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A History of Plant Ecology in Belize

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Abstract

This paper recounts the history of plant collecting and plant ecology in Belize and describes current work in these fields. Scientific plant collecting and systematic description of vegetation in Belize began in the late nineteenth century. By the early twentieth century collecting flourished, due to the work of Peck, Schipp, and others. In the 1920s and 1930s, Hummel, D. Stevenson, Bartlett, and Lundell gave the first scientific descriptions of Belize's vegetation, while N. Stevenson articulated the basis for a profound and useful understanding of vegetation in Belize. This was realized in the great work, *Land in British Honduras*, published by Wright, Romney, Arbuckle, and Vial in 1959, in which principles of soil-moisture-plant relationships were used to describe and map 77 vegetation types in Belize. Up to that point maps had shown no more than seven vegetation types in the country. Lundell, N. Stevenson, and Smith carried out the first quantitative plot studies in Belize in the 1930s and 1940s, followed by a hiatus of nearly 40 years, after which such work became widespread, with the added purpose of recording vegetation dynamics. From the beginning plant ecologists in Belize have speculated on the effects of land use by the ancient Maya on today's vegetation, but research has been little and inconclusive. Beginning in the 1970s, quantitative research focused on soil-plant relationships. Furley described the soil catena and its effects on vegetation structure and species richness. Kellman did experiments on the long-standing question of the relationship between forest and savanna, and showed how forest could invade savanna. Kellman then studied gallery forests within the savanna, demonstrating how unique features of these forests sustain more species richness than expected in habitat fragments. Belizean plant ecology was much advanced in Central America before work in

other countries of the region began to catch up. With its extensive natural vegetation and healthy populations of large herbivores and top carnivores, Belize could lead in research on relatively intact tropical ecosystems.

Introduction

Flying into Belize today you see beneath your plane a mosaic of natural vegetation types. Terrestrial travelers to this Central American country in the nineteenth and early twentieth centuries also noticed these patterns. They suggested that variations in soil and moisture explained them. But they also knew about the ancient Maya, and so they proposed historical explanation for vegetation pattern as well. These early observers wanted to understand plants and vegetation to help them better exploit and conserve Belize's natural resources. We still seek this knowledge, and for the same reasons. Thus there is a long history of studies on floristics and plant ecology in Belize (Table 1), motivated by the need to use and conserve Belize's natural heritage, and enlivened by striking variation in vegetation cover and a dramatic past of land use and disturbance. I recount that history of research in this essay. I include all the relevant work I know of, but I exclude the large body of work on mangroves, more capably reviewed by Zisman (1997), and the strictly silviculture studies.

The history of plant ecology in Belize includes three related types of inquiry, each of which began early and continues but achieved sequential prominence. The first line of inquiry concerns what plants are present, answered by collecting plants and compiling floras. The second concerns the patterns formed by those plants, answered by distinguishing and mapping vegetation types. The third line of inquiry, prominent today, concerns the processes underlying those patterns, answered by comparative, experimental, and long-term studies. This essay begins with a brief description of the environment of Belize; then pursues these subjects of plant collecting, vegetation patterns, and ecological processes; and ends each subject with a description of contemporary research in that area. It will be seen that certain themes have dominated plant studies in Belize, namely: classification of vegetation types to guide land uses and conservation; the impact of the Ancient Maya on present-day vegetation; and plant-soil-moisture relations, especially as they influence the forest-savanna boundary. These themes have developed in the context of broad issues in ecology, and they have advanced not only our understanding of Belize's ecology but those broad issues as well.

Table 1.1: - Chronology of events in Belizean plant collecting and ecology. Dates given for studies are publication dates; fieldwork obviously occurred earlier.

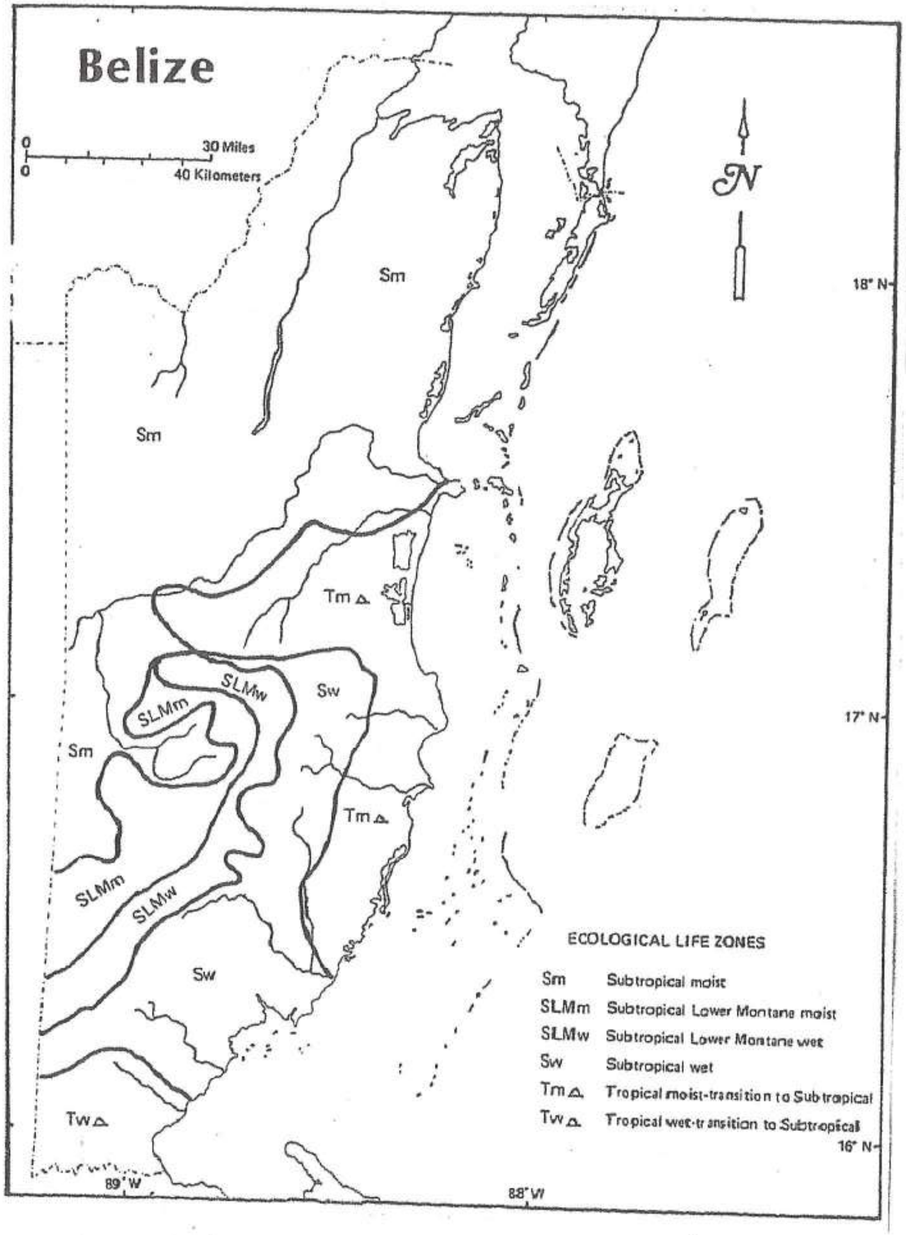
DATE	EVENT	REFERENCE
1883	Morris describes "pine ridge", "broken ridge", and "cohune ridge"	Bartlett 1935
1905-1907	Peck collects 900-1000 plant specimens	Spellman et al. 1975
1925	Hummel describes forests of Belize	Hummel 1925
1928	D. Stevenson classifies Belize vegetation into seven types	Stevenson 1928
1929-1937	Schipp collects c. 11,700 specimens	Lowden 1970
1931-1958	Gentle collects largest number of different, individual plants of any botanist in Belize	Spellman et al. 1975
1933	First vegetation map of Belize, showing seven classes, probably work of N. Stevenson	Anonymous 1935
1936	Standley and Record publish a flora of Belize	Standley & Record 1936
1937	Lundell publishes a classification of vegetation of Petén	Lundell 937
1938	N. Stevenson establishes principles for a useful classification of vegetation	Stevenson 1938
1940	Lundell carries out plot studies on Vaca Plateau	Lundell 1940
1940	Charter suggests successional sequence from forest to savanna	Charter 1940 in Beard 1953
1942-1945	N. Stevenson and Smith carry out plot studies in Stann Creek and Cayo	Stevenson 1942, Smith 1945a,b
1959	Wright, Romney, Arbuckle, and Vial publish country-wide description of soil-moisture-vegetation relationships and a map showing 77 vegetation types	Wright et al. 1959
1972-1975	Missouri Botanical Garden collects intensively	Spellman et al. 1975
1974	Furley explains details of topography-soil-moisture-vegetation relationships	Furley 1974a, 1974b, 1976
1978	Lambert and Arnason describe vegetation	Lambert & Arnason

	on Maya ruins	1978
1979-1989	Kellman shows how forest can invade savanna with soil nutrient changes	Kellman 1979, etc.
1991-1996	Kellman describes effects of fragmentation from studies on gallery forest	Kellman et al. 1996, etc.

Environment of Belize

Belize, formerly known as British Honduras, lies roughly at 15°-19° N and 87°-90° W. It covers 22,963 km^2 (9185 mi^2) of land area (including the cays). Belize has mostly a subtropical environment, including four subtropical life zones: *moist, wet, lower montane moist, lower montane wet*; and a smaller area of two tropical life zones: *moist-transition to subtropical, wet-transition to subtropical* (Fig. 1). Rainfall declines from 4000 mm (160 in) per year in the south to 1500 (60 in) per year in the north. Hurricanes periodically strike the country (see below). The northern part of Belize is mostly a low-lying, former seabed, gradually raised from the ocean during the Pliocene (2-13 million YBP) and now supporting a mosaic of limestone and sandy soils. The south of the country also has low-lying, limestone and sandy areas but is dominated by the Maya Mountains, rising to 1124 m (3709 ft), and by the Mountain Pine Ridge, the oldest land surface in Central America. These mountains consist of quartzites, shales, and slates, with granitic intrusions, dating from the Carboniferous and Permian (c. 250-300 million YBP). Karst foothills surround the southern mountains. As we shall see, these gradients in rainfall, topography, and soil support a variety of vegetation types. (The above is mostly from Hartshorn et al. [1984] and Wilson [1995].)

Figure 1.1



Plant Collecting and Floras in Belize

Plant collecting in Belize for scientific purposes began in the nineteenth century, as described in a history of collecting in Belize (Spellman et al. 1975, and Bartlett, 1932). However, less than 20 specimens had been collected before 1883, while few were added in the rest of that century. Between 1905 and 1907 Morton Peck collected more than 900 species for Harvard University. His grass collections indicated the West Indian affinities of Belize's flora (Bartlett 1932). Twenty years passed before the next serious collectors, Samuel Record in 1926, Cyrus Lundell in 1928-1929, and J.S. Karling in 1928, worked in Belize. Lundell's was the first collection constituting an adequate flora of any particular area of Belize (Honey Camp in the present Freshwater Creek Forest Reserve).

William A. Schipp was an especially important early collector (Lowden 1970). Schipp was born in Australia in 1891 and made his living collecting plants for subscribing herbaria in the U.S. and Europe. He collected in Belize from 1929 to 1937 and sent specimens to Paul Standley, at the Field Museum of Natural History, Chicago, and other specialists for identification, resulting in 154 taxa new to science, including two new genera, *Schippia* Burret and *Schizocardia* A. C. Smith & Standley (= *Purdiaea* Planchon). Schipp (1933-1934) published a catalogue, *Flora of British Honduras, Pricelist of Seeds & Material*. In 1970 there were 11,702 plus specimens collected by Schipp known to be present in 11 herbaria, including 1934 specimens in the Field Museum. Based on the notes attached to the 1462 Schipp specimens in the Belize Forest Department Herbarium, Lowden (1970) was able to map Schipp's collecting trips in Stann Creek and Toledo Districts in 1929-1935.

Between 1931 and 1951, Percy Gentle, a Belizean, collected amassing nearly 10,000 specimens, the largest number from different individual plants of any botanist in Belize (Schipp's total included multiples collected from one plant). Gentle's contributions deserve more detailed presentation, but I have no other information on him. An effort such as Lowden (1970) made for Schipp would produce an interesting account of Gentle's achievements. Many other botanists have collected in Belize (Spellman et al. 1975), but a great deal of the work has been done by collectors from the Missouri Botanical Garden, St. Louis, where the best collection of Belize plants is housed. Systematic collecting, by Michael Balick and Rosita Arvigo, continues, in order to screen Belize's plants for chemicals active against AIDS and cancer.

Schipp's catalogue was an informal flora of the lower elevations in the Stann Creek and Toledo Districts. It was soon superseded by Standley and Record's (1936). Beginning in 1946, volumes of the *Flora of Guatemala* began appearing and were intended to include all species known in Belize. From these and other sources, Spellman et al. (1975) listed the dicots, Dwyer and Spellman (1981) the monocots, and Hartshorn et al. (1984) the trees of Belize. Currently, the massive, gradually issued, *Flora Meosamerica* will include Belizean species.

Numerous authors have presented species lists for local areas or study plots in Belize. Lundell (1940) published lists of species according to life form in the Vaca Plateau and Mountain Pine Ridge. Lists have also been published for Shipstern Nature Reserve (Meerman 1993), Columbia River Forest Reserve (including a surprisingly large number of species new to Belize, as well as three new families (Holst 1993a, 1993b, and Smith 1995), Bladen Nature Reserve (Iremonger & Sayre 1994, Iremonger et al. 1995), and the area near Belize's highest elevation, informally known as Doyle's Delight (Allen 1995). This last list included liverworts, lichens, mosses, ferns and allies, as well as higher plants, and it recorded many new species to Belize. 'M Balick (unpublished) has listed and mapped the collection sites of plant species endemic to Belize.'

All this plant collecting and compiling of species lists has helped researchers see patterns in Belize's vegetation, leading to the descriptions of vegetation types, classification schemes, and vegetation mapping that I discuss next.

Studies of Vegetation Patterns in Belize

Vegetation types and their classification

Daniel Morris, in 1883, wrote the first description of Belize's vegetation that the researcher has seen (in Bartlett 1935). In his book, *The Colony of British Honduras*, Morris described three forest types: "pine ridge", characterized by *Pinus caribaea*; "broken ridge", a broadleaf forest of particularly uneven canopy; and "cohune ridge", a broadleaf forest with many tall *Attalea cohune* Mart. palms (*Orbignya cohune* (Mart.) Dahlgren ex Standl (Henderson et al. 1995). The term "ridge" means forest in Belize and implies nothing topographical, although it must derive from some early perception of the uplands as distinct from the lower-lying rivers along which early Belizeans tended to travel. Whatever the nomenclature, describing vegetation types goes hand-in-hand with attempts to classify those types into a system that shows relationships among them. For instance, Morris (1883) said that broken ridge was an intermediate type between the other two. Then in 1928 Duncan Stevenson (1928), Belize's Deputy Conservator of Forests, divided Belize's vegetation into five main classes (with subclasses): 1) mangroves, 2) savannas (wet and dry), 3) pine forests, 4) primary rain forests (swamp, intermediate, advanced, mountain), and 5) secondary rain forests. Standley and Record (1936) also tried to provide fuller descriptions of Stevenson's five classes. These efforts, however, certainly did not do justice to the variety of vegetation types in Belize. '(Hummel, [1925] and Burdon, [1932] also described Belize's forest vegetation, but I have not seen those documents.)'

Indeed, was it possible to classify vegetation containing so many plant species and in combinations that often varied gradually across the landscape? The botanist Harley Harris Bartlett (1935) confronted this problem in Belize during the great debate between those who viewed the vegetation in a particular area as a collection of species responding individually to the environment (Gleason, 1926) and those who viewed it as a community of interdependent species (Clements, 1936). Emboldened by the ability of local people to recognize and name vegetation types, and the obvious connections between those types and physiography, Bartlett (1935) declared that classification was possible on the basis of dominant species.

Cyrus Lundell was the first to classify regional vegetation. His scope ranged from the whole of the Yucatan Peninsula (south to Sibun River), to the different vegetation types in a landscape, to the details of forests differing largely in species composition along a local topographic gradient. Using physiographic and climatic variables Lundell (1934) divided the vegetation of the Yucatan Peninsula into five regions. Most of the Belize section was included in his "Eastern Coast" region, with just a sliver along Belize's western boundary belonging to the "Northern Petén" region. Unfortunately, in his monograph he only discussed the three regions not pertaining to Belize. Likewise, his monumental *The Vegetation of Petén* (Lundell, 1937), concerning the department of Guatemala that borders Belize, is not about Belize, but its detailed qualitative descriptions of different vegetation types, including physiognomy, species, successional processes, and topography-soil-vegetation relationships, are useful for Belize. Lundell adopted the locally used system in which a vegetation type was named by adding "al" to the name of a dominant species, for example, *ramonal* where the ramón tree (or breadnut, *Brosimum alicastrum*) was common. This system was analogous to the European system of adding "etum", to produce, for example, *pinetum*.

However, Lundell did focus some of his work on Belize. As mentioned, he collected at Honey Camp; he seems to have been the first to do quantitative plot studies of vegetation in Belize (see below); and in 1945 he summarized knowledge of vegetation in Belize. Lundell (1945) described the similarity between the forests of northern Belize and those in northern Petén and southern Quintana Roo and Campeche, the similarity between Belize's savannas and those in Florida and Cuba, patterns of endemism and discontinuous distributions, and the major vegetation types, with their most characteristic species. Despite there attempts, classification of Belize's vegetation was still rudimentary.

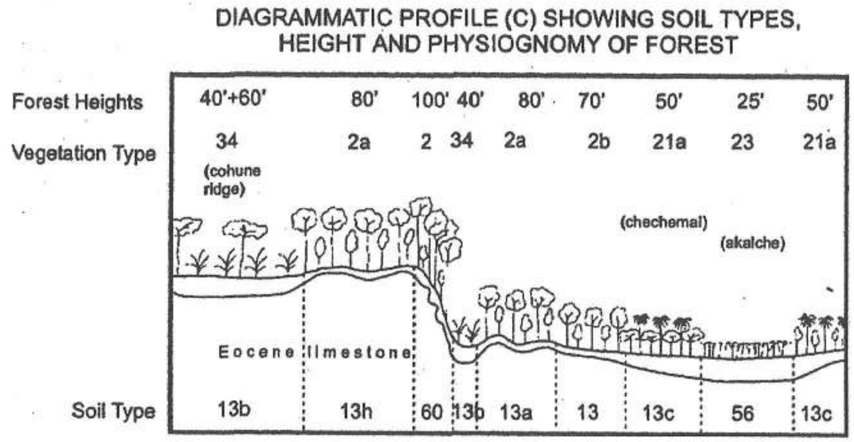
Neil Stevenson, Conservator of Forests (and not to be confused with D. Stevenson), did not revise the still simple vegetation classification for Belize, but his work contributed to its later, tremendous improvement. He wrote the first comprehensive treatment on the environment of Belize. Stevenson recognized the strong links among soils, moisture, and vegetation, and his "The evolution of vegetation survey and rural planning in British Honduras" (Stevenson 1938) contains geology, topography, rainfall, and simple vegetation maps of Belize. Stevenson knew that the best uses for land could be planned from knowledge of soils and vegetation, and to obtain an overview of the country he collated Forest Department ground surveys of topography and vegetation (using the "al" classes mentioned above). He described these difficult surveys in a poorly accessible country, for which contemporary maps still showed a large area of *terra incognita*. To further the process of classification Stevenson also led quantitative studies on particular forest types (see below). Other contributions by Neil Stevenson were collecting the type specimen of the valuable rosewood, *Dalbergia stevensonii* (Standley, 1927), and writing about the species himself (Stevenson 1927a); working on mahogany (*Swietenia macrophylla*) silviculture (Stevenson 1927b); and writing on the ecology and management of the cohune palm (Stevenson 1932). But his largest contribution, was the conceptual framework on vegetation survey and rural planning, in which he linked geology, topography, soils, moisture, and vegetation, for this is much the same framework supporting the great landmark of Belizean plant ecology published by Wright *et al*., in 1959.

In 1959 Charles Wright, D. H. Romney, R. H. Arbuckle, and V. E. Vial published *Land in British Honduras*. Its goal was to describe the agricultural potential of Belize. The first sentence they wrote was:

"We, the members of the team who made this Survey, have derived great pleasure from our task", and they do seem to have applied a loving and industrious passion to their work. This well-written book contains an amazing amount of information, enlightening maps and diagrams, and interesting perceptions, all based on intimate acquaintance with Belize. Following earlier workers, Wright et al. (1959) emphasized the importance of soil-moisture-plant relationships, and they thoroughly discussed and illustrated the geology, soils, and climate of the country. They contributed so much to plant ecology because they used natural vegetation to indicate agricultural potential, and thus took great pains to describe, classify, interpret, and map Belize's vegetation types. To get a systematic view of the distribution and relationships among topography, soil, and vegetation, Wright and his colleagues made cross-country traverses on foot, and they analyzed aerial photographs.

Wright et al. (1959) based their classification on the life zone system used by Holdridge for Guatemala (Holdridge no date, in Wright et al. (Ibid), the physiognomic system used by Beard (1944) for the neotropics, and patterns they saw that distinctively reflected differences in soil type and moisture in Belize. The result was 18 main classes, which, with sub-classes, amounted to a total of 77 varieties. These included 50 types of broadleaf forest (subdivided according to the abundance of "lime-loving species", degree of deciduousness, and canopy height), 3 types of shrubland, 7 types of savanna, 14 types of marsh and swamp, 2 types of littoral forest, and cohune palm forest. Each of these 77 types was described in terms of characteristic height, dominant species and plant growth form, and soil type and moisture. To illustrate the basis of their scheme, and help the reader identify types in the field, they presented eight profile diagrams showing gradients of topography, soil types, and vegetation types, with the height and physiognomy of characteristic plants (Fig. 2). Wright et al. (1959) also provided a cross-referenced list of scientific, Creole, Maya, and Spanish names of trees in Belize.

Figure 1.2: A Topography-Soil-Vegetation Profile Diagram



Land in British Honduras (1959) was the great leap forward for plant ecology in Belize. However, another vegetation classification scheme was devised by Iremonger and Brokaw (1995) to use in determining which vegetation types were under- or poorly-represented in Belize's system of protected areas. These ecologists wanted a scheme that was readily understood by the international conservation community. They used contemporary terminology and took concepts from the classification system adopted by UNESCO (Mueller-Dombois & Ellenberg 1974), while relying heavily on Wright et al. (1959) and their own field experience. Their system was hierarchical and organized like a taxonomic key. It first distinguished among forest, scrub, and herbaceous communities, then subdivided these according to water table, soil, species, and additional structural details. The result was 51 vegetation types, including 36 forest, 9 scrub, and 6 herbaceous types. Each was described in terms of height and dominant plant life form and species, with soil descriptions from Wright et al. (1959).

Others have classified particular groups of vegetation types. Rejmánková et al. (1996) distinguished types of herbaceous wetlands in Belize, based on physiochemical site characteristics, soils, and plant species and stature, and the University of Edinburgh is currently classifying savanna vegetation in the Rancho Dolores area. Another approach has been to classify in detail the variety of types in a certain locale, including: Vaca Plateau and Mountain Pine Ridge (Lundell 1940), Lamanai ruins (Lambert & Arnason 1978), Cockscomb Basin (Kamstra 1987), Community Baboon Sanctuary (Horwich & Lyon no date), Rio Bravo Conservation and Management Area (RBCMA) (Brokaw & Mallory 1993), Shipstern Nature Reserve (Meerman & Boomsma 1993), and Bladen Nature Reserve (Iremonger & Sayre 1994). Both the local and the country-wide classification systems have been used to map vegetation, a unified subject treated in the next section.

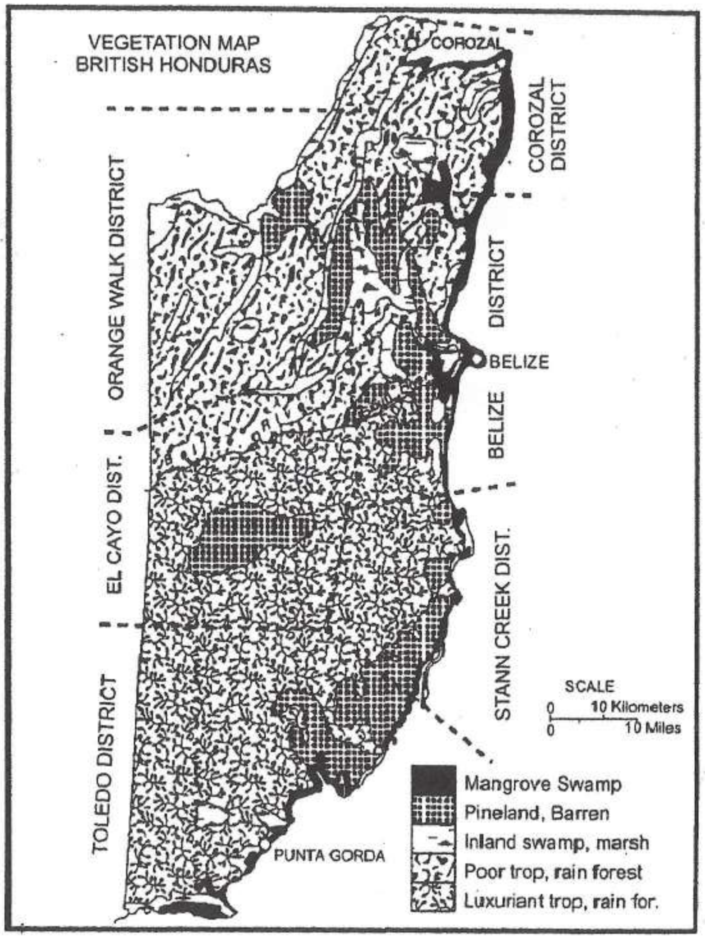
Vegetation maps

There have been three important vegetation maps published for Belize, appearing in 1933, 1958, and 1995 respectively. The 1933 map seems to have resulted from the foot surveys described by Neil Stevenson (1938), and it was probably produced by him. It was published by the Surveyor General's Department, British Honduras. This map showed the distribution of seven vegetation types. These were the main and sub-classes of vegetation as described by D. Stevenson (1928), slightly recombined and with the class "second growth forest" apparently replaced by "existing or abandoned cultivation". A large area in the south of the country was left blank on the map and inscribed with "probably advanced and mountain forest". The scale was accurate in some places, with polygons less than a scale mile across in some dimension. This map seems to have been re-published at least three times, each time altered according to the author's interpretations and intentions rather than on the basis of substantial new information.

Neil Stevenson (1938) presented a simplified version of the 1933 map in his paper on vegetation survey and rural development. He lumped polygons by collapsing the seven vegetation types in the previous map to four, while retaining the additional class of "existing and abandoned cultivation". The blank area was now marked "unexplored". Lundell (1945) simplified the map again, showing only four types of polygons corresponding to four vegetation classes with new names (mangrove swamps, pinelands and barrens, inland swamps and marshes, rainforest). Lundell apparently wanted to show potential natural vegetation, for he did not show cultivated areas. The

"unexplored" area was at last classified, as quasi-rainforest and rainforest. Finally, Victor Shelford (1963) in a summary of his career's work, *The Ecology of North America*, presented yet another version of the 1933 map (Fig. 3). This version was modified from Lundell's (1945) map by slightly simplifying Lundell's polygons and using his vegetation classes, except that "quasi-rainforest and rainforest", which had been used for upland broadleaf forest throughout the country, was divided into "poor tropical rain forest" in the north and "luxuriant tropical rain forest" in the south.

Figure 1.3: Simple Vegetation Map of Belize



The map of 1958 was based on Wright et al. (1959), and, like the book, was a great leap forward: from 7 to 77 vegetation types mapped. The map, based on ground traverses and aerial photographs, was finely detailed; many polygons throughout the map had areas with one dimension less than 0.5 scale mile. And it was beautifully and clearly rendered, such that the vegetation types are easy to distinguish. The goal was to illustrate potential natural vegetation as an indicator of agricultural potential, thus cultivated areas were not shown. The 1958 map was the first and most accurate of the three.

The 1995 map on the other hand depicted Iremonger and Brokaw's (1995) classification. It was based on the 1958 map plus satellite imagery and detailed information for some local areas. Developed for use in conservation planning, it showed actual, not potential, vegetation, as well as cultivated and urban areas. The distributions of 49 of the 51 vegetation types in their classification were shown, leaving out two herbaceous communities occurring in small patches. The boundaries of protected areas were overlaid on this map, enabling the planners to calculate with GIS the amount of each vegetation type that was protected.

There are several other vegetation maps of local areas in Belize: Lamanai ruins (Lambert & Arnason 1978), the Cockscomb Basin (Kamstra 1987), the western part of the RBCMA (Brokaw & Mallory 1993), the Community Baboon Sanctuary (Horwich & Lyon no date), and Bladen Nature Reserve (Iremonger & Sayre 1994). These are also the sites of quantitative descriptions of vegetation.

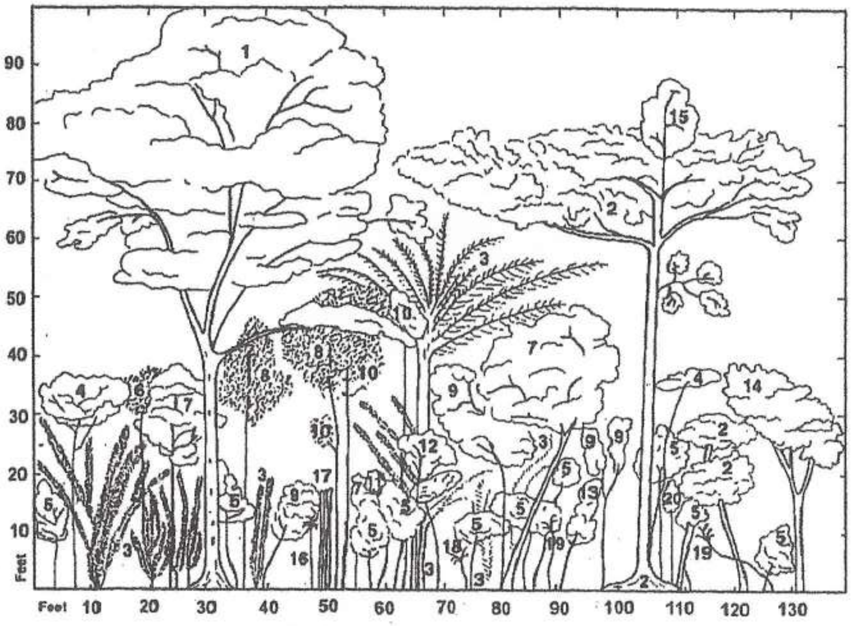
Quantitative vegetation plot studies

In the early days, Forest Department surveyors recorded topography and dominant species while they hiked along forest trails, noting direction with a Boy Scout compass and estimating distance by travel time (Stevenson 1938). Then about 1940 Lundell and Neil Stevenson, independently, carried out the first quantitative plot studies in Belize.

Lundell (1940) was interested in plant geography, local variation in forest structure and composition, and the environmental legacy of the ancient Maya (see below). He recorded the species and diameters of trees in belt transects (479-1829 m^2) in broadleaf forests at valley, hillside, and hilltop sites near Valentín (a few kilometers from Caracol) on the Vaca Plateau, and in a belt transect of 11,163 m^2 in pine ridge near San Agustín (now DaSilva) in the Mountain Pine Ridge. The Valentín studies quantified the existence of relatively taller forest with large palms in the deeper, moister soil of valleys, a characteristic pattern in Belize (Furley & Newey 1979). Lundell (1940) states that in the valleys some emergent trees reached 60 m and that the main canopy was 25-40 m in height. Apparently, Hurricane Hattie in 1961, selective logging of the bigger trees, and post-disturbance fires have reduced this magnificent stature, for today's forest in this region is shorter (personal observation). Lundell (1940) also noted the high percentage of trees in the Valentín forest that were known only from the Yucatan Peninsula.

Neil Stevenson and his coworker J. H. Nelson Smith conducted plot studies in order to classify forest types and understand regeneration for management. About that time there was much interest in classifying neotropical vegetation (e.g., Beard 1944), and the editor of the *Caribbean Forester* was urging ecologists to carry out standardized plot studies for comparisons (Editor's Note in Stevenson, 1942). Stevenson (1942) responded with a detailed description of a 392 m^2 plot representing the *Orbignya-Dialium-Virola* association in Silkgrass Forest Reserve. His report includes information on the environment and land use history of the plot; results concerning tree diameters, vertical structure and physiognomy (Fig. 4), life forms, leaf types, buttresses, stilt roots, epiphytes and lianas (listed by hosts); and comments on seed production, floristics, and successional development. Based on the diameter-class distribution of mahogany in the plot he suggested that it had experienced a drastic disturbance about 1865 that promoted mahogany regeneration.

Figure 1.4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Smith (1945a, 1945b) reported on 14 plots (588-784 m^2) in the *Orbignya-Dialium-Virola* association, and in what he termed broken ridge, chicle, and bamboo associations, at sites in the Dry Creek area of eastern Cayo District and nearby in the Manatee area of southwestern Belize District. He provided the same type of information as Stevenson (1942), but he provided more nearly complete plant lists, and he commented on the additional subjects of deciduousness, light penetration, spatial clumping of species, and how cohune presence is negatively related to understory tree density.

After these studies were published in the 1940s there was little quantitative vegetation description in Belize until recently. Lambert and Arnason (1978) used transect data to describe plant communities in the vicinity of the Lamanai ruins, and Kamstra (1987) followed a 5.4 km transect in the eastern Cockscomb Basin recording various information on forest structure and composition. His results highlighted the effects of recent natural and human disturbance on the vegetation.

By the 1990s inventories of trees ≥ 10 cm diameter at breast height (DBH; breast height is 130 cm) in 1-ha plots had become a standard for comparing tree species richness (number of species) among tropical forests (Gentry 1988), and many have been established in Belize: in the upper Raspaculo Branch watershed (Sutton, 1991, and Brokaw, 1991), the RBCMA (Brokaw & Mallory, 1993), gallery forests in the Mountain Pine Ridge (Kellman et al., 1994), and the upper Bladen Branch watershed (Brokaw et al., 1997). Guided by Neil Bird, the Forest Planning and Management Project (FPMP), in the Ministry of Natural Resources, has established throughout Belize thirty 100 x 100 ha plots, in which all trees ≥ 10 cm DBH have been mapped, measured, and identified (Smith, 1995). The goals for all these 1-ha plots is both to describe the current forest and, after remeasurements, describe forest dynamics.

Among the 17 1-ha plots in Belize for which I have results, the number of tree stems ≥ 10 cm DBH ranged from 318 to 973 ha^{-1}, and the number of species represented by those stems ranged from 39-77 (summarized in Brokaw et al., 1997, with additional data on basal area and diameter-class distributions). The richest sites in Belize, and those with the largest trees, are in Toledo District (but with fewer species than occur in forests nearer the equator (Gentry, 1988). Currently, Keith Shawe, with the FPMP, is conducting a series of transect studies in the less understood vegetation types of Belize to evaluate their structure and species richness. An efficient method for estimating tree species richness in tropical forests was recently developed by Tackaberry et al. (1997), using the RBCMA plots mentioned above.

The past century of plant collecting and descriptive studies have produced a good understanding of patterns in Belize's vegetation. In the next section I will discuss the efforts of ecologists to understand the processes and underlying mechanisms that have produced those patterns.

Studies of Processes in Belizean Vegetation

Legacy of the Ancient Maya, Breadnut, Cohune

The surprising discovery of charcoal widespread in the soils of the Amazon basin (Sanford et al. 1985) recently alerted ecologists to the pervasive influence of past land uses on today's tropical forests (Clark, 1996). In the Yucatan area, however, ecologists have long assumed that the composition and structure of present vegetation reflected land uses of the populous ancient Maya (Barrera et al., 1977).

Duncan Stevenson (1928) considered much of the forest in Belize to be secondary, having grown up following ancient Maya agriculture. In "A biological survey of the Maya area", Bartlett (1932) stated the goal of learning to distinguish primary from secondary forest, in order that archaeologists could determine what land had been under cultivation by the Maya. Ower (n.d. in Bartlett, 1935) asserted that all limestone land had been occupied by the Maya, and that mahogany grew in old cultivated sites. All the forest in Maya area had been influenced by humans, according to Lundell (1934), and he thought that no other region in the Yucatan Peninsula showed as much evidence of ancient Maya occupation as the Vaca Plateau, with its high frequency of ancient agricultural terraces. Furthermore, he suggested that low species richness of plants and the presence of xeric-adapted species in the Plateau area might reflect ancient clearing. Maya agriculture was, of course, not confined to uplands; botanists working with archaeologists have shown from pollen cores that the ancients intensively farmed wetlands (references in Bradbury et al. 1991, and see discussion of marshes below).

Early ecologists noted the frequency of certain tree species, such as breadnut and sapodilla (*Manilkara zapota*), in the vicinity of Maya ruins, and attributed this to ancient cultivation or protection of these species (Lundell, 1934; Bartlett, 1935). Indeed, there are many plant species characteristic of ruins areas, as demonstrated quantitatively in transect studies over various substrates at Lamanai (Lambert & Arnason, 1978). However, at Tikal, Guatemala, breadnut grows as abundantly on natural substrates similar to those provided by Maya ruins as it does on ruins, thus breadnut presence on ruins may simply be an ecological response, and there is no need to invoke human purpose to explain its abundance there (Lambert & Arnason, 1982). Nonetheless, breadnut trees at Tikal appear to differ genetically from those elsewhere, suggesting that local genotype, if not abundance, is due to the ancients (Peters, 1983).

High densities of cohune palm in today's "corozals" have also been attributed to the ancient Maya, and to more recent farmers, who supposedly spared cohunes when other trees were cleared (Stevenson, 1932). However, McSweeney (1993 and 1995, concerning cohune uses) found that six comparably dense corozals at widespread locations in Belize did not share similar histories, and dense stands were not necessarily sites with a long history of farming. She argued instead that corozals develop naturally on especially fertile soils, consistent with Huston's (1994) claim that species dominance is likely on rich substrates. It has long been known that cohune mainly occurs on fertile soil, and Wright et al. (1959) suggested that cohune helps create such soil. Cohune does this both by contributing organic debris to the soil and by leaving large, deep stump holes that fill with organic matter, thereby inverting and enriching the soil profile (Furley, 1975).

Although it is certain that ancient agriculture has had a significant impact on today's vegetation, there is no study showing causal links between land uses of the ancient Maya and specific features of today's vegetation, such as the distribution and abundance of particular vegetation types or plant species (but see Peters, 2000). A definitive study is now more feasible, since archaeologists have begun focusing on settlement patterns and soil features (e.g., Fedick, 1995), and such work is underway where vegetation is relatively undisturbed since the time of the ancients (Guderjan, 1991). As suggested by the studies on breadnut and cohune, this definitive study would require good understanding of soil-plant relationships, one of the better-studied subjects in Belizean plant ecology and our topic in the next section.

Soil-moisture-plant relationships

Native farmers recognized the connection between vegetation and "types of land" in Belize (Bartlett, 1935), and the earliest scientists similarly attributed the dramatic shifts from one vegetation type to another, such as forest to savanna, and less subtle shifts, as among forest types, to soils. Morris (1883 in Bartlett, 1935) emphasized soil depth; D. Stevenson (1928) mentioned drainage; Ower (n.d. in Bartlett, 1935) emphasized parent material (limestone versus other rock); and Charter (1940b in Shelford 1963) discussed concurrent soil and vegetation development. Professor F. Hardy, of Trinidad, visited Belize in 1934 and particularly focused attention on soil and topographic properties (grain size, slope, etc.) that affect soil moisture and therefore vegetation (Stevenson, 1938). All these perspectives were integrated and applied in great detail to interpret correlations of soil with vegetation in *Land in British Honduras* (Wright et al. 1959).

Peter Furley, however, was the first to do quantitative studies on soils and vegetation in Belize. In a series of papers on catenas in the Mountain Pine Ridge, Bald Hills, and the Granite Basin area, Furley (1974a, 1974b, 1976) showed how soils, moisture, and plant community varied along the summit to footslope gradient. Summits have intensively weathered soils and the thinnest, species-poorest vegetation. Footslope soils have highest values of organic carbon, exchangeable magnesium, calcium, and potassium, and available water, and they support the highest biomass and diversity of plant species. These slope/soil features are clearly reflected by the vegetation and can be extrapolated to the larger gradient from plateau to valley bottom. After Hurricane Hattie devastated forests in 1961, Furley and Newey (1979) showed how catena effects interacted with succession at a site near Belmopan, and they emphasized the paramount importance of soil moisture in determining vegetation biomass and species diversity. His understanding of soil-vegetation relationships led Furley (1987) to warn against clearing and farming on cone karst, as leading to soil degradation. (See Baillie et al. (1991) for a description of the negative effects of slash and burn agriculture on soils and vegetation in Belize.)

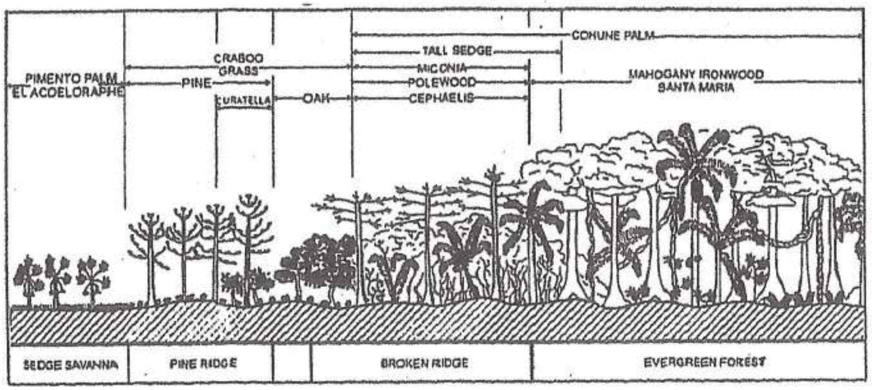
Although soil-plant relationships have been emphasized in Belizean plant ecology, nutrient cycling has been studied only by Lambert et al. (1980). Over the course of a year in a 45 year-old forest at Indian Church, they measured above-ground biomass and nutrients for the whole forest, for certain plant species, and for different plant parts, and they determined seasonal amounts and nutrient content of litter and soil. Half the nutrients in standing vegetation were in the leaves and these nutrients were returned annually to the soil, a big influx occurring at the start of the wet season, presumably when increased moisture accelerates fungal and microbial decomposition of dry season leaf fall. In a current study, O'Hara (1994) has shown that the botán palm (*Sabal maritiiformis*) has exceptionally high levels of the limiting nutrients phosphorous and potassium and that these are mineralized relatively slowly from the leaves. Thus she is studying the effect of harvesting botán leaves for thatch on community nutrient cycling and on the growth and population dynamics of the species.

Other current soil-plant studies are Furley's work on soil-vegetation relationships in the FPMP's experimental silvicultural plots in the Chiquibul forest and research he is helping lead on the savanna at Rancho Dolores. Questions about the dynamic tension between savanna and forest have led to the most fully developed and important plant ecology research in Belize.

Savanna Versus Forest

Savannas (grasslands with scattered trees) abut forests at many sites in the neotropics, posing the question of what conditions produce savanna, as opposed to forest, and whether either is transitional to the other (Beard, 1953). Stevenson (1927) thought pine savanna in Belize gradually changed to forest, which then reached a climax as cohune ridge. He though that forest in Belize had one of two origins: it was either regrowth after ancient Maya agriculture or it was the coalescence of small islands of broadleaf trees in a former pine savanna. Bartlett (1935) thought that pine savanna only changed to forest where soil was enriched and altered by overflows of silt and calcareous water, eventuating in a mahogany-sapodilla forest. The soil scientist Charter (1940a, in Beard, 1953) studied soils and vegetation in Belize and described a detailed process of soil development that he asserted led to savanna (Fig. 5). Beginning as wet alluvial deposits with river-edge vegetation of bamboo and herbaceous plants, soils in the first stages developed vertical structure and better drainage and gradually supported increasingly luxuriant forest. With later soil development, drainage is increasingly impeded, and the vegetation changes to broken ridge, to pine ridge, and finally to a sedge-grass savanna with scattered palmettos (*Acoelorraphe wrightii*). Wright et al. (1959, citing Charter, 1941) agreed with this, and thought, like Bartlett (1935), that this succession was only checked or reversed where soils were improved, as on slopes where weathering brings decomposing rock to the surface, or at sites of alluvial deposition. Curiously, Shelford seems to have completely misinterpreted Charter (1940b, in Shelford, 1963), by implying that the usual sequence, according to Charter, was from sedge-grass savanna to high forest. Finally, in the 1970s, research began to address this question.

FIGURE 1.5



Martin Kellman, in a series of papers based on observations and field experiments in the Mountain Pine Ridge (MPR), demonstrated how savannas could be invaded by broadleaf trees and become forested. Kellman (1975) showed from charcoal in the Bald Hills, carbon-dated to about 11,200 BP, that fire may have deforested this region, leading to erosion and the establishment of savanna on the resultant less fertile soils. The soil-vegetation system of savannas in the MPR has a smaller sink of, and requirement for, nutrients than forests do (Kellman, 1979, Kellman & Sanmugadas, 1985). But savanna vegetation conserves nutrients well after burning (Kellman et al., 1985, Kellman, 1985b), due to rapid immobilization in the soil and uptake by quickly sprouting graminoids and shrubs (Kellman et al., 1987). Thus savannas in the MPR survive fire, but they are more prone to burning than forest is, potentially leading to a positive feedback between fire and savanna that tends to exclude fire-sensitive forest (Kellman, 1984).

How then does nutrient-demanding, fire-sensitive forest survive on the margins of savanna, or encroach on savanna? Kellman showed that native, woody savanna plants in the MPR, such as craboo (*Byrsonima crassifolia*), facilitate colonization by forest trees, aided by a previously unappreciated source of added nutrients and possible when fire is infrequent. He transplanted seedlings of mahogany, polewood (*Xylopia frutescens*), and santa maría (*Calophyllum brasiliense*) from the forest to beneath and beyond savanna trees (Kellman, 1985*a*). Mahogany did not survive, but polewood and santa maría, which are capable of sustained slow growth in low nutrient soils, survived and grew better beneath than beyond the savanna trees (Kellman & Miyanishi, 1982). He concluded that forest establishment is multi-stage process begun by species like polewood at the fringes of woody savanna vegetation.

The key to an invasion by forest trees is that soil under native, woody species in the MPR savanna is nutrient enriched (Kellman, 1979). As explanations for this, Kellman ruled out deep rooting to decomposing rock, high cation exchange in the soil, or high water retention in the soil. Instead, the added nutrients are captured by savanna trees from nutrients dissolved in rain, locally enriching the soil (Kellman & Carty, 1986). This process can shift the balance to forest, but about 500 years of nutrient accumulation, the invasion of transitional species such as polewood, and low fire frequency are required for true forest to establish (Kellman, 1989). Within the MPR, forest may invade savanna from gallery forests along streams.

The Ecology of Gallery Forests and the consequences of Fragmentation

His work in the MPR savannas led Kellman and co-workers into detailed study of bordering gallery forests. They are usually less than 100 m wide and occur in the bottoms of small valleys where higher soil moisture and nutrient levels support trees(cf. Furley, 1976). Given their narrow width and the probability that they have been isolated as forest fragments since the Pleistocene, one would expect from the theory of island biogeography (MacArthur & Wilson, 1967) that these gallery forests would be species poor (cf. Turner & Corlett, 1996). Yet in 1-ha gallery forest plots species richness of trees is about equal to that in 1-ha plots in continuous forest in the region (Kellman et al., 1994). Nor do the gallery forests show "peninsula effects", a corollary of island theory predicting reduced species richness with distance from base to tip of habitat peninsulas (Tackaberry & Kellman, 1996).

Kellman and his co-workers set out to explain this apparent anomaly, which was all the more interesting because the ecology of the present MPR gallery forests may resemble that of the postulated forest refugia that persisted in the Amazon basin during xeric phases of the Pleistocene (Haffer, 1969). Thus understanding the factors that maintain species richness in MPR fragments could help us understand the remarkable richness of today's Amazon forests. Moreover, lessons from the gallery forests could help us conserve species in our world of increasing habitat fragmentation.

The critical question was: what factors mediate the coexistence of tree species in gallery forests that do not operate in continuous forest and would therefore compensate for pauperizing island effects? One factor is the "density effect" (Denslow, 1995): individual gallery forest trees are smaller than trees in typical continuous forest, so relatively more individuals occupy a given area, and thus, other things being equal, more species are likely to be represented in that area (Kellman et al., 1994). Another contributing factor, somewhat peculiar to gallery forest, is differential adaptation to the microenvironmental gradient along the slope from forest edge to the central stream (Kellman et al., 1996). The light gradient from edge to interior is, however, short and steep due to a special set of tree species, including many in the family Melastomataceae, that grows thickly at the edge and cuts off light to the interior (MacDougall & Kellman, 1992). These edge trees resist fire and thus prevent drastic damage to the interior forest. Nevertheless, fire does penetrate the forest in places, but this augments species richness, because it kills few large trees while providing unique seedbeds for recruitment of specialized tree species (Kellman & Tackaberry, 1993, Kellman & Meave, 1997).

Thus the factors unique to gallery forests that would promote tree species richness are the density effect together with specializations for establishment after fire, for growth and fire resistance on the forest edge, and, less importantly, for occupying different positions along the topographic gradient. Two other distinctive features of gallery forest tree communities are that a relatively large proportion of the species have fruits for bird consumption, which can provide relatively long distance seed dispersal, thus tending to augment richness in any fragment, and that a relatively small proportion are dioecious (having separate male and female plants), which could hinder pollination in fragmented populations (Kellman et al., 1996). If these same features characterized Pleistocene forest remnants they could well have harbored an unexpectedly large amount of biological diversity (Meave et al., 1991).

Looking to the future, if the long-fragmented gallery forests of the MPR have unique characteristics that tend to maintain species richness, then loss of diversity in fragments may not be inevitable (Meave et al., 1991). The gallery forests fragments are not, however, microcosms of continuous forest, because they have relatively few dioecious species and tree species dispersed by large animals, and they include specialized edge species. Kellman (1996) concluded that to conserve diversity in newly created fragments, they should not be managed as remnants of continuous forest, but, instead, managed with an understanding of the unique, diversity sustaining features of fragments. For instance, the edges of newly created fragments could be planted with the specialized edge species to seal the boundary against fires and excessive light. Conservation of fragments is also not a complete substitute for conservation of continuous forest.

Martin Kellman has also studied pine woodlands in the MPR. This and other research on processes in Belizean vegetation will be briefly described in the next section.

Other process studies on Belizean vegetation

Pine Woodlands

Pines in the MPR are a valuable timber resource, so there has been concern about the possible negative effects on pine populations of fire, broadleaf competition, and repeated nutrient removal in harvests. Kellman and co-workers showed that, within limits, these processes were not a great problem. Pine establishes after fire (Kellman, 1976); broadleaf trees tend to enrich the soil, benefiting pine, and pine competes well because it requires less fertile soils than broadleaf trees do (Kellman & Hudson, 1982, Kellman, 1976); and atmospheric nutrient inputs compensate for harvest removals (Stewart & Kellman, 1982, Kellman & Carty, 1986).

Weed composition and distribution.

Kellman studied weed seeds in soils at Central Farm to suggest methods for weed control (e.g., Kellman, 1980b). He found that there were an average of 6488 weed seeds of 54 species per m^2 to a depth of 4.2 cm (Kellman, 1974). Comparing pastures with cultivated fields, weed seeds in pastures differed somewhat in species composition and were more abundant, more species rich, more evenly distributed, and concentrated at a lower depth in the soil (Kellman, 1973, 1978). These differences in part reflected a faster turnover of weed seeds in fields, resulting from more frequent plowing, which promotes germination and exposes seeds to predation. For much the same reason cultivated fields have fewer and different weed species than are found at sites of swidden agriculture (Kellman & Adams, 1970). Taking a broader view, different scales of variation in the weed flora can be recognized: intra-regional, as influenced by soil and land use; inter-regional, as influenced by biogeographic history; and pan-tropical (Kellman, 1980a; Kellman & Adams, 1970). Inter-regional differences are being swamped as pan-tropical elements spread in the wake of intensive agriculture.

Marsh Types and Marsh History

Marshes (herbaceous wetlands) in Belize have only recently been studied. According to Rejmánková et al. (1995, 1996) there are three basic types, characterized respectively by a rush (*Eleocharis cellulosa*), a sawgrass (*Cladium jamaicense*), and a cattail (*Typha dominguensis*). Because these marsh types consistently differ in soil type, water depth, and water chemistry, one can predict future, and interpret past, changes in these wetlands resulting from changes in sedimentation, water level, and nutrient input (Rejmánková et al., 1995). For example, increased salinity caused by rising sea level or ditching will favor *Eleocharis* and *Cladium* marshes, whereas fertilizer runoff and erosion will favor *Typha* and *Cladium* marshes. The authors suggest that the peatlands farmed by the ancient Maya were transformed by rising water to lakes and mudflats, then, after siltation and succession, changed to the present marshes. In another study, remote sensing indicated that methane emission from Belize's wetlands contributes little to global CH_4 (Rejmánková & Post, 1996).

Community plant Phenology

Plant phenology (seasonal patterns of leaf, flower, and fruit production) is a pivotal process in community ecology, because it strongly reflects climate while it strongly influences consumers (Bullock & Solís-Magallanes 1990). Two studies of phenology have been made in Belize, partly with the aim of understanding how nectar and fruit consumers are sustained through the year.

In the Community Baboon Sanctuary at Bermudian Landing, the amount of newly flushed leaves among all individuals of the common tree species tends to peak at the dry-to-wet season transition; flowering peaks mainly in the dry season, with sometimes a secondary peak after the wet season; and fruiting peaks irregularly (Horwich & Lyon n.d., Lyon & Horwich, 1996). While each fluctuates in availability, the combination of edible new leaves, flowers, and fruits was adequate at any given time to sustain the local howler monkeys (*Alouatta pigra*). Nearby, in forests of the western part of the RBCMA, community flowering of trees and shrubs exhibited a major peak in March and minor peak in August and September over a two year period (Hess 1994). Fruiting peaked in April and May the first year, but in the second year it rose in those months but then continued fairly heavily through the year, with another high in December. These variations seemed to be related to marked variation in annual patterns of rainfall. Although there were periods when little fruit was available in some parts of the forest, there was always fruit elsewhere that could sustain consumers. In particular, there were always fruiting individuals of the understory palms *Cryosophila stauracantha* and *Chamaedorea* spp. at some place in the forest.

Hurricane Effects on Vegetation

Since 1785 a storm of known hurricane strength (18 total) has struck Belize every 12 years on average, and, altogether, these have crossed nearly every part of the country. Friesner (1993) has provided a valuable account of these storms, and 15 others of possibly hurricane strength, giving (where known) storm date, strength, and path; describing resultant damage and interpreting it as a function of storm strength, topography, soil, forest type (pine versus hardwood), and particular tree species; and relating what is known about post-hurricane regeneration. The most famous of these storms was Hurricane Hattie in 1961, which damaged 4290 km^2 (1650 mi^2) of forest in a 48 km (30 mi) swath across the country (Wolffsohn, 1961; Lindo, 1968, Johnson & Chaffey 1973).

There has been little follow-up on observations of hurricane damage in Belize. However, elsewhere on the Caribbean coast and in the West Indies studies have revealed how profound are the short- and long-term effects of these storms (Walker et al., 1991). Initial impacts are dramatic, but recovery is fairly rapid (e.g., Scatena et al., 1996), because many forest organisms are adapted to these disturbances. One important consequence is that hurricanes, especially followed by fire, have repeatedly created over the centuries the sort of forest clearings where rich stands of mahogany get their start (Snook, 1997).

Conclusion

There is little published about the ecology of Belize in comparison with, for example, Costa Rica or Panama, where there have been lavish funds, facilities, and fellowships for research. But if you have read this history of plant ecology in Belize, you may agree with me that Belize was once preeminent in Central American plant ecology. And if you have visited Belize, you may also agree that it could lead today in some plant ecology fields, because Belize offers a research setting that is absent or dwindling elsewhere.

The evidence of past preeminence is clear in Shelford's *The Ecology of North America* (1963). He used Neil Stevenson's (1942) profile diagram of the *Orbignya-Dialium-Virola* association to illustrate tropical forest structure, because Stevenson's work was perhaps the first comprehensive plot study in Central America. He used Lundell's (1945) map of Belize's vegetation because Belize's vegetation was then one of the best mapped. And, even if Shelford did get it wrong, he used Charter's (1940) diagram of vegetation development from forest to savanna because scientists in Belize were then leading the field of soil-vegetation studies in the region. However, putting Shelford aside, just a quick perusal of the breadth and depth of *Land in British Honduras* (Wright et al. 1959), and of the detail in the accompanying vegetation map, should convince you that before 1960 plant ecology in Belize was preeminent on the isthmus.The evidence for potential preeminence is clear from my last visit to Las Cuevas, in the Chiquibul. During my ten days there, while going about my routine plant studies, I saw a Great Curassow, Scarlet Macaws, white-lipped peccaries, and a jaguar. You will not see any of these at the famous field stations in Central America. These animals are "The big things that run the world" (Terborgh 1988), or did until humanity overwhelmed nature. Compared with their numbers, these large consumers and top carnivores have a disproportionate effect on the vegetation. In the absence of large consumers, large-seeded trees do not get their seeds dispersed or predated, as the case may be. In the absence of large carnivores, small consumers flourish and eliminate the seeds and seedlings of some species. For these reasons, much of the forest in Central America, where these large animals have been hunted out, is indirectly but drastically being altered by humanity, without a tree being cut. But in Belize you can still study extensive ecosystems with these original parts and processes intact.

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FIGURE LEGENDS

Figure 1 - Holdridge Life Zones of Belize (Hartshorn et al. 1984).

Figure 2 - A topography-soil-vegetation profile diagram from Wright et al. (1959). Vegetation key: 2 = sapote-silion forest, 2a = sapote-silion forest variant, 2b = sapote-ramón-spice forest, 21a = botan-chechem forest, 23 = chucum-logwood-palmetto assemblage, 34 = cohune palm forest. Soil key: 13 = jolja clay; 13a = jolja clay, gravelly clay; 13b = jolja clay, dark grey-brown clay; 13c = jolja clay, mottled clay; 13h = jolja clay, gravelly clay, hill soil; 56 = chucum clay; 60 = Xunantanich rocky clay loam (used by permission of Her Majesty's Sationery Office).

Figure 3 - Simple vegetation map of Belize (Shelford 1963, used by permission of University of Illinois Press). This map was the last of several reinterpretations of a map first published in 1933, probably by Neil Stevenson.

Figure 4 - Profile diagram of a 392 m^2 plot representing the *Orbignya-Dialium-Virola* association in Silkgrass Forest Reserve (Shelford 1963 after Stevenson 1942, used by permission of University of Illinois Press).

Figure 5 - Vegetation and soil profiles showing a proposed chronological sequence of vegetation types in Belize growing on soils that develop from alluvium to a soil with poor drainage (Shelford 1963 after Charter 1940, used by permission of University of Illinois Press).