvalues (after fitting covariables)					2.578
					0.066

Monte Carlo test summaries (99 permutations under full model):
Test of significance of first canonical axis: eigenvalue = 0.04; $F = 1.71$; $p = 0.06$;
Overall test: Trace = 0.07; $F = 1.39$; $p = 0.05$;
Test of significance of environmental variables: (1) disturbance age: $F = 1.46$; $p = 0.10$;
(2) disturbance intensity: $F = 1.32$; $p = 0.07$.

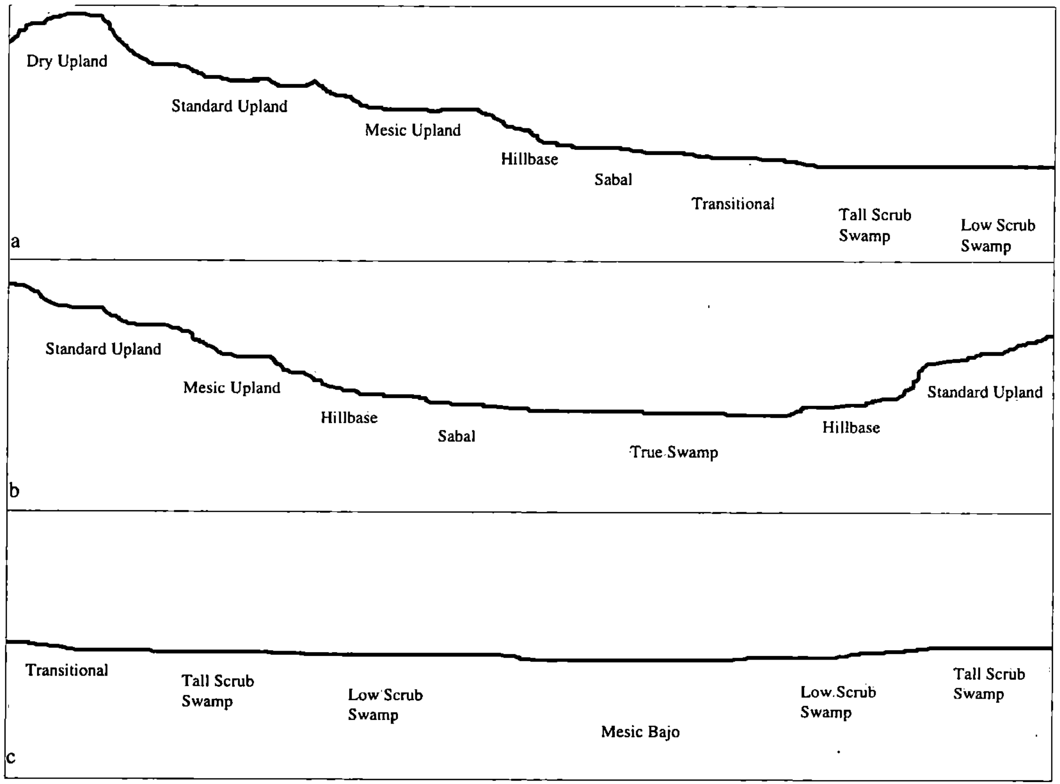
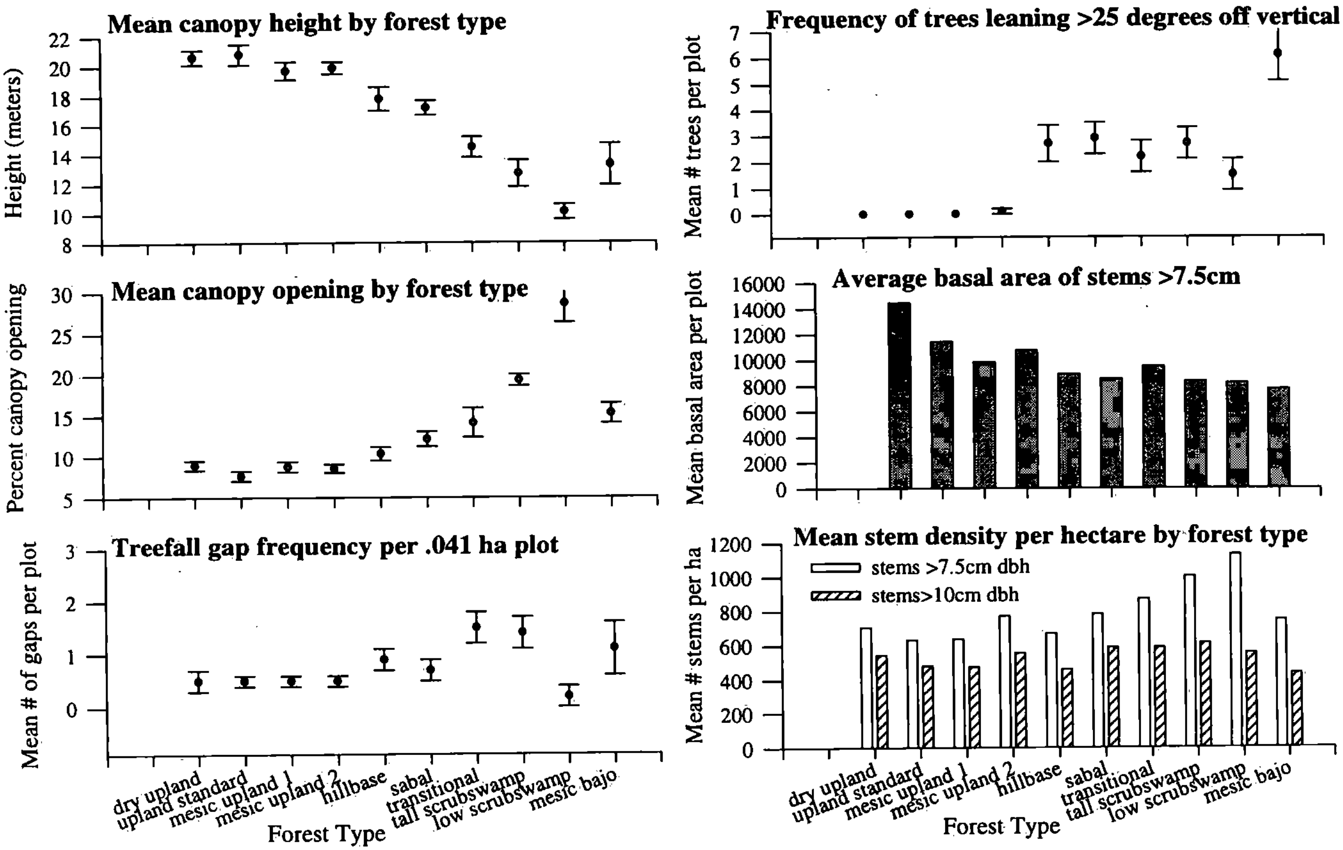


Figure 11. Graphic representation of topographic gradients in Tikal National Park, Guatemala, with associated forest types: a) complete gradient from a dry upland hilltop to the center of a lowland depression; b) a narrow lowland depression between two upland areas; c) illustration of the dramatic influence exerted on vegetation by subtle topographic changes within lowland depressions.



Mean canopy height by forest type

Frequency of trees leaning >25 degrees off vertical

Mean canopy opening by forest type

Average basal area of stems >7.5cm

Treefall gap frequency per .041 ha plot

Mean stem density per hectare by forest type

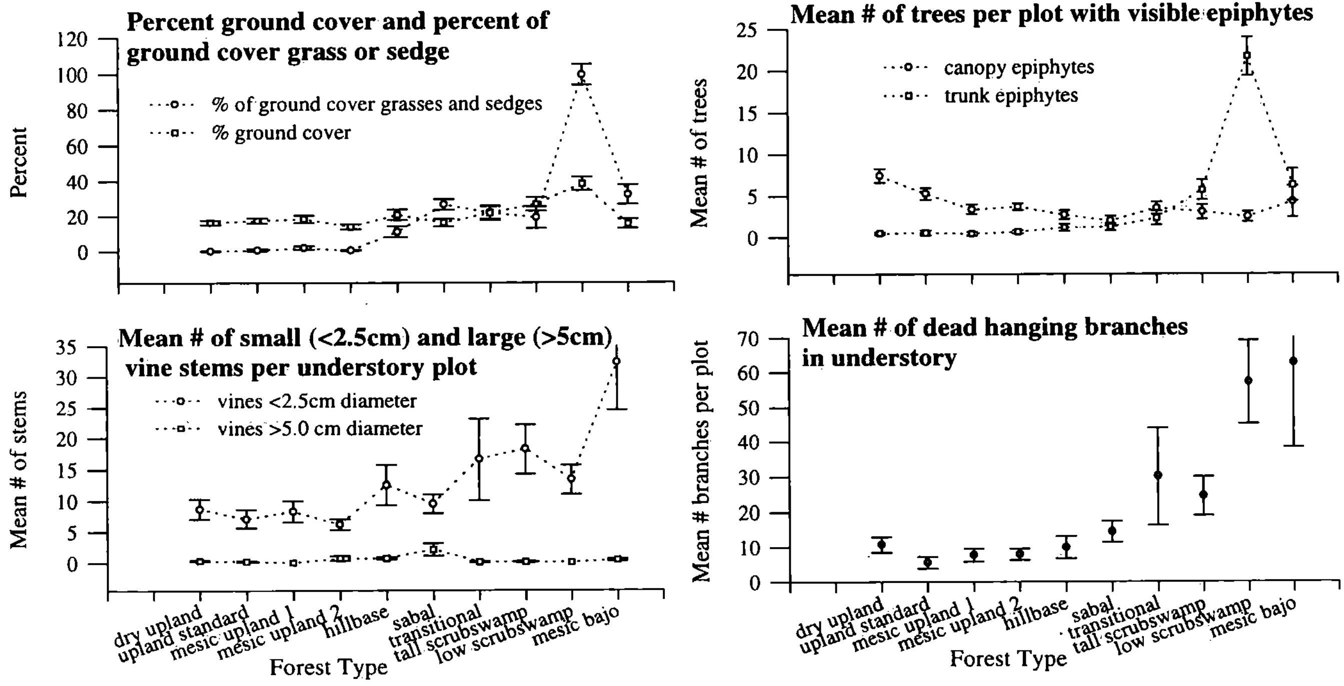
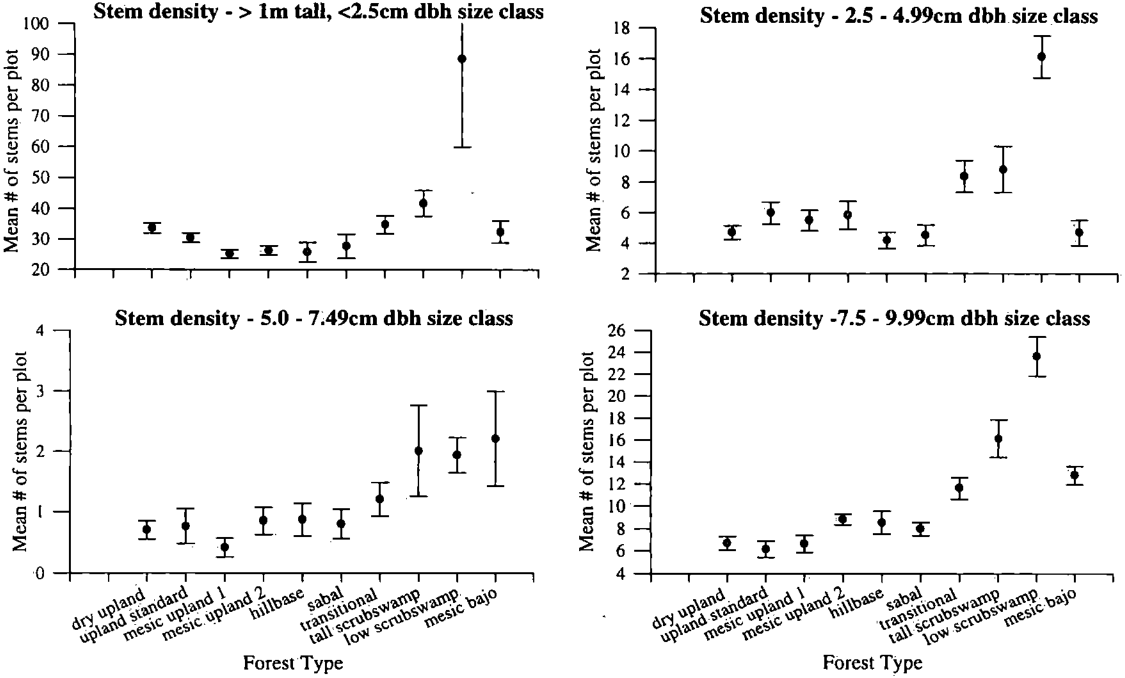


Figure 12. Variation of key structural characteristics of forest vegetation across the dominant environmental gradient, Tikal, Guatemala. Values are presented as means per forest type (= topographic position), ± 1 standard error.


Stem density - > 1m tall, <2.5cm dbh size class
Mean # of stems per plot
100
90
80
70
60
50
40
30
20
Stem density - 2.5 - 4.99cm dbh size class
Mean # of stems per plot
18
16
14
12
10
8
6
4
2
Stem density - 5.0 - 7.49cm dbh size class
Mean # of stems per plot
4
3
2
1
0
dry upland
upland standard
mesic upland 1
mesic upland 2
hillbase
sabal
transitional
tall scrubswamp
low scrubswamp
mesic bajo
Forest Type
Stem density -7.5 - 9.99cm dbh size class
Mean # of stems per plot
26
24
22
20
18
16
14
12
10
8
6
4
dry upland
upland standard
mesic upland 1
mesic upland 2
hillbase
sabal
transitional
tall scrubswamp
low scrubswamp
mesic bajo
Forest Type

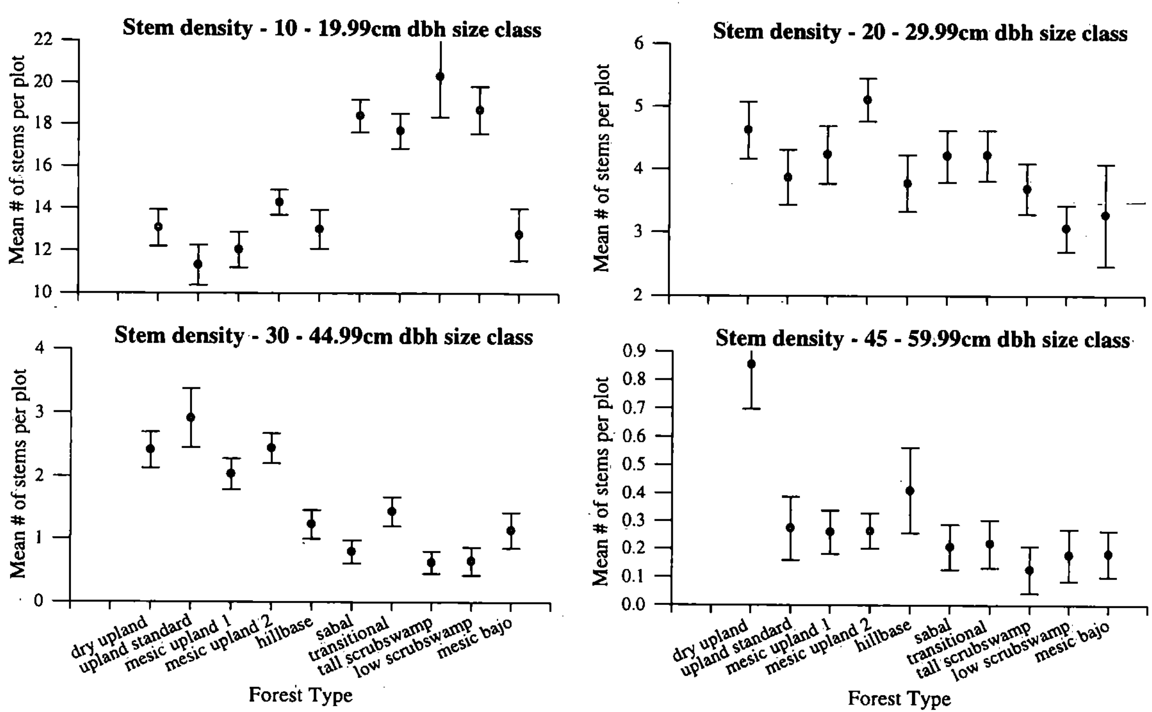
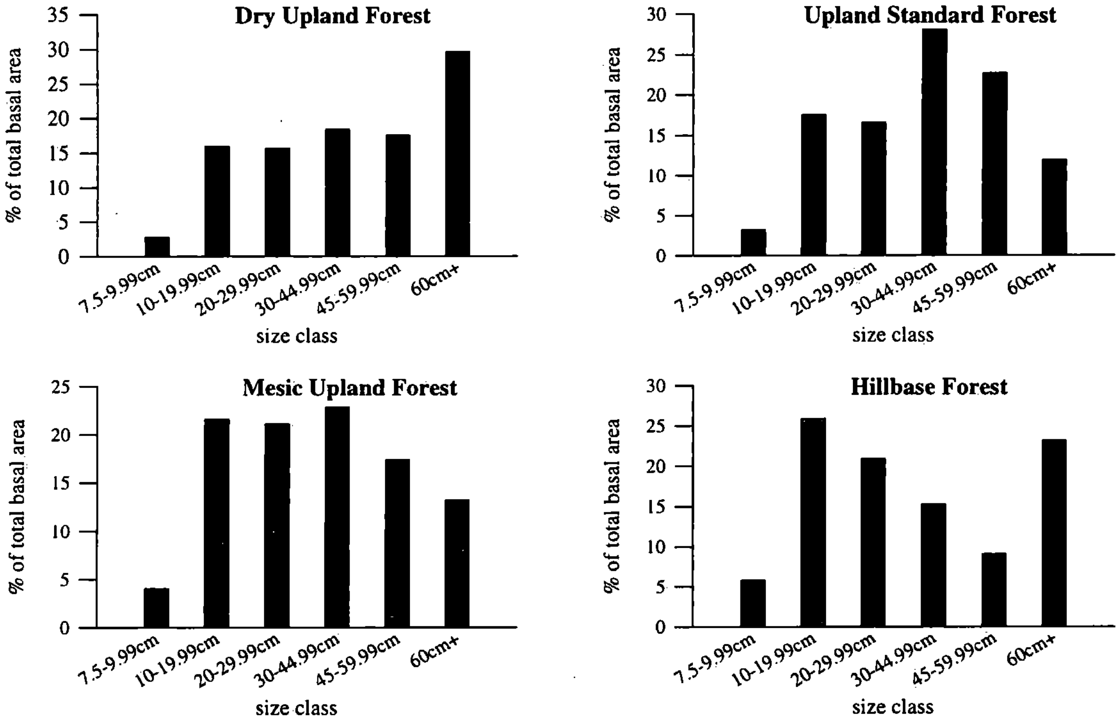


Figure 13. Variation in stem density by diameter class for forest types across the dominant environmental gradient, Tikal, Guatemala. Values given are means per forest type (topographic position), ± 1 standard error. Stems >60 cm d.b.h. are not presented graphically; for this size class, means are as follows from Dry Upland to Mesic Bajo: 0.85; 0.28; 0.27; 0.27; 0.42; 0.21; 0.22, 0.13; 0.17; 0.19.


Dry Upland Forest
% of total basal area
0
5
10
15
20
25
30
35
7.5-9.99cm
10-19.99cm
20-29.99cm
30-44.99cm
45-59.99cm
60cm+
size class
Upland Standard Forest
% of total basal area
0
5
10
15
20
25
30
7.5-9.99cm
10-19.99cm
20-29.99cm
30-44.99cm
45-59.99cm
60cm+
size class
Mesic Upland Forest
% of total basal area
0
5
10
15
20
25
7.5-9.99cm
10-19.99cm
20-29.99cm
30-44.99cm
45-59.99cm
60cm+
size class
Hillbase Forest
% of total basal area
0
5
10
15
20
25
30
7.5-9.99cm
10-19.99cm
20-29.99cm
30-44.99cm
45-59.99cm
60cm+
size class

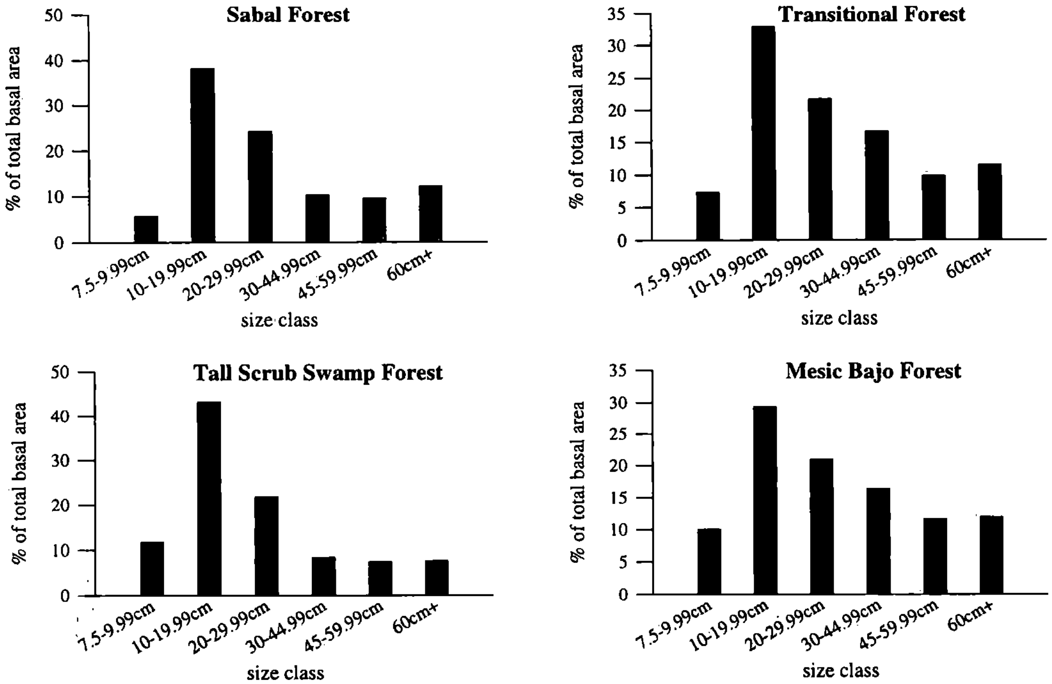


Figure 14. Variation in tree size class structure across the dominant environmental gradient, Tikal, Guatemala. Values given are the percent of total average basal area accounted for by a given diameter class.

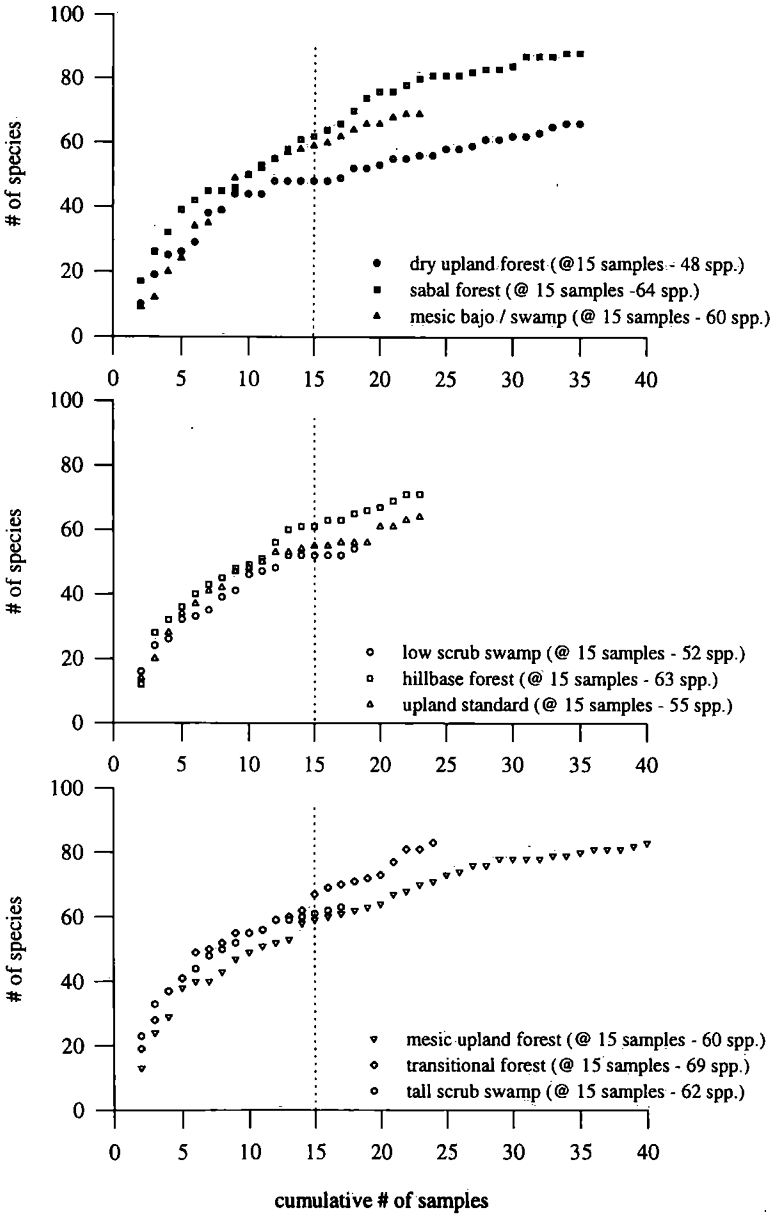


Figure 15. Species accumulation curves per sample effort for nine forest types sampled in Tikal National Park, Guatemala. Samples were 0.041 ha (0.1 acre) in area.

Figure 16. Dry Upland Forest, Tikal, Guatemala. Rarity of understory palms such as *Cryosophila stauracantha*, and prevalence of *Piper psilorrachis* and a dense collection of tree saplings in the understory are typical; vine density is low.

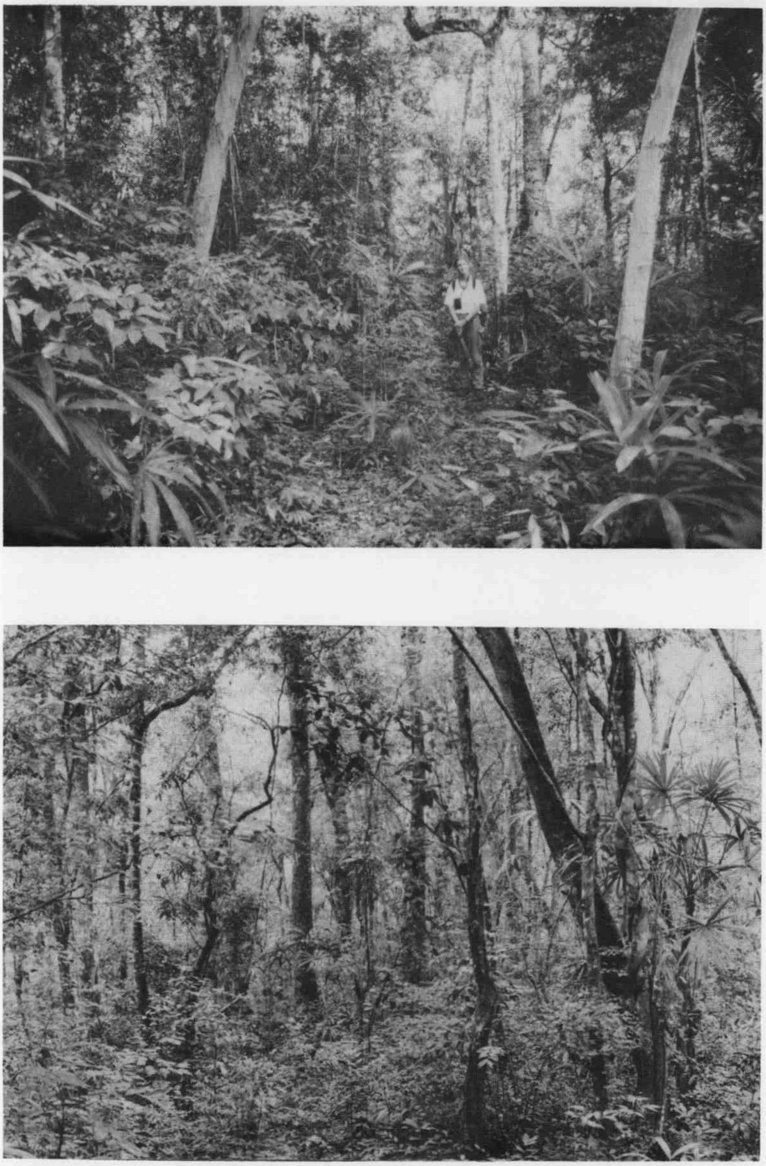


Figure 17. Upland Standard Forest, Tikal, Guatemala. The palm *Cryosophila stauracantha* generally dominates the understory, with *Piper psilorrachis* abundant but of secondary importance; sapling density is moderate and vine density typically low.

Figure 18. Mesic Upland Forest, Tikal, Guatemala. The palm *Cryosophila stauracantha* dominates the understory while *Piper psilorrachis* is only sparsely distributed; vine density is low.

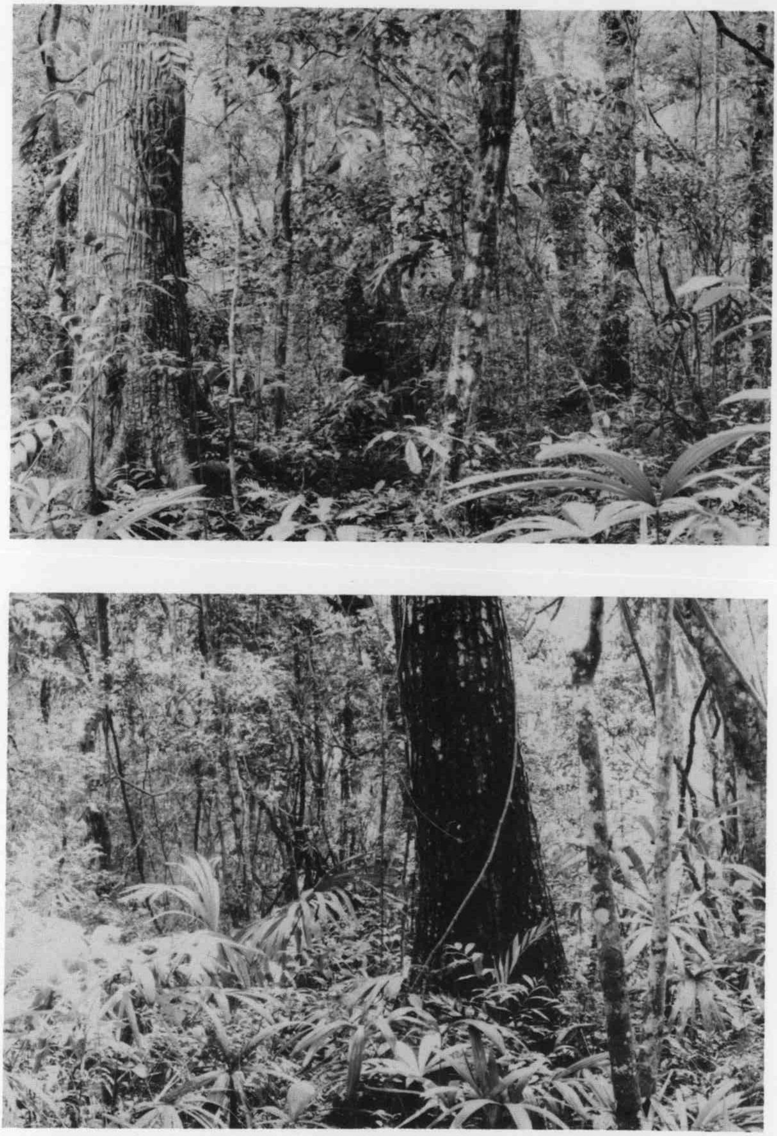


Figure 19. Hillbase Forest, Tikal, Guatemala. Usually occuring in a narrow zone up to 100-150 m from areas of upland relief, this forest type has canopy slightly lower than that of Upland forest, and often very irregular in height. Vine density is high, with most trees having at least a few large, woody vines in their crowns, while density of understory shrubs and saplings is usually not much greater than in Upland forest.

Figure 20. Sabal Forest, Tikal, Guatemala. Generally occurring in nearly level areas 100-400 m from a hill base, this forest, at a mean height of 17 m, has even more broken canopy structure than does Hillbase Forest. Many small light gaps are created by abundant leaning trees, treefalls, and around the small crowns of the palm *Sabal mauritiiformis* which abounds. Vine density varies dramatically over short distances, probably largely as a result of treefall history.

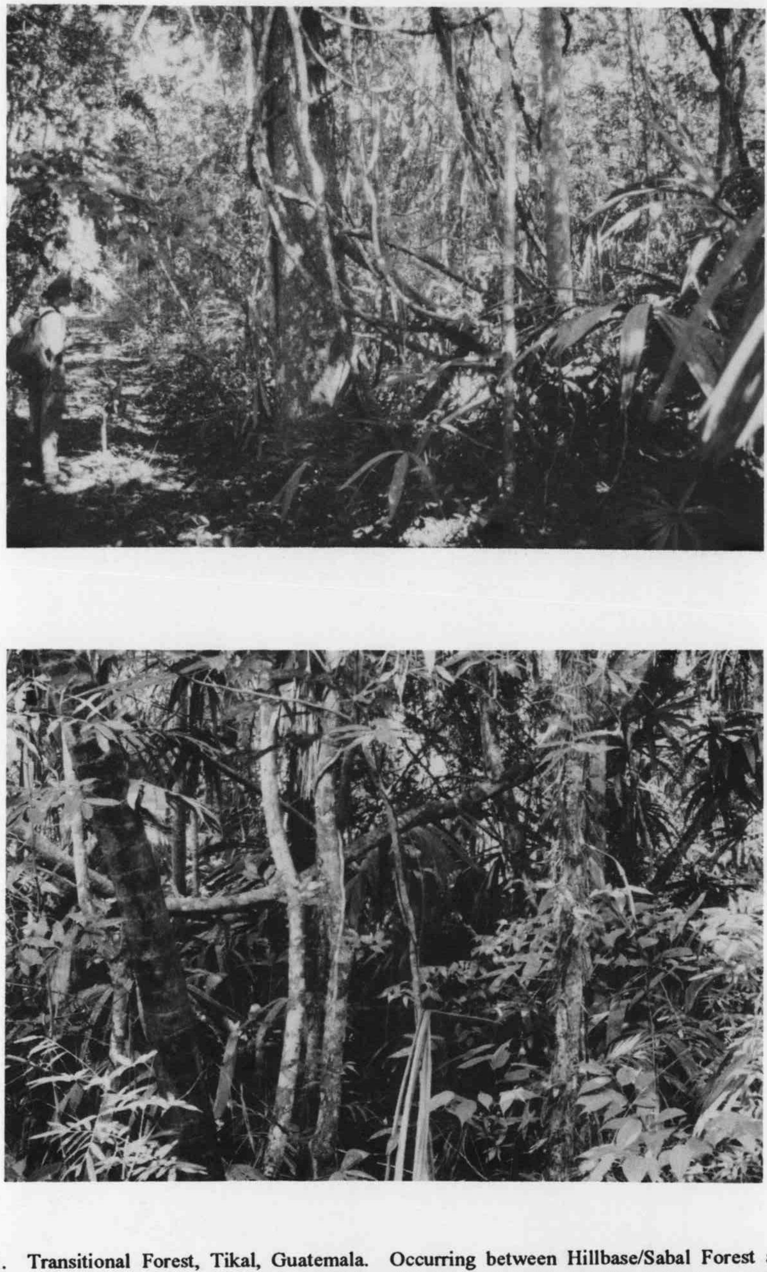


Figure 21. Transitional Forest, Tikal, Guatemala. Occurring between Hillbase/Sabal Forest and xerophytic Scrub Swamp, this forest type is transitional in terms of structure and composition. Mean canopy height is 14.5 m, with emergents averaging 19 m and lowest canopy areas averaging 11 m. While the understory is dense, with abundant vines, shrubs, and saplings, trees often reach 20-30 cm in diameter, creating a more structurally diverse canopy and less dense understory than in Scrub Swamp.

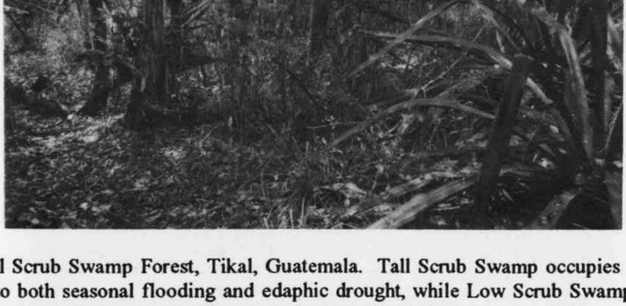


Figure 22. Tall Scrub Swamp Forest, Tikal, Guatemala. Tall Scrub Swamp occupies peripheries of basins subject to both seasonal flooding and edaphic drought, while Low Scrub Swamp occupies the central portions of such basins. In Tall Scrub Swamp, canopy height averages 12.7 m, with emergents averaging 18 m and lowest canopy averaging 9 m. *Bucida* and *Swietenia* are often present as large emergents in Tall Scrub Swamp, less commonly in Low Scrub Swamp. Small vines are abundant and there is a high density of small diameter trees.

Figure 23. Low Scrub Swamp, Tikal, Guatemala. In Low Scrub Swamp, mean canopy height is 10.1 m, emergents average 12 m, and lowest canopy averages 8.1 m. While both Tall and Low Scrub Swamp have relatively open canopy, this is more pronounced in Low Scrub Swamp, where grasses and sedges dominate the ground cover and epiphytes are abundant on boles. At its extreme, scrub swamp is an almost impenetrable thicket of small vines, saw-sedge, and stunted, sapling-sized trees.

Figure 24. Arroyo Forest, Tikal, Guatemala. Occurring along seasonal waterways through basins dominated by Scrub Swamp, this forest type differs from the latter in structure more than in species composition.

Figure 25. Mesic Bajo Forest, Tikal, Guatemala. Included within the spatial matrix of xerophytic Scrub Swamp, this forest type occupies areas less prone to dry-season edaphic drought, with standing water remaining through at least some dry seasons. Canopies are at least as tall as in Tall Scrub Swamp, significantly more closed, and highly irregular; in areas without recent natural disturbance, canopy is tall and dense, but adjacent may be areas comprised of a dense tangle of vines, saplings, and bamboo.

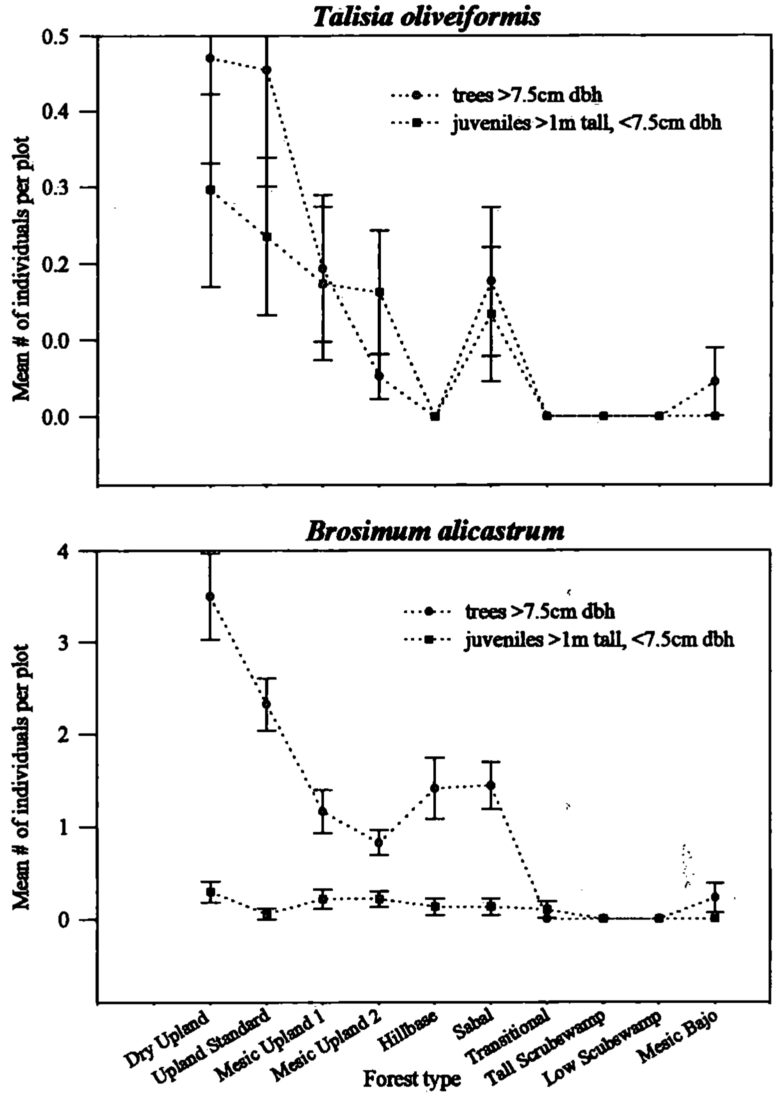


Figure 26. Representative distribution plots for Type 4 (values given as mean ± 1 standard error): "Xeric Upland Dominants" - Peak abundance in Dry Upland Forest, dropping significantly in Mesic Upland, Hillbase and Sabal forest, although many of these species are still frequent in this range, and then virtually non-existent in Transitional Forest and Xerophytic (Tall and Low) Scrub Swamps, and infrequent or absent from True Swamps. Both widespread, common species and rare, restricted species are included in this category. Species: *Brosimum alicastrum, Talisia oliveiformis, Trichilia minutiflora, Thouinia paucidentata, Pouteria campechiana, Malmea depressa, Piper psilorrachis, Diospyros campechiana, Forchammeria trifoliata, Bernoullia flammea,* and *Celtis trinerva.*

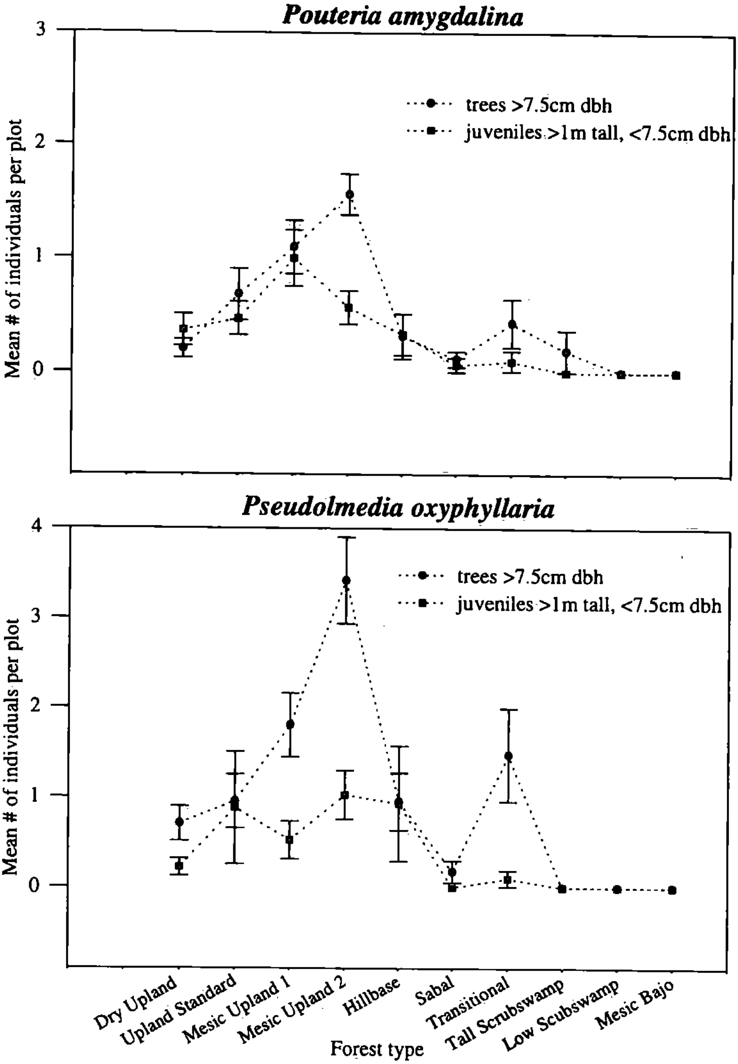


Figure 27. Representative distribution plots for Type 1 (values given as mean ± 1 standard error): "Mesic Upland Species" - present from Upland Dry to Transitional Forest, but significantly more abundant in mesic/low relief upland (Mesic Upland), uncommon in Hillbase or Sabal Forest, and often increasing slightly in abundance in Transitional Forest. Species: *Pouteria amygdalina, Pseudolmedia oxyphyllaria, Casearia bartlettii, Cordia gerascanthus, Aspidosperma cruenta, Sebastiana longicuspis, Zanthoxylum procerum, Hirtella americana, Exothea paniculata, Annona sp, Cymbopetalum penduliflorum, Cryosophila stauracantha, Chamaedorea sp2, Nectandra salicifolia, Stemmadenia donnell-smithii,* and *Alseis yucatanensis.*

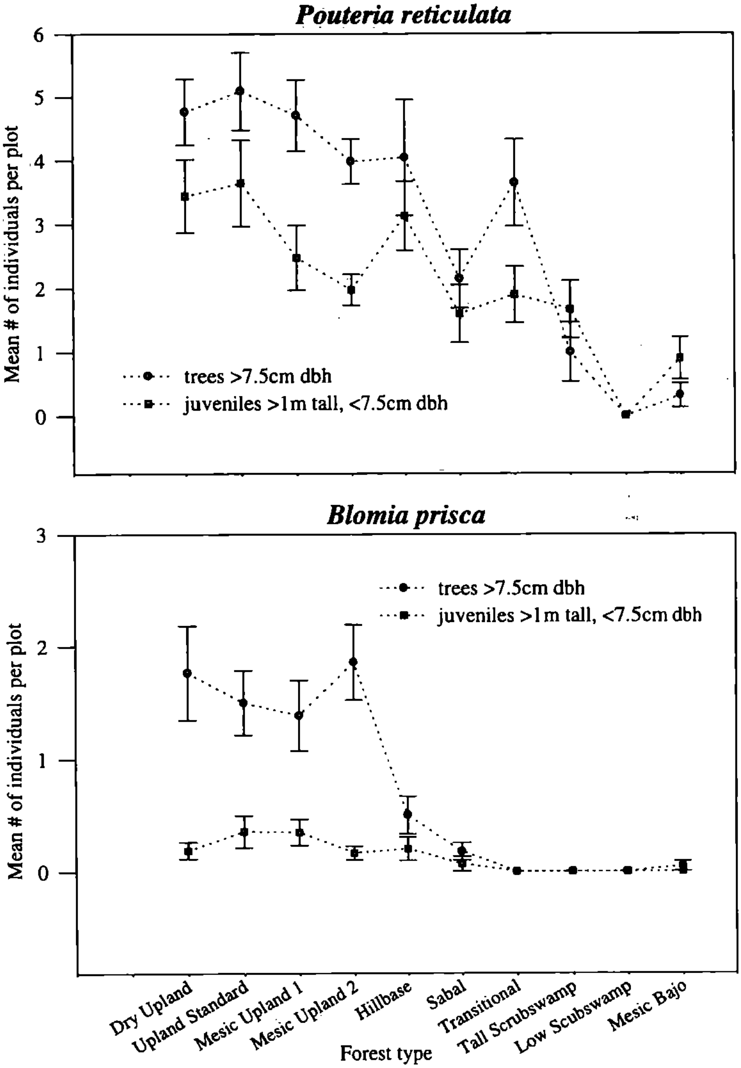


Figure 28. Representative distribution plots for Type 3 (values given as mean ± 1 standard error): "Upland Generalists" - Relatively high abundance in all upland areas, decreasing significantly in abundance by Hillbase (or even Mesic Upland) Forest but continuing at some low frequency until Transitional Forest or Tall Scrub Swamp; absent from Low Scrub Swamp. Species: *Pouteria reticulata, Blomia prisca, Pimenta dioica, Trichilia pallida, Chamaedorea* sp.1, *Chamaedorea pacaya, Cedrela mexicana, Dendropanax arboreus, Cecropia peltata, Aegiphila monstrosa, Wimmeria concolor, Mastichodendron foetidessimum, Aspidosperma megalocarpon, Coussapoa oligocephala, Malpighia glabra, Piper sempervirens, Trichilia havanesis,* and *Swartzia cubensis.*

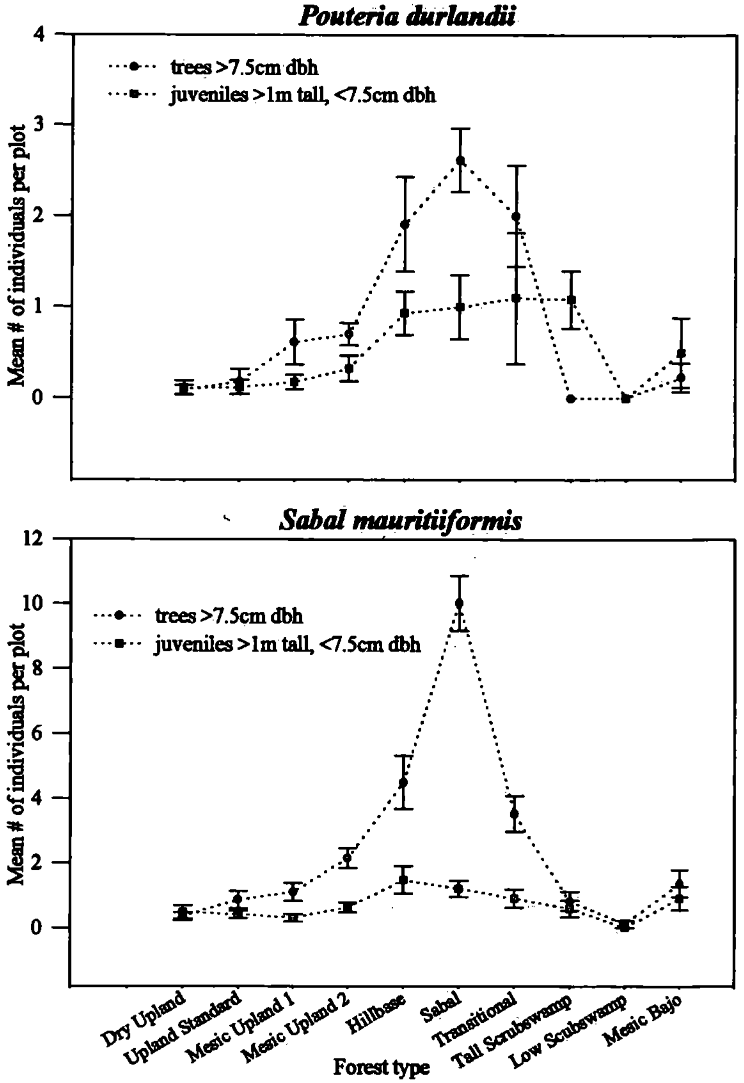


Figure 29. Representative distribution plots for Type 2 (values given as mean ± 1 standard error): "Mesic Forest Species" - low abundance in Dry Upland, increasing in Mesic Upland with a large peak in Hillbase/Sabal forest, with decreased or similar abundance in Transitional, decreasing to absence in Tall and Low Scrub Swamp. Many of these species display slightly higher abundance in Mesic Bajo and True Swamp than in Tall and Low Scrub Swamp. Species: *Trophis racemosa, Guarea glabra, Vatairea lundellii, Sabal mauritiiformis, Ampelocera hottlei, Psychotria* sp.1, *Protium copal, Quararibea funebris, Pouteria durlandii, Tabebuia* sp., *Piper* cf. *aduncum, Zuelania guidonia, Cupania belizensis, Simira salvadorensis, Cassipourea guianensis, Alibertia edulis, Spondias mombin, Acacia cookii, Ocotea* sp., *Chrysophyllum mexicanum, Astronium graveolens, Castilla elastica, Ficus glabra, Rehdera penninerva, Pouteria sapota, Costus* sp. (a non-woody plant), and *Simarouba glauca.*

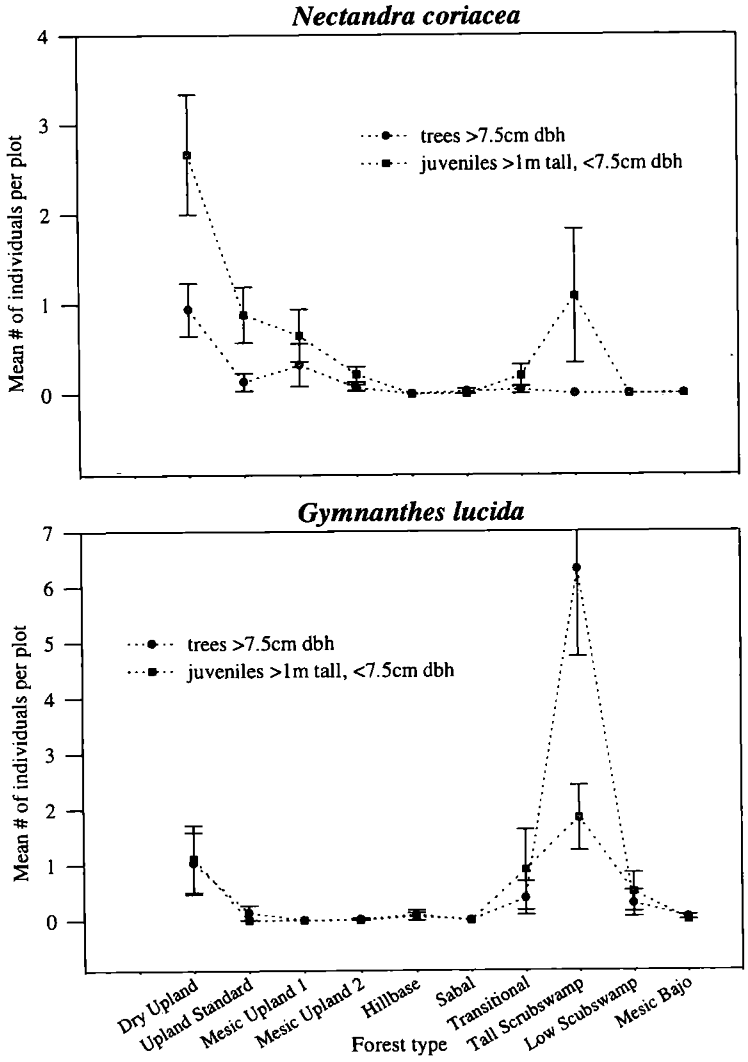


Figure 30. Representative distribution plots for Type 5 (values given as mean ± 1 standard error): "Bimodal Xerics" - several species have a strong bimodal distribution, with relatively high abundance in Dry Upland Forest and in Tall Scrub Swamp and/or Transitional Forest. Species: *Gymnanthes lucida, Nectandra coriacea, Laetia thamnia, Drypetes lateriflora, Clusia* sp., *Amyris elemifera, Eugenia* sp., *Gaussia maya, Metopium brownei, Krugioendron ferreum, Pseudobombax ellipticum,* and *Talisia floresii,* although the patterns for the last 4 species are not well represented in the sampling data.

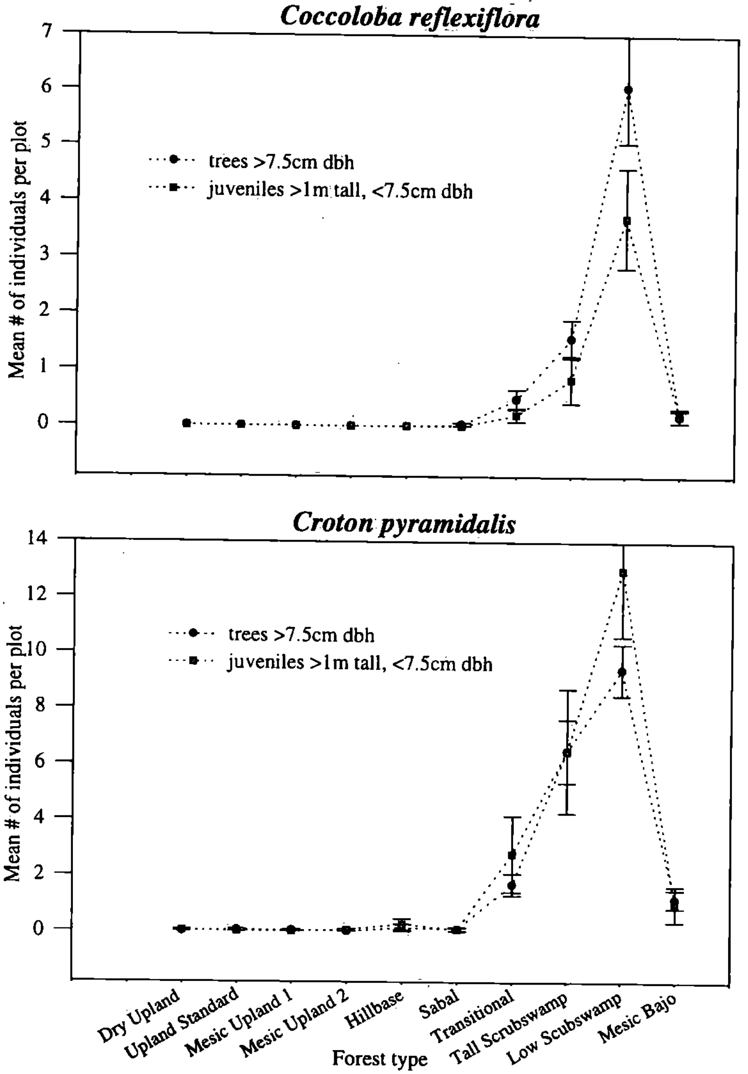


Figure 31. Representative distribution plots for Type 7 (values given as mean ± 1 standard error): "Scrub Swamp Specialists" - Low frequency of occurrence in upland areas building to a peak in Tall and Low Scrub Swamp, but with noticeably lower abundance in, or absent from, Mesic Bajo and True Swamp. Species: *Croton pyramidalis, Croton reflexifolia, Coccoloba cozumelensis, Coccoloba reflexiflora, Byrsonima bucidaefolia, Gliricidia sepium, Ardisia densiflora, Plumeria obtusa, Hampea trilobata, Lonchocarpus rugosus, Rapanea guianensis, Erythroxylon guatemalensis, Chysobalanus icaco, Myrica cerifera, Myrtaceae* **1,2 & 3,** *Cordia sebastena, Xylosma* **sp.,** *Phyllanthus nobilis, Guettarda combsii, Haematoxylum campechianum,* **and** *Cameraria latifolia.*

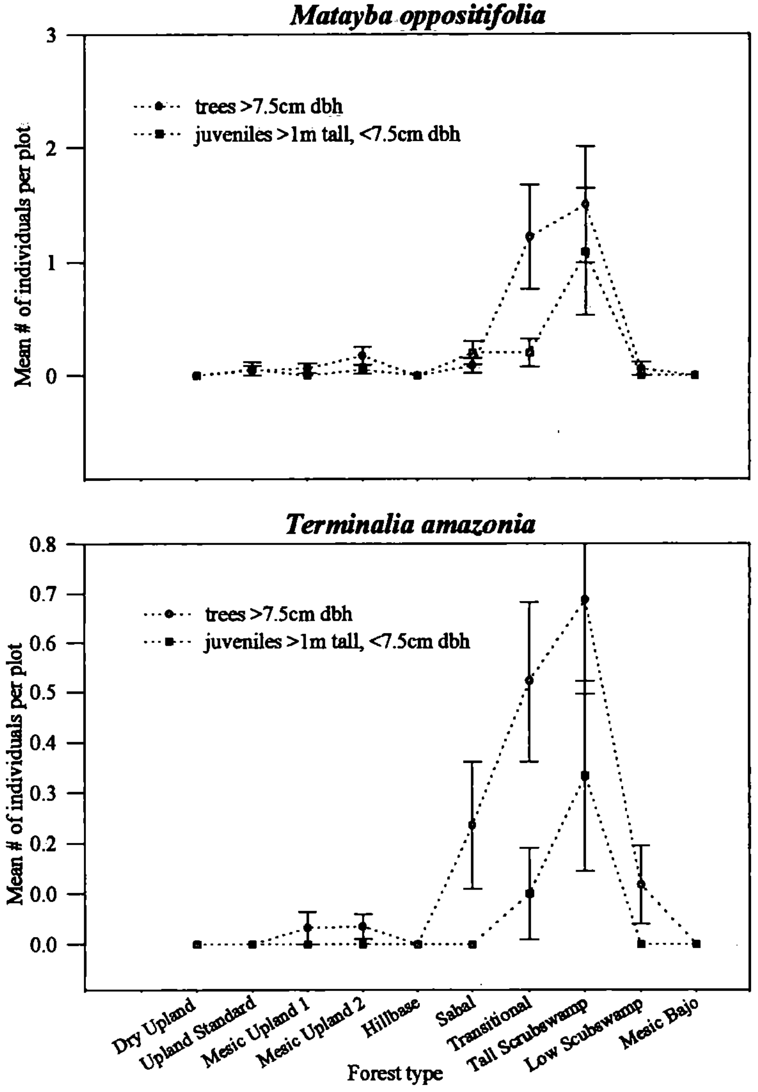


Figure 32. Representative distribution plots for Type 6 (values given as mean ± 1 standard error): "Transitional Forest Species" - These species are widespread, but are patchy in Upland forest and reach highest densities in Transitional Forest or Tall Scrub Swamp, with low densities in the extreme Low Scrub Swamp. Species: *Bursera simaruba, Vitex gaumeri, Coccoloba acapulcensis, Matayba oppositifolia, Terminalia amazonia, Licaria peckii, Lonchocarpus castilloi, Ardisia paschalis, Thevetia ahouai, Bactris major, Ouratea lucens, Jacquinia sp.*, and *Lonchocarpus latifolius.*

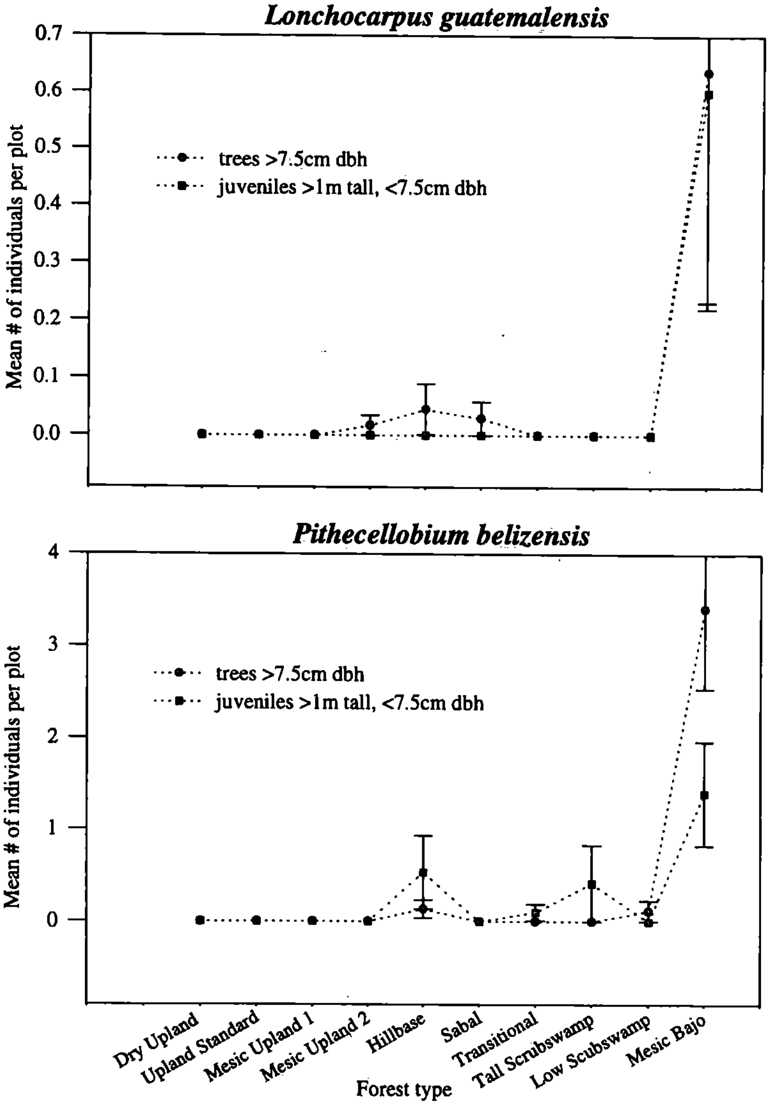


Figure 33. Representative distribution plots for Type 9 (values given as mean ± 1 standard error): "Swamp Obligates" - Species which occur virtually only in areas subject to high seasonal waterlogging of soils, but not excessive drought conditions in dry season. These conditions occur along arroyos (seasonal streams), swampy depressions in otherwise upland areas, and at the very bottom of the topographic gradient, below the Scrub Swamps, where surface water may be present throughout the year. Some of these species occur sporadically in Sabal forest but can't be considered a regular component of this forest. The majority of these species are also characteristic of riparian forests in other parts of Petén and Belize. Species: *Pachira aquatica, Inga edulis, Pithecellobium belizensis, Lonchocarpus guatemalensis, Casearia corymbosa, Cassia grandis, Chamaedorea* sp.4, *Calyptranthes chytriculia, Sapium nitidum, Zanthoxylum caribaeum* and "bamboo sp".

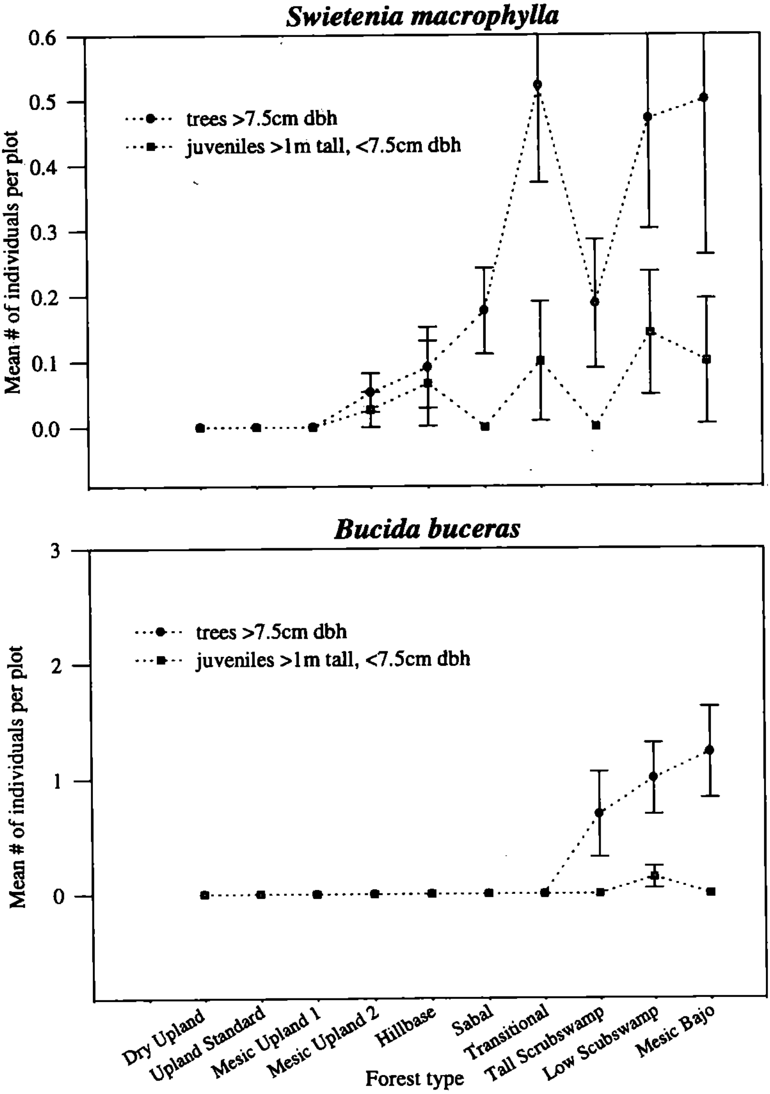


Figure 34. Representative distribution plots for Type 8 (values given as mean ± 1 standard error): "Lowland Generalists" - These species have low frequencies or are absent from upland forests down to Transitional Forest, with a much higher frequency in Scrub Swamps and equal or even higher frequencies in Mesic Bajo and True Swamps. Species: *Bucida buceras, Swietenia macrophylla, Allophylus comina,* and *Margaritaria nobilis.*

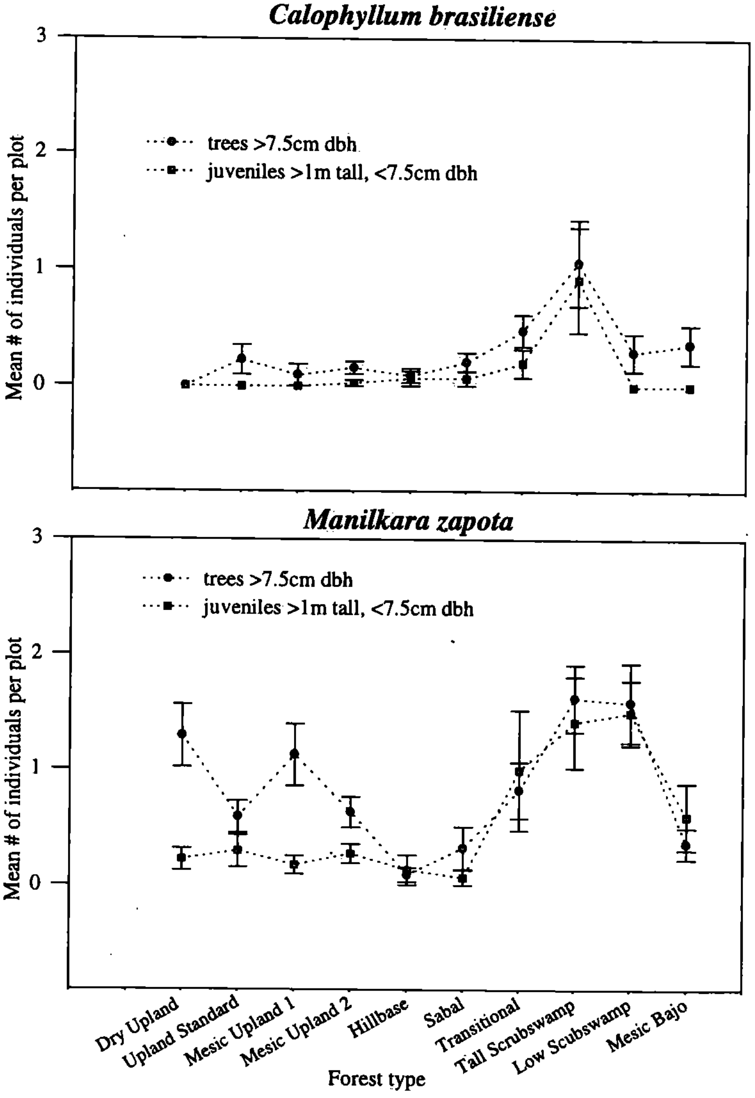


Figure 35. Representative distribution plots for Type 10 (values given as mean ± 1 standard error): "Topographic Generalists" - Several species were common throughout the environmental gradient in Tikal, and did not appear to be limited by edaphic extremes. While these species were not uniformly distributed among forest types, they were not significantly associated with any region of the topographic gradient. Species: *Trichilia moschata*, *Manilkara zapota*, and *Calophyllum brasiliense*.

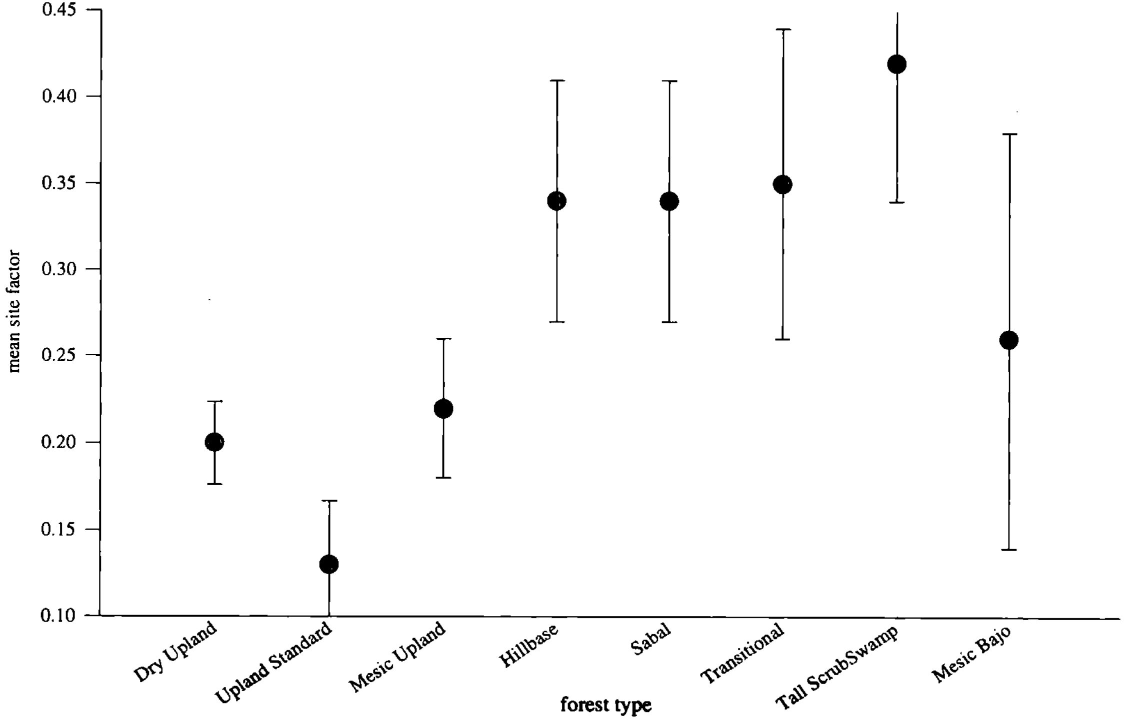


Figure 36. Comparison of mean light intensity at 1 m above ground level in eight forest types. Values given as mean total site factor, as calculated from hemispherical photographs using Hemiphot, with standard deviations. All photographs were taken under uniform cloudy sky conditions in early morning, in areas lacking evidence of canopy disturbance (i.e. treefall gaps). Fourteen photographs were taken per forest type.

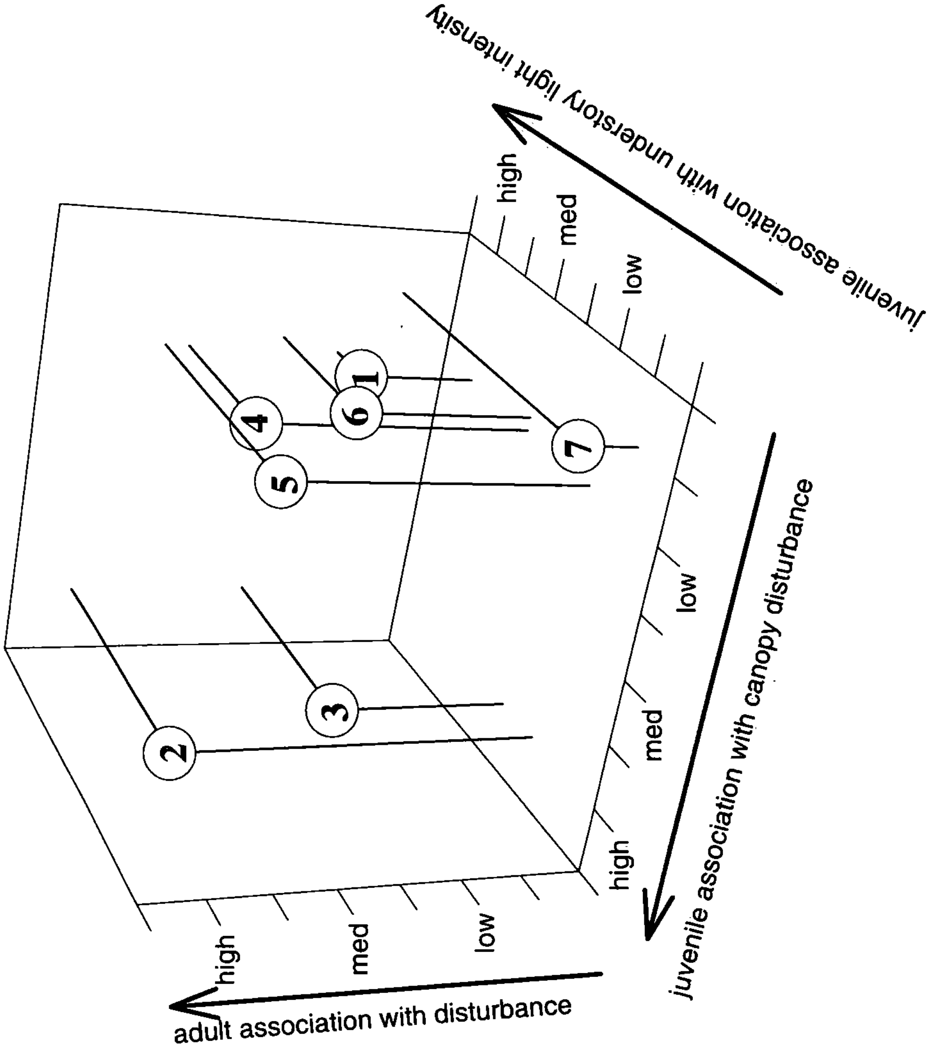

juvenile association with understory light intensity
high
med
low
juvenile association with canopy disturbance
low
med
high
adult association with disturbance
high
med
low
1
2
3
4
5
6
7

Figure 37. Idealized representation of seven species light intensity/canopy disturbance response types along three response axes. Numbering is in order of increasing shade tolerance: 1 = Highly shade-intolerant, non-gap species; 2 = Large-gap colonizers; 3 = Gap generalists; 4 = Moderately light-demanding species; 5 = Gap recruiters; 6 = Semi-shade-tolerant species; 7 = Shade-tolerant species.

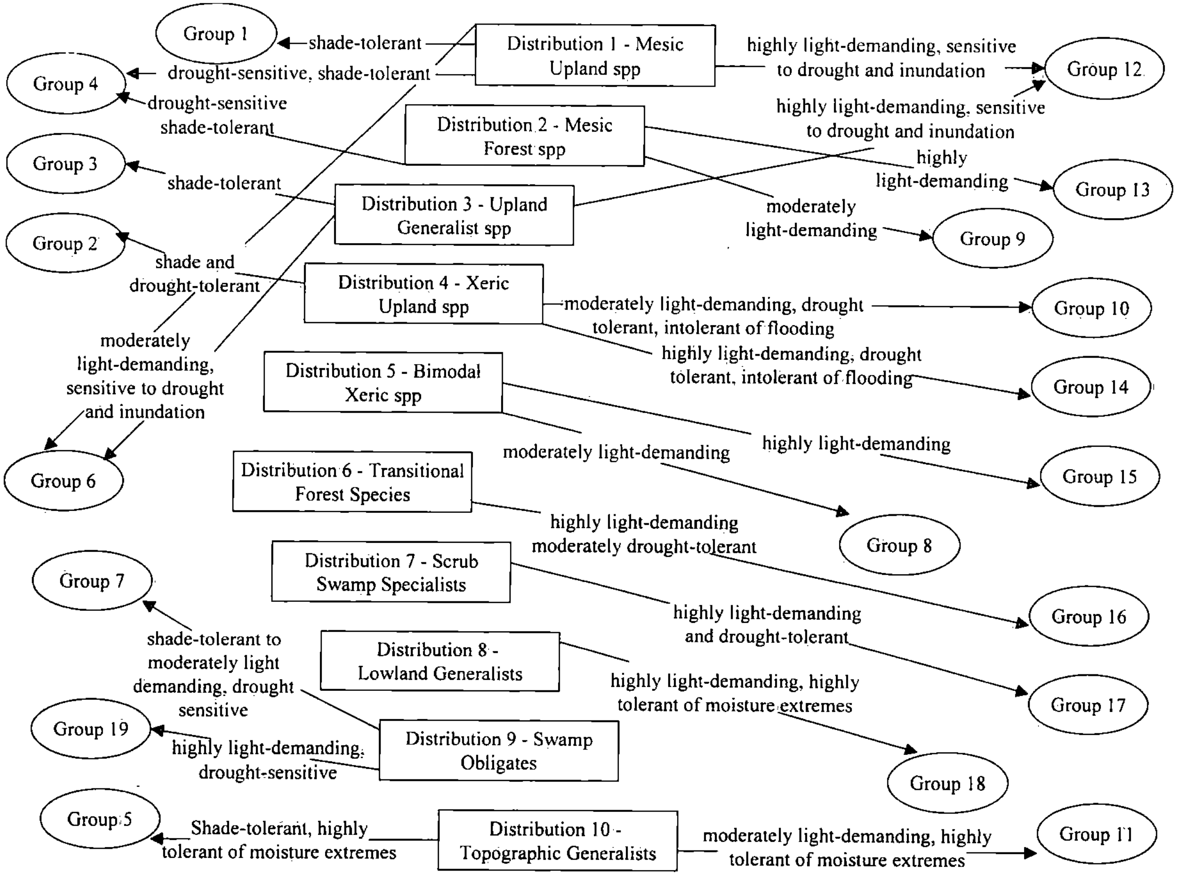

Group 1
shade-tolerant
Distribution 1 - Mesic Upland spp
highly light-demanding, sensitive to drought and inundation
Group 12
Group 4
drought-sensitive, shade-tolerant
drought-sensitive shade-tolerant
Distribution 2 - Mesic Forest spp
highly light-demanding, sensitive to drought and inundation
Group 3
shade-tolerant
highly light-demanding
Group 13
Distribution 3 - Upland Generalist spp
moderately light-demanding
Group 9
Group 2
shade and drought-tolerant
Distribution 4 - Xeric Upland spp
moderately light-demanding, drought tolerant, intolerant of flooding
Group 10
moderately light-demanding, sensitive to drought and inundation
highly light-demanding, drought tolerant, intolerant of flooding
Group 14
Distribution 5 - Bimodal Xeric spp
moderately light-demanding
highly light-demanding
Group 15
Group 6
Distribution 6 - Transitional Forest Species
Group 8
highly light-demanding moderately drought-tolerant
Group 7
Distribution 7 - Scrub Swamp Specialists
Group 16
highly light-demanding and drought-tolerant
shade-tolerant to moderately light demanding, drought sensitive
Distribution 8 - Lowland Generalists
highly light-demanding, highly tolerant of moisture extremes
Group 17
Group 19
Distribution 9 - Swamp Obligates
highly light-demanding, drought-sensitive
Group 18
Group 5
Shade-tolerant, highly tolerant of moisture extremes
Distribution 10 - Topographic Generalists
moderately light-demanding, highly tolerant of moisture extremes
Group 11

Figure 38. Ecological groupings of forest tree species studied at Tikal, Guatemala. Groupings reflect patterns of species occurrence along topographic/edaphic and light/disturbance gradients, as depicted in Figs. 26-35 and summarized in Appendix 1.

Supergroup 1: Shade-tolerant species able to germinate and persist as saplings beneath intact upland forest canopy.

Group 1 - Species negatively impacted by excessive inundation and drought, with optimal survival and colonization in mesic upland areas.

Group 2- Tolerant of excessive drainage, seasonal moisture stress and shallow soils, and displaying highest survival and/or competitive advantage in upper regions of slopes and other upland regions with excessively drained, shallow, rocky soils (i.e. Mayan temple mounds). These species show decreased survival ability/competitive advantage in mesic upland areas, and drastically lower survival in areas of prolonged inundation, particularly Scrub Swamps (which also experience intense seasonal drought).

Group 3 - Species reaching optimal densities in all upland regions, but with strongly negatively impacted survivorship only in areas of extreme seasonal drought and/or prolonged inundation (Scrub Swamps, True Swamps).

Group 4 - Highly drought-intolerant species, tolerant of some degree of soil saturation. The majority of these species are typical of wetter climates and are only marginal members of the Tikal tree community.

Group 5 - Highly tolerant of moisture extremes.

Supergroup 2: Moderately light-demanding species - germination and/or sapling persistence under intact or light forest canopy.

Group 6 - Able to colonize small to large gaps in upland forest, moderately sensitive to drought and inundation, showing significantly higher densities/survival ability in Mesic Upland, Hillbase and Sabal forest.

Group 7 - Adapted to conditions of perennial soil saturation and inundation, and highly intolerant of edaphic drought.

Group 8 - Able to reproduce under light canopy cover (>10% opening), highly resistant to drought and inundation; not adapted for high success in colonizing tree fall gaps in upland areas.

Group 9 - Able to reproduce in large gaps in Upland forest, small to large gaps in lowland forest, or under very light canopies (>20% open) in the absence of tree fall gaps. Not adapted for high competitive success against true pioneer species in large gaps in Upland areas (due to slower growth rates), but are more successful in lowland sites that are marginal for these true pioneer species. These species are sensitive to seasonal moisture stress but not inundation.

Group 10 - Highly drought tolerant, intolerant of inundation.

Group 11 - Highly tolerant of moisture extremes.

Supergroup 3: Extremely shade-intolerant species - germination and/or seedling survival very low beneath canopy cover.

Group 12 - Successful colonists of moderate-sized or large gaps in upland areas (fast growth, wide seed dispersal), sensitive to edaphic drought and inundation.

Group 13 - Sensitive to drought, tolerant of inundation.

Group 14 - Highly resistant to drought stress and shallow rocky soil, but intolerant of inundation. These species show restricted ranges along environmental gradients and low abundance.

Group 15 - Highly tolerant of drought, moderately tolerant of inundation.

Group 16 - Tolerant of most edaphic conditions, but with low survivorship under the most extreme edaphic drought conditions of Low Scrub Swamp.

Group 17 - Highly shade-intolerant (requiring canopy opening >20% for regeneration), tolerant of extreme edaphic stress (drought and inundation) but with lower competitive success in perennially mesic areas; not adapted for high success colonizing tree fall gaps in upland or mesic lowland areas (due to slow growth, small adult stature, patchy or localized seed dispersal).

Group 18 - Highly shade-intolerant, requires very large gaps or other disturbance events for colonization of uplands; tolerant of full range of edaphic extremes.

Group 19 - Highly sensitive to drought stress, highly tolerant of inundation.

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All illustrations are referred to as figures. They must comply with the following standards: Photographs should be sharp, with good contrast, and printed on glossy paper, or the originals submitted. If the background of photographs (especially those of specimens) is not desired, amberlith should be cut out and used to cover the background. Drawings should be made with dense black waterproof ink on quality paper or illustration board. All figures should have a cover sheet. All lettering will be medium weight, sans-serif type (e.g. Futura Medium, News Gothic) in cutout, dry transfer, or lettering guide letters. Make allowance so that after reduction no lower case letter will be less than 1 mm high (2 mm is preferred) nor any capital letter greater than 5 mm high. The maximum size for figures is 9" x 14" (twice BULLETIN page size); figures should not be less than typepage width (4½"). With soft lead pencil, on the back of each illustration, designate the top and identify each by author's name, manuscript title, and figure number.

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Managing Editor of the BULLETIN
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Phone: 352-392-6724
FAX: 352-846-0287
email: rjbryant@flmnh.ufl.edu