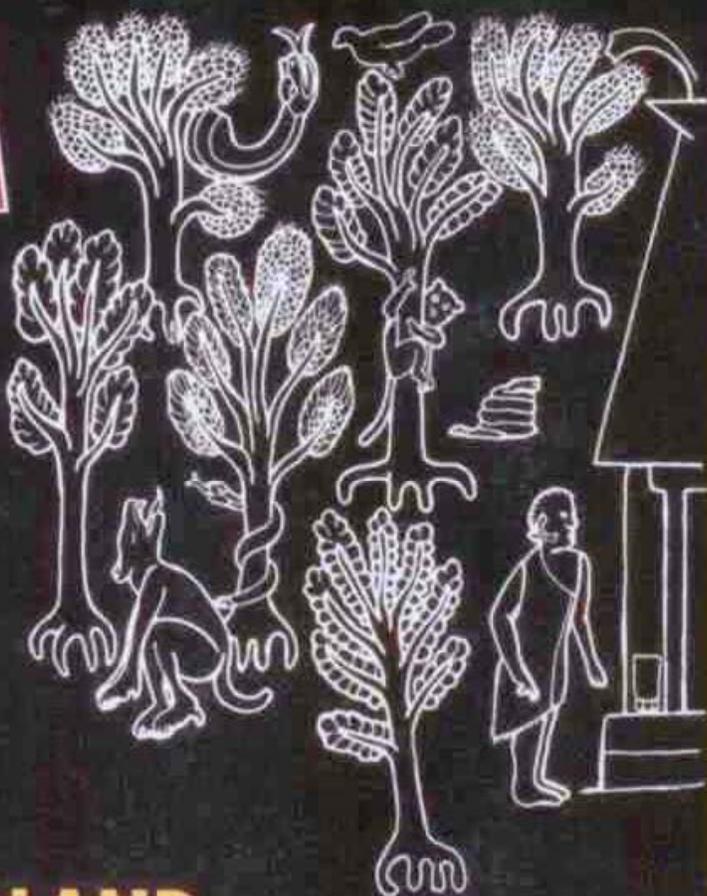


THE LOWLAND MAYA AREA

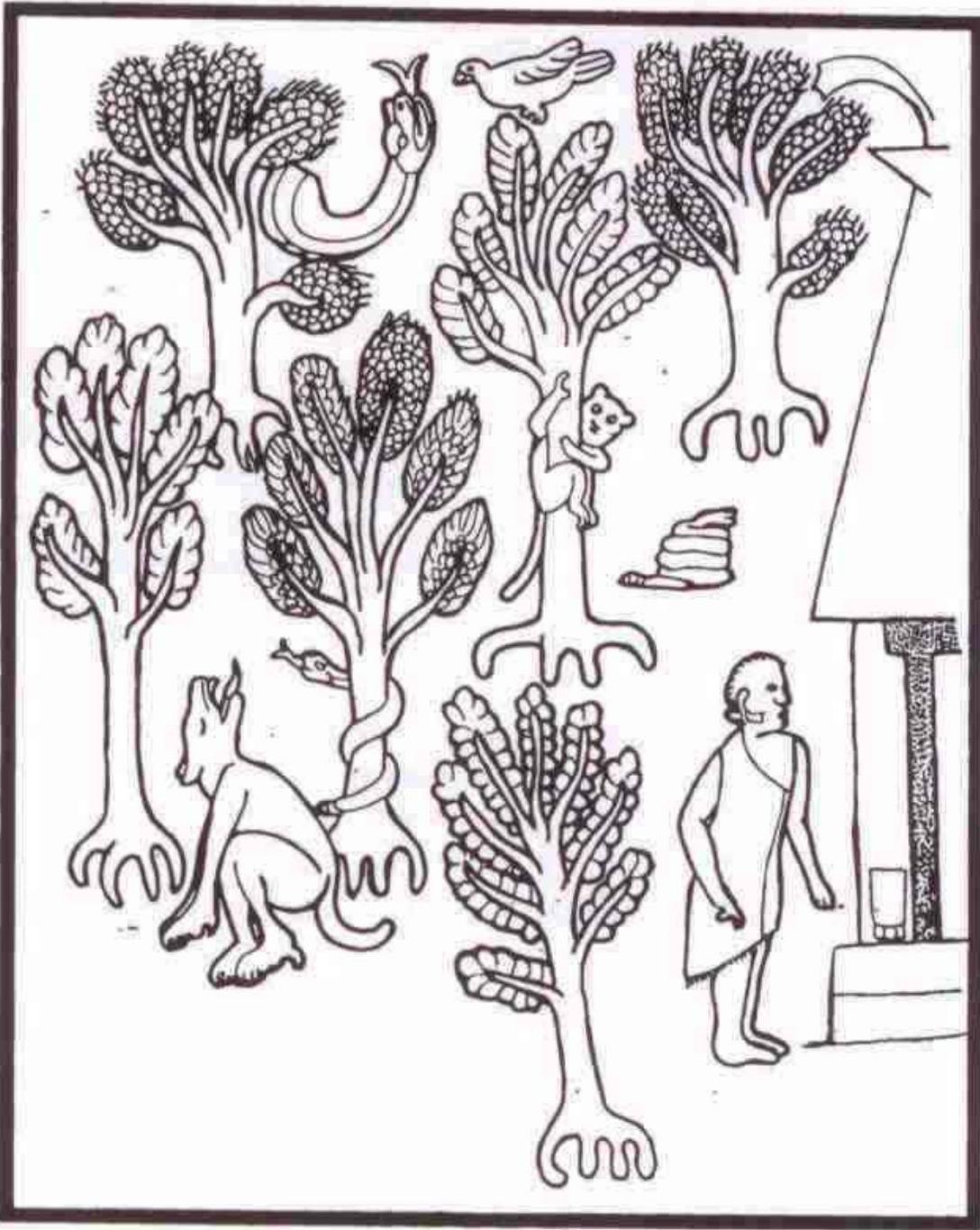


**THREE
MILLENNIA
AT THE
HUMAN-WILDLAND
INTERFACE**



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EDITORS



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PART I:
INTRODUCTION

Chapter 1

Research Challenges for the Lowland Maya Area: An Introduction

Arturo Gómez-Pompa

When I was asked to organize the 21 st Symposium of Plant Biology, I saw a great opportunity to bring together a group of scientists from different disciplines in order to address the complex topic of human-plant-environment interactions over time. My proposal was approved; this approval then provided an opportunity to explore a wide variety of topics of relevance to plant biology.

The focus of this symposium is the ongoing research of one culture, the Maya, and the geographical area that they have inhabited for more than 3,000 years. This is the second symposium that the University of California at Riverside has organized on the Maya. The last one, in 1991, was on ancient Maya agriculture and resource use; from that symposium came the outstanding book, *The Managed Mosaic* (Fedick 1996).

One question you might be wondering is the following: Why another symposium on the Maya? The Maya culture and the region in which they live have attracted the continuous attention of a distinguished set of scholars and institutions from many different disciplines over the years. This continued attraction is fully justified for several well-known reasons. The Maya, according to Coe (1984:7), were “in degree of cultural development... head-and-shoulders above the rest of the American Indians in the hemisphere.” In spite of more than 25 Mayan dialects known to exist, the Maya had an astonishing fundamental unity in their subsistence techniques, religion, cosmovision, mathematical time calculation, and hieroglyphic writing” (Coe 1984). The Maya are the best-known cultures in tropical America. Archaeological research has produced an impressive body of knowledge about the ancient Maya and their magnificent monumental centers.

The Maya civilization has captured the imagination of writers who either have exaggerated and glorified their accomplishments, or vilified their

failures (Fash 1994). The disparity of these views can be explained by the great amount of things that we ignore about the Maya culture and its environment. Although we possess a great deal of knowledge about their elites and rulers, little is known about the majority of the population—that is, the rural Maya people and their environs. These people did not leave written records of their lives and their agricultural systems and resource management activities did not leave clear archaeological clues regarding the plants and animals they used, or their techniques and methods of food production. But it was the technological innovations of these people that allowed the spectacular cultural centers to establish and flourish.

The Maya civilization evolved mainly in the tropical lowlands. This is a historical anomaly because few advanced civilizations evolved in such a challenging environment. The tropical lowlands remain a hostile, often unhealthy, and difficult environment for human development and agricultural production. It is in this “hostile” environment, however, that the Maya developed one of the most sophisticated and advanced civilizations in the ancient world.

Based on archaeological evidence (Turner 1990), the Maya reached a high population density (up to 200 people per square kilometer in rural areas) that is found today only in a few highly populated regions within Central America and Asia. This figure remains unchallenged and suggests that the Maya were able—for centuries—to feed a population several times larger than the population of today in a tropical environment with soils that most agronomists would describe as marginal for agricultural purposes. There are two alternatives: either we assume that the population density figure is exaggerated, or we accept the figure and look for an explanation. Both options are challenging. The first alternative remains uncontested by archaeologists, but the second has been explored by scientists from different disciplines.

How did the Maya feed their people? Although several research projects and symposia have explored this question, the answer is still unknown. We know that the Maya practiced intensive agriculture, but we are not sure what species they used or how they managed them. Was corn-bean-squash shifting cultivation the principal food production system? Did they practice intensive rain-fed agriculture or agrosilviculture? What other staple foods did they cultivate in addition to corn, beans, and squash? What was the importance of chinampa-like agriculture? One approach to answer these questions has been the study of present-day traditional agriculture. From the bulk of data available, we have been able to propose many hypotheses on ancient systems of Maya agriculture and resource utilization, but we have very few projects that actually have tested them (Gómez-Pompa et al. 1982; Jimenez-Osornio and Rorive 1999).

The Maya culture reached its peak in the years 300–900 A.D. (i.e., the Classic Maya period) in the tropical lowlands of the Yucatán Peninsula, ranging from Tabasco and northern Chiapas to the lowlands of Guatemala, Belize, and Honduras. They created a network of population centers with spectacular architectural stone buildings and monuments. At their peak, the Maya were feeding several million people—most of whom lived in a transformed environment that challenges our imaginations. This surplus is not evident even today.

What were the environmental and cultural conditions that favored the development of this civilization in a lowland tropical environment? We do not know for certain the reasons for their success. The Maya were able to create surplus in the face of increasing demands for food and materials through a continuous process of agricultural innovation that enabled them to change from an extensive shifting agriculture to an unknown intensive agriculture. The production of surplus food was a necessity in order to feed nonproducers such as rulers, priests, warriors, builders, artists, poets, and scientists.

This remarkable culture experienced a major collapse during the first half of the ninth century. Monuments ceased to be constructed, and population centers were deserted. Many hypotheses have been suggested to explain this collapse. The most well-known hypothesis suggests an ecological collapse brought on by overexploitation of the environment; nutrient depletion of agricultural soils; deforestation and defaunation; pollution of water sources, erosion, and siltation of water bodies; and major diseases affecting humans and crops (Rice and Rice 1984). This ecological collapse has been the most popular hypothesis for the Maya Collapse, and it is used over and over again as an example of a culture that overused their resources because of overpopulation. However, this explanation may be grossly oversimplified.

A recent explanation for the Maya Collapse (Hodell, Curtis, and Brenner 1995) suggests that an arid event in the region coincided with the collapse of the Maya civilization. This timing is congruent with other hypotheses that attribute the collapse to warfare between powerful chiefdoms (Demarest 1993), which was brought about by the breakdown in agricultural production. We do not need great imaginations to picture a rebellion involving masses of hungry peasants urged to increase food production to feed the elites, or efforts by the elites to secure food supplies from other neighbors. Climate change in the Maya region is a very important topic of research that is helping us understand the large picture of the ecological history of the region.

The geographical lowland Maya region contain a great diversity of environments, including all kinds of tropical forests (wet to dry), savannas, palm stands, and many kinds of wetland vegetation communities. This region is known to be one of the most important biological regions of

the Americas. It is considered a site of several centers of plant diversity (Davis, Heywood, and Hamilton 1994–1997)—a biodiversity hotspot for its exceptional concentration of endemic species, which is undergoing an exceptional loss of habitat (Myers et al. 2000).

The sustaining of the high biodiversity of this region is an intriguing fact that puzzles conservationists. In spite of its long history of human-environment interactions—some of them extremely intense—there is no evidence of any major biological collapse produced by ancient Maya activities (Gómez-Pompa and Kaus 1999). There is no record of any biological extinction, past or present, in the Lowland Maya region due to ancient or modern Maya traditional agricultural practices.

It is assumed that the biodiversity of the Maya region is well known, but this is far from the truth. Although there are a few good inventories of the vascular plants and vertebrates from certain regions within the Maya area, detailed ecological studies are scarce. Very little is known of the diversity of nonvascular plants and invertebrates. In-depth studies of the biodiversity and ecological history of certain sites may help us better understand the human impact on the biodiversity of the lowland Maya region. In-depth studies of sites where we can integrate biological, archaeological, and environmental data for comparisons are needed.

For this reason, a group of conservationists interested in the topic of Maya subsistence create an experimental protected area that was not only dedicated to research and education on biodiversity conservation and management, but also the additional goal of trying to reconstruct human and ecological history of the site. This was the beginning of the research program of the El Edén Ecological Reserve, a nongovernmental-protected area, approximately 1,500 hectares (ha) in area, in northern Quintana Roo, Mexico, which is run by a not-for-profit Mexican organization <http://maya.ucr.edu/pril/el_eden/home.html>. The El Edén location was chosen because it represented all major ecosystems of the region: different successional stages of a tropical semievergreen dry forests, swamp forests, savannas, and wetlands. Archaeological investigations presented in this symposium show the presence of early Maya populations in this site.

In this symposium, we are including results from this interdisciplinary and multi-institutional research project. We believe that by concentrating our efforts in one site, we will be able to understand better the ecological and biological history of one site. We have not resolved any single problem yet, but we have opened new lines of research and education in archaeology, ecology, and biodiversity of a poorly-known region of the Yucatán Peninsula. It is one more piece of the puzzle concerning the managed ecological mosaic of the ancient Maya.

If the Maya, at their peak, used all available land for agriculture, where have all the rare and endemic species gone? Is the biota that we have today

an impoverished biota that is the product of a few centuries of intense transformation of native habitats? Or is it an astonishing biota, resilient to human actions? These are extremely important questions that are very difficult to answer. Our level of knowledge of the biota of any site in the Maya region is at the level of early alpha taxonomy, with some groups (e.g., flowering plants and large vertebrates) better known than others (e.g., microorganisms, nonvascular plants, and invertebrates). We need to know the in-depth biodiversity of today in order to understand changes that might have occurred in the past.

It has been suggested that the Maya maintained a great diversity of forest gardens where they domesticated, semidomesticated, cultivated, or semi-cultivated many plant and animal species (Wiseman 1978; Gómez-Pompa 1987; Atran 1993). These sites may have been the source areas where many wild species were able to survive. Are these sites the ecological refuges that allowed most of the flora and fauna to survive the intensification of land use at the end of the Classic Maya period? Some recent findings in traditional coffee and cacao plantations seem to support such a hypothesis (Gómez-Pompa 1997).

We know that deer, peccary, and turkeys were used extensively (Pohl and Feldman 1982). We have no idea what management approach the Maya might have used to sustain the abundance of these animals. It was known that deer, peccary, and ocellated turkey were so abundant and tamed in some areas that they seemed domesticated (Díaz del Castillo 1927). The only explanation for this abundance was the existence of large areas of managed forests and secondary forest lands where these animals, plus large carnivores, were able to thrive. These places were likely crucial ecological refuges. Studies on the ecology of regeneration and on the biodiversity of managed forests and secondary forests at different stages of development in the Maya region can help us understand their role as refuges and possible ancient wildlife management approaches. The use of nontraditional taxa as indicators of diversity could be an important contribution.

We may never know what flora existed in pre-Maya times. The pollen and phytolite record gives only some broad taxonomic information at the genus or family level. Great advances have been made in the study of pollen profiles of Maya lakes that have provided insight into the ecological history at a local level (Rice, Rice, and Deevey 1985). A better knowledge of the ecology of local species that are good ecological indicators could help us to have a better interpretation of the pollen and phytolite profiles within certain localities.

Today, we are struggling to find better approaches for a sustainable use of natural resources. We know that the ancient Maya, in spite of their extensive and intensive use of the area, were able to sustain their biological resources over several generations. In this intensively managed mosaic, the

old Maya were able to conserve the biodiversity they used and then pass this diversity to the next generation. This was their conservation strategy (Gómez-Pompa 1996). How can we use this knowledge to develop better and more accepted conservation approaches?

The Maya culture is alive and well. Today, they comprise more than 2 million people who live in the same geographic area as their ancestors: southeast Mexico and northern Central America. These people face similar challenges in food production and other activities as did their ancestors, but most of them face new challenges posed by the activities of dominant cultures. The knowledge of traditional Maya systems of agriculture and resource management is a key to decipher the past, and perhaps a path for the future for us all. Unfortunately, we are losing this knowledge at a rapid rate.

Many of these questions and topics are discussed in this book. It is my hope that these readings will stimulate further research on this unique culture and fascinating ecological region of tropical America.

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***PART II:
THE BIOLOGICAL AND PHYSICAL
ENVIRONMENT***

Chapter 2

The Changing Global Environment and the Lowland Maya: Past Patterns and Current Dynamics

Michael F. Allen
Emmanuel Rincon

INTRODUCTION

Images of the ancient Maya focus on a culture that built science, art, and architecture equivalent to the most advanced civilizations of their time. This culture, however, also experienced an almost complete political and cultural collapse of enormous magnitude, which resulted from the overuse of a fragile environment during periods of rapid climate change. Unfortunately, our images of the ancient Maya do not convey the unique aspects of both the rise and the change in culture of the region, or what lessons we can apply to our own times. Forests in the Maya region are actually quite resilient, as shown by their high biodiversity and stability in the face of continuing disturbance. The Maya people are not gone—they are the largest indigenous group of Native Americans in North America. As with most cultures, they have changed; their historical roots and current practices, however, have much to teach the rest of us.

The Maya civilization was born during one climate regime, expanded during a different climatic period, then retracted and changed over a third. The ancient Maya dramatically altered their surroundings, and then abandoned the more advanced scientific and artistic elements. They dropped drastically in population and returned to a simpler lifestyle—more

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susceptible to their surroundings, but likely also more attuned to their environment. As such, they developed institutions and technologies based on one set of ecosystem parameters, expanded and enhanced their population under different ecosystem properties, and then finally abandoned what had been a successful lifestyle under a third set of ecosystem limitations.

The failure of the cultural attributes of the Classic period to provide for existence during the changing conditions of the Postclassic period should not be a surprise. What should be of greater interest is developing an understanding of how the Maya persisted through many different environmental and cultural changes. Despite very high human population densities, elements of the wildland ecosystem persisted, adequate to reclaim most of the region when human numbers declined and areas were abandoned. This response to environmental change appears to be rather unique among human adaptations. As we change our own environment, are there lessons that can be learned from the Maya experience? If so, to what extent can we compare those changes that the Maya survived with changes prevalent in our own time?

Cultural practices may have important implications to wildland ecosystems. Religion is tightly coupled to food production and stability (*agri-culture*) in the Maya culture just as elsewhere. Similarly, we must search for solutions to cope with environmental change if wildland ecosystems and high levels of biodiversity are to persist. Terrestrial tropical ecosystems appear to hold important keys to both the release and sequestration of carbon (C), as well as to global climate. The functioning of ecosystems in the Yucatán Peninsula, both past and current, appears to hold important clues to these keys.

In this chapter, we provide an overview of the ecosystem characteristics of the Yucatán Peninsula, evaluate those changes that may have been critical to supporting the developing civilization as well as influential in its collapse, and provide some projections of the types of changes underway for our own time.

PAST ENVIRONMENTS AND THE YUCATÁN PENINSULA

Distinct Maya cultural activity can be traced at least three thousand years into the past, which coincided with rather dramatic shifts in climate. We introduce only the types of change here; further detail is presented elsewhere in this book.

Hunter-gatherers used the more arid shrub/grassland regions of the Yucatán Peninsula as far back as the Pleistocene epoch. As the climate grew wetter and warmer, seasonal tropical forests became more expansive—creating a difficult region in which large-scale agriculture could establish.

In drier regions of North America and South America, such as the desert of Peru, ancient civilizations arose some 4,000 years ago that were equivalent to those in Africa and the Middle East (Solis, Haas, and Creamer 2001). Three millennia ago, Preclassic civilizations arose in southern Mexico and Guatemala coincident with a drying of the environment. Although surface waters were still present, levels of inundation were less apparent than today. Severe drought coincided with the collapse of the Classic Maya civilization, but the returning wetter regimes appear not to have supported any recovery of the earlier urban life in the southern lowlands. In the northern lowlands, Maya civilization changed dramatically, supporting first an urban civilization, then smaller cities and village lifestyles that survived through Spanish colonization, and up until today.

The ancient Maya faced one problem that persists today—namely, conversion of land from wild forest to one supportive of agricultural crops. Despite the use of forest resources, opening fields for maize, beans, squash, and other crops requiring high light intensity was essential. To support the incredibly high population density that existed in the past, vast amounts of land were converted from forest to cultivated lands. Although the ancient Maya retained certain trees such as *Ceiba pentandra* in the middle of agricultural fields, the problem of feeding large populations required extensive land clearing. This is apparent in the changing pollen analysis during the times of human occupation.

One particular difference between the environment of the ancient Maya and today needs further consideration. During the rise and fall of the Maya civilization, the atmosphere contained less than 250 parts per million (ppm) of carbon dioxide (CO₂). It had likely been as low as 190 ppm during the Pleistocene, gradually rising to about 250 ppm during the Industrial Age, when the dramatic increases that are characteristic of our own times became apparent. This means that during the Maya agricultural hiatus, CO₂ was likely a limiting factor—not an excess resource. Both land conversion and CO₂ concentrations have major impacts on how ecosystems work that are crucial to understanding past human activities and predicting where the Yucatán Peninsula is headed today.

THE EL EDÉN TROPICAL SEASONAL FOREST: CURRENT ECOSYSTEM STRUCTURE

Little is understood of the functioning of wildland ecosystems in the Maya lowlands. Models of ecosystem processes have been generated in the Florida Everglades, or in areas such as La Selva in Costa Rica, or Barro Colorado Island in Panama. While these areas provide insights into tropical

ecosystem theory, the details of how the ecosystems work remain largely unknown.

A site in southeastern Mexico has studying for soil and plant dynamics in conjunction with other ongoing research on biodiversity and restoration. The site is located at the El Edén Ecological Reserve, situated within northern Quintana Roo, Mexico. This site contains a wide range of environmental conditions, from cenotes and wetlands to upland mature forests and secondary forests. These conditions represent most ecosystem types in the area, with the exception of coastal areas. As a test case for environmental change and ecosystem functioning, we will examine the information gathered largely at this site and in the surrounding areas.

Climate

The climate at El Edén is characterized by an extended winter/spring drought, with the wet period commencing in June or July. The total precipitation averages 1,200 millimeters/year (mm/yr.). This results in a tropical seasonal forest. The wetlands result from a high water table and a flow northward through the limestone. In the wet season, the water table is high enough that the wetland resembles a slow-moving, northward-flowing river. During the dry season, only the cenotes contain standing water.

The climate is strongly influenced by the Gulf of Mexico, the Caribbean Sea, and the North Atlantic. Importantly, we have found little evidence that El Niño has a major impact on the Yucatán Peninsula. La Niña, however, may play a major role; during La Niña periods, hurricanes appear to peak, and almost every major hurricane during recorded history has appeared during a La Niña period. Water inputs also support the influence of La Niña (Figure 2.1). Precipitation is consistently higher in La Niña periods than during El Niño years.

Soils

The soils of El Edén are typical of the Yucatán Peninsula. The forest soils consist largely of limestone covered with a thin [1–4 centimeters (cm)] veneer of soil. Most plant growth exists in small potholes filled with extremely rich soil that is really a mulch mix. These soil patches are extremely high in organic matter (O.M.), ranging from 15 to 30% organic carbon (C), and are surprisingly rich in nutrients that support rapid plant growth (Table 2.1).

In the uplands, a layer of red soil can be found. We have not studied this soil in detail, but it contains a high clay content and holds considerable moisture. In other regions, similar soils tend to be high in iron (Fe), deficient in available phosphorus (P) and organic carbon (C), and can become lateritic [i.e., high in aluminum (Al)] when repeatedly cropped.

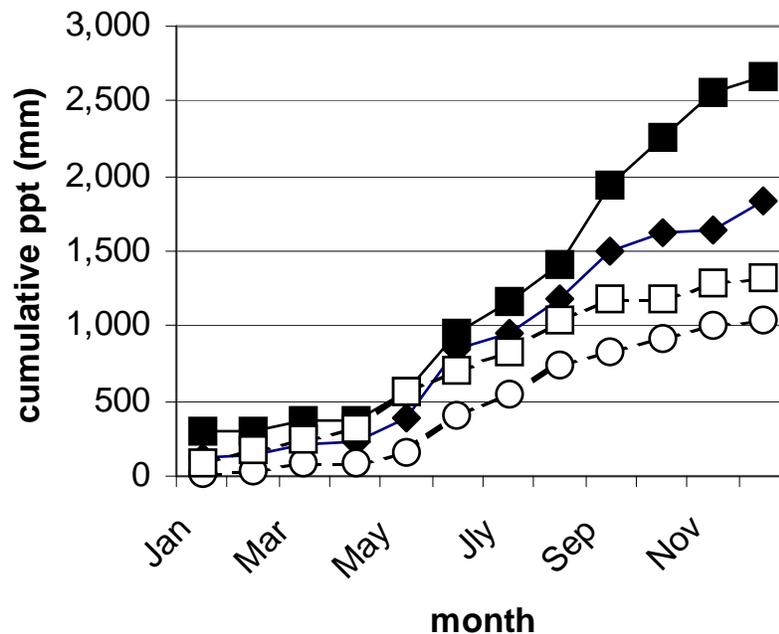


FIGURE 2.1. Comparative precipitation (ppt) of La Niña years (1964 [closed diamond], 1988 [closed square]) versus El Niño years (1991[open circle], 1997[open square]) at Kantunilkin, Quintana Roo, Mexico.

In the wetlands, the soils tend to be largely muck with high clay content, relatively rich in phosphorus (P) but low in nitrogen (N) (Schultz, unpublished data). In one sense, this is surprising in that there is a very high density of cyanobacteria that are rapidly fixing atmospheric nitrogen (N_2). This may be due to high rates of denitrification. Conditions for denitrification, high organic matter, warm temperatures, and low oxygen tensions are perfect for rapid rates.

Soil Organisms

Although we understand little about the soil organisms in these regions, what we do know is very interesting. In the acahual and in the mature forests at El Edén, the dominant type of mycorrhizae are arbuscular mycorrhiza (AM). In this system, the fungal hyphae are very dynamic—extending outward a few centimeters from a root and extracting largely plant-available nutrients, but turning over rapidly. The fungal hyphae also respire, locally mineralizing phosphorus (P) as the increasing CO_2 in solution becomes bicarbonate (Figure. 2.2).

In patches of mature forest, older acahual, and especially in the tintal, we also find species of *Amanita*, *Boletus*—even *Suillus*—as well as other genera of ectomycorrhizal fungi. The presence of these fungi indicates that

TABLE 2.1. Soil nutrients in the research plot at El Edén Ecological Reserve. Soil samples were collected at four different times: from the mature forest, before burning (Preburn), in the restoration plot following burning (Postburn), and at two years after planting

	15 June 1997	17 June 1997	4 July 1997	12 July 1999
	<u>Mature Forest</u>		<u>Restoration Plot</u>	
	<u>Inoculum</u>	<u>Preburn</u>	<u>Postburn</u>	<u>At two years</u>
pH	7.2	7.7	7.6	7.5
ug/g total P	710.6	564.6	591.1	nd
S.E.	88.0	55.2	49.8	
ug/g extr P	20.2ab	29.1b	29.4b	14.5a
S.E.	6.4	3.0	2.5	1.6
% O.M.	26.8a	34.0a	15.9b	43.2c
S.E.	6.8	1.2	0.7	1.1
% total N	2.04a	1.39a	1.52a	0.87b
S.E.	0.65	0.08	0.09	0.05

nd = no data; P = phosphorus; N = nitrogen; O.M. = organic matter; S.E. = [standard error of the mean]

nutrients, particularly nitrogen (N), are likely directly transported from litter to plants in the form of amino acids, not only following mineralization. In some cases, mats can be distinguished with large amounts of thick, white hyphae—suggesting that oxalates are abundant that bind calcium (Ca^{2+}) and other cations. These organic acids bind and concentrate cations such as Ca^{2+} and Al^{3+} , which simultaneously release the complexed phosphorus (P) (see fig. 2.2). Orchids have their own distinctive mycorrhizal fungi that extract nutrients and often sugars and carbohydrates from the substrate on which they are growing. While these plants are not known to be of high importance to forest ecosystem dynamics, they are commercially important and interesting from the perspective of both biodiversity and conservation.

Nitrogen-fixing bacteria that are symbiotic with legumes play an extremely crucial role in these forests. Most of the rapidly growing tree seedlings are legumes, and examination of these plant roots reveals high densities of red nodules, which indicate active fixation. We do not know much about the diversity of these bacteria, their species associations, and their efficiencies; we do know, however, that these bacteria are so efficient

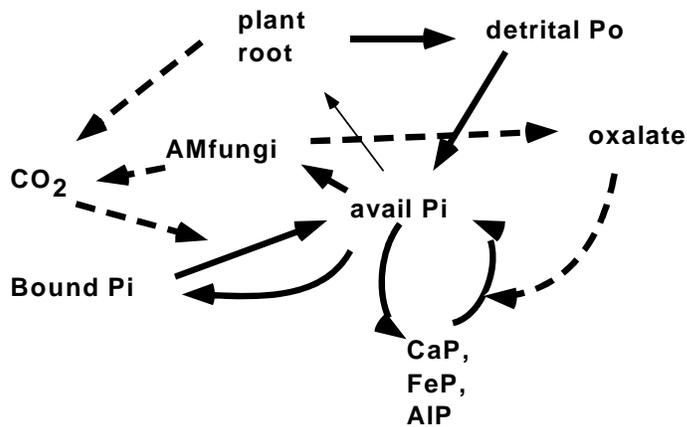


FIGURE 2.2. Phosphorus (P) cycling in the forest soils of El Edén. (Source: Adapted from Allen 1991.)

that the N/P ratios of most of the acahual forest trees range from 20 to 40, which suggest that the plants tend to be deficient in P, but not N.

Together, N₂-fixing bacteria and mycorrhizal fungi are critically important for these communities. Not only do these organisms aid the nutrient status of their immediate host, but the mycorrhizal fungi also connect multiple plants. Nitrogen has been fixed by a N₂-fixing host (beans), and then transported to a second host (maize) by the fungi (Bethlenfalvay et al. 1991). We have recently found that deep water can be taken up by a host plant, then transported to a mycorrhizal fungus by hydraulic lift (Querejeta, Egerton-Warburton and Allen, unpublished data), which allows nutrient uptake to occur in dry soils. We are currently attempting to determine if this water can be transported to a neighboring plant.

Vegetation Structure

Although wildland communities are described in detail elsewhere in this volume, there are some additional issues that are critical for discussion here. These include the photosynthetic pathway and water-use efficiency, as well as rooting structure and water access.

First, the large majority of the plants are C₃, or cool-season, species. In the presence of light, the stomata of these plants open and allow water to escape, while simultaneously allowing CO₂ to diffuse in. Through the Calvin cycle, CO₂ is fixed into glucose in the mesophyll cells immediately inside the stomata and throughout the leaves. Leaves maintain optimum temperatures (20–30°C) through transpiration, but this entails sensitivity to drought. Thus, water loss can be high. Water-use efficiency (WUE) is defined as the number of water (H₂O) molecules lost to CO₂ molecules gained. In most C₃ plants for this region today, a general figure is around

318 H₂O molecules per CO₂ molecule. This number will become important later in the discussion.

Second, a few of the forest succulents (e.g., Bromeliaceae) contain the Crassulacean Acid Metabolism (CAM). CAM plants open their stomata at night and fix CO₂ into malate. Even though the stomata are closed during the daytime, enough light is available for the malate to be converted back into CO₂, and then fixed into glucose through the Calvin cycle. WUE can be quite high, as water is not lost from the plant during the day when transpiration rates are high. Few plants in the wildlands are C₄, or warm-season, plants. C₄ plants have a distinct anatomical and physiological shift. In the mesophyll cells, CO₂ is fixed into malic acid and aspartic acid. These C₄-acids are then transported to bundle sheath cells where glucose is made. These plants are very efficient in obtaining CO₂ at low concentrations, and therefore have rather high WUE. They also efficiently fix CO₂ up to 35°C. Only a few grasses in the wildlands are C₄, but maize is a C₄ plant, which could have major implications for ancient agriculture.

Third, the structure of forest roots is also of interest in areas where water is especially crucial. Forests are largely C₃, releasing large amounts of water, and thus have lower WUE. Some of these trees have deep roots that access water, especially in the northern part of the Yucatán Peninsula where the water table is relatively shallow. Observations such as the drawing by Catherwood of the Cave at Bolonchen (see Stephens 1843) show that roots extend deep into the limestone. Data from El Edén (Figure 2.3) show that there are some important differences among species. Some, such as *Ceiba pentandra* or *Leucaena leucocephala*, maintain a high water potential (low water stress) into the dry season. This indicates that these plants have deep roots tapping into the groundwater. Others, such as *Havardia albicans* or *Acacia pennatula*, undergo severe drought stress, which suggest the presence of shallow, spreading roots that exhibit rapid growth during the wet season. These are different strategies for coping with the dry season.

Agriculture

Increasingly, lands are being converted from forest to agricultural production. In the more traditional agricultural practices, this conversion involves short-term use followed by a long-term fallow rotation system. In the Yucatán Peninsula throughout the pre-Hispanic period, the Maya did not use large animals as manure producers, which would have allowed a three-field rotation system. Thus, the land-ownership concept that existed in Europe differed radically from that in the Maya lowlands. Fertility resulted from N₂ fixation by multicropping with legumes, and from fallow periods that extended upwards for about two decades.

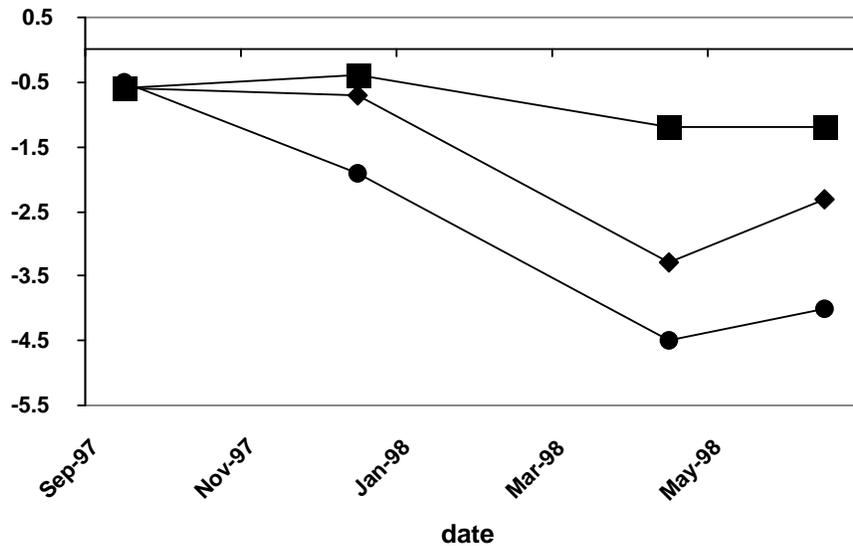


FIGURE 2.3. Water potentials (measured in MPa) of plants from a mature forest and seedlings from a restoration experiment at El Edén; measurements were taken in the wet season and continued through a dry season. Shown are *Ceiba pentandra* in the restoration plots (square), and *Havadia albicans* in the restoration plots (diamond) and in the forest (circle). *C. pentandra* is an example of a species with rapid and deep root growth, while *H. albicans* has shallow, spreading roots.

There is an additional consideration. Anderson (pers. comm.) pointed out that during traditional agriculture, some species of trees (e.g., *C. pentandra*) were left alone, as well as many resprouts. Some concern has been expressed as to why these trees were untouched because they compete with crops for light and nutrients. Were these left for shade, for religious reasons, or for other unknown purposes?

There may, however, be other compelling reasons. Of the mixture of species left untouched, some species appear to have roots that reach groundwater. For these trees, there is a high likelihood that hydraulic lift occurs during the early part of the drying cycle. Water is picked up in the deeper roots and is transported horizontally to the surface soils during the night (Jackson, Sperry, & Dawson 2000). As both the trees and crop plants form arbuscular mycorrhizae, the possibility that this water could play a critical role in maintaining the water status of nearby crop plants cannot be underestimated.

In the southern and western part of the peninsula, agricultural techniques are changing. Mechanized agriculture (where possible) and commercial fertilizers have change the system to a monoculture in which N_2 fixation within a maize field (from co-cropped beans) has been eliminated. If it is assumed that the remaining trees are removed, then any importance of

hydraulic lift is lost. Often, because of increasing demands for food, the fallow period is eliminated with unknown consequences.

ECOSYSTEM DYNAMICS: CURRENT VERSUS PAST

Water dynamics regulate virtually all processes in the Yucatán Peninsula, as with most locations. Rainfall tends to be high, but very seasonal—increasing from the northern lowlands to the southern lowlands, and then into the highlands. This seasonality, coupled with the porous limestone and lack of soil, means that little water is held in the surface for plant use. In some regions such as the Yalahao, however, the groundwater is close enough to the surface to be important. These characteristics are essential to understanding the dynamics of these ecosystems.

Three features in water dynamics are crucial to comparing the ecosystems of ancient times with those of today. The first (and foremost) feature is probably the differing CO₂ regimes of 1,500 years ago and today. Prior to the Industrial Revolution, atmospheric CO₂ was only about 210 to 250 ppm (versus 370 today). WUE would have been extremely poor for C₃ plants. For example, for each CO₂ molecule fixed in about 900 A.D., 532 molecules of H₂O were lost. This compares to a H₂O:CO₂ ratio of 318:1 today and, potentially, a ratio of 197:1 by the end of the next century. One impact would have been that during the Classic period, failure or low rainfall would have been much more devastating to production of C₃ crops (beans, squash, and chilies) and trees than today.

One important exception is C₄ maize. C₄ plants have a high WUE that produces much more mass per molecule of H₂O than an equivalent C₃ plant. This is important to agriculture and human nutrition as well. During drought years, one could readily envision a steady production in maize, with other crops (e.g., beans and squash) declining. How this might play into human nutrition is speculative; during marginal years and times of social unrest, however, this exception could prove important.

A second impact on water dynamics is the forest itself. Because of the high leaf area of the forest, transpiration rates can exceed the rates of water loss from open pans. As one moves inland, greater amounts of water in the atmosphere continue to come from vegetation, not from the ocean (Hayden 1998). This process has clearly been demonstrated in the Amazon basin. This is also apparent in weather satellite images and in precipitation patterns in the Yucatán (see Orellana, 1999).

In inland areas such as the Petén region, then, a large fraction of atmospheric water and precipitation likely was derived from transpiration during Preclassic and Early Classic Maya times. With a low WUE across the forest, and an onshore breeze associated with inland heat, a large

fraction of the atmospheric water would have come from the forest itself. With extensive deforestation (bare soil) and increasing coverage of the land with C₄ maize, as the dominant plant, this water would not necessarily be put back into the atmosphere at inland regions.

The final pieces in this puzzle are the microbial symbionts themselves, particularly mycorrhizal fungi and N₂-fixing bacteria. Under low atmospheric CO₂ concentrations, mycorrhizae are limited in C (Treseder & Allen 2000). With drought, these fungi also do not produce the extensive hyphal networks necessary to take up limiting nutrients efficiently. These fungi are responsible for creating soil aggregates that are essential to soil structure and moisture-holding capacity, and soil aggregates are reduced with low atmospheric CO₂ levels (Rillig et al. 1999). Mycorrhizal fungi are also very sensitive to disturbance and land clearing. Experimental tests have demonstrated that levels of these fungi are dramatically reduced if forests are removed by burning (E. Allen et al., this volume). These fungi are responsible for most of the P uptake into plants. Phosphorus is not readily mobile in the soil solution. The extensive hyphal network radiates out and transports the available P back to the host in exchange for sugars. In calcareous soils or high cation soils, the CO₂ respired by these fungi weather P and also produce organic acids that maintain the P in solution for uptake (e.g., Allen et al. 1996).

Nitrogen fixation into crops such as beans for essential amino acids is energy limited, and, thus, water limited. A single protein molecule such as hemoglobin requires 146 molecules of NH₃⁺, which needs a large amount of energy (12 ATPs/N₂ fixed) and, thus, assimilated C. Assuming that the average Maya required 50 g protein (as today), gained mostly from beans, then the plants would have transpired 44 liters (l) of water for CO₂ fixation (compared with 26 l today). As drought proceeds, photosynthesis and N₂ fixation rapidly decline, and so does protein from agricultural sources. This places an additional burden on hunting and increases the sensitivity of the population to game depletion.

Thus, virtually all ecosystem processes—from forest nutrient turnover, to fertility, to protein—is dependent on the water regime of a region. The forests are not only users of regional water, but also creators. We are learning that water is coupled tightly to the functioning of an ecosystem. Changing the proportion of land in various components (e.g., converting wetlands and forests to large-scale agriculture) had the potential to alter virtually every aspect of agricultural production during the Classic period.

As WUE declines with decreasing CO₂ levels, nutrient-use efficiency increases. N and P concentrations go up at 250 ppm CO₂, as compared with ambient (Allen, unpublished data). This could mean two things for the ancient Maya compared with today. First, following opening of a forest for crop production, nutrients were probably not limiting. Even today, P and N concentrations in soil, even following burning, are very high (see Table 2.1). Estimates of nutrient removal suggest that, even with many years of

agriculture, nutrient levels were unlikely to be limiting in at least northern Yucatán. With continual production, however, cation immobilization of P is still likely important. In terms of long-term agriculture, we still suggest that nutrients would not limit production as much as in today's environment. The increasing N concentration, however, has a secondary effect. Thus, secondly, insect and pathogen activity may increase markedly in response to increasing N concentration of the leaves because leaf material is simply more nutritious. With increasing N, however, plants can also produce more secondary defense chemicals, which, in turn, would negatively affect grazers (and humans). These dynamics clearly need better understanding of basic plant ecological interactions.

CURRENT AND PROJECTED ENVIRONMENTAL CHANGE AND THE YUCATÁN PENINSULA

Global concentrations of CO₂ are rising dramatically. From 250 ppm pre-Industrial Age, to over 370 ppm today, this exponential rise is expected to continue well into the next century, rising to at least 550 ppm. Although some models show a leveling off at around 550 ppm, these estimates are based on some dramatic changes in cultural practices that are not supported by the current political climate. Elevated CO₂ levels have some benefits for crop production (discussed above), but also have potential dramatic consequences to climate and ecosystem processes.

The changing global climate is not only a function of elevated CO₂ from North American manufacturing and European industry. Forest clearing not only directly increases CO₂ loss from decomposing organic matter in the soil, but also reduces the ability of the ecosystem to absorb CO₂. As previously discussed, deforestation also potentially reduces transpiration and dramatically affects soil processes. Finally, increasing urban growth and industrialization fragments the region and places increasing demands on local production for food and water.

We have evaluated the data from two sources near El Edén to better understand the potential effects of global climate change issues on the region of our study area. These two sources are the weather records from Kantunilkin and Solferino. With a twofold increase in CO₂ concentrations (i.e., 350 to 700 ppm) because of rising ocean-heat loading, rainfall in the Caribbean region is expected to increase 20 to 40% with a 1–2°C rise in annual temperature and a 5 mm/yr. increase in sea level. Over the last 200 years, CO₂ concentrations rose 48%, with most of that increase within the last 50 years. Both sites have experienced changes in climate over the last 40 years. At Kantunilkin, precipitation has increased an average of 6.2

mm/yr. since 1961, at $p = 0.23$. While this is of marginal significance, the monthly pattern of that increase is of much greater interest. The bulk changes occur in April, May, and November (fig. 2.4). These are significant enough to warrant the need for additional monitoring. These changes also occur at the end of the growing season and could be adequate to extend the growing season on either end. At Solferino, the precipitation pattern is similar, but not statistically significant.

Minimum temperatures also provide an interesting clue about a potentially changing environment (fig. 2.5). At Solferino, the minimum temperature has increased since 1970 for each month except March. During the rainy season, these increases are highly significant (June, $0.105^{\circ}\text{C}/\text{yr.}$, $p < 0.0001$; July, $0.09^{\circ}\text{C}/\text{yr.}$, $p = 0.003$; August, $0.106^{\circ}\text{C}/\text{yr.}$, $p = 0.0002$; September $0.095^{\circ}\text{C}/\text{yr.}$, $p < 0.0001$; October, $0.062^{\circ}\text{C}/\text{yr.}$, $p = 0.11$). Minimum temperatures reflect the dew point temperatures; as the relative humidity rises, so does the minimum temperature associated with the increasing ocean temperatures.

At Kantunilkin, however, the opposite pattern emerges. Since 1961, minimum temperatures have declined in every month except November. This is especially apparent in June ($-0.103^{\circ}\text{C}/\text{yr.}$, $p = 0.003$), July ($-0.075^{\circ}\text{C}/\text{yr.}$, $p = 0.004$), August ($-0.083^{\circ}\text{C}/\text{yr.}$, $p = 0.011$) and September ($-0.65^{\circ}\text{C}/\text{yr.}$, $p = 0.015$). Why the difference? The sites are only a few kilometers apart, and the precipitation is increasing at Kantunilkin. The most likely explanation exists in recent satellite images. The new moderate resolution imaging spectroradiometer (MODIS) satellite clearly shows a brown region extending eastward across the northern part of the Yucatán

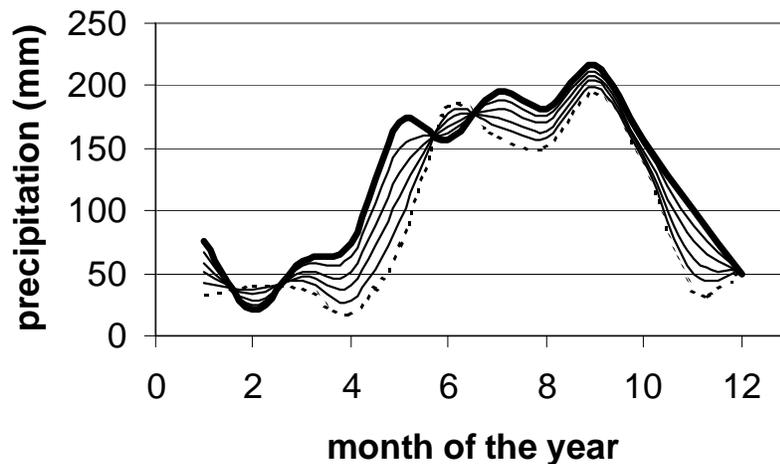


FIGURE 2.4. Precipitation structure at Kantunilkin for decadal intervals from 1960 (dashed line) to 2010 (solid heavy line). These projections are based on the increasing rates of precipitation since 1961 in the growing season, including April ($p = 0.12$) and May ($p = 0.15$), and again at the end of the growing season in November ($p = 0.12$).

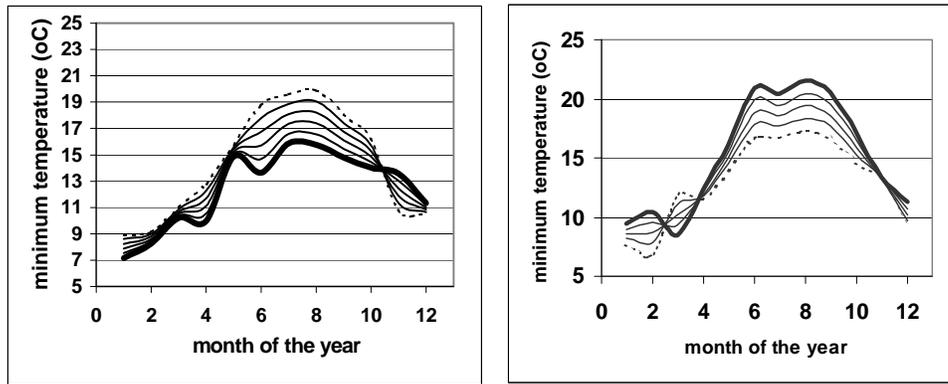


FIGURE 2.5. Minimum temperature structure at Kantunilkin (left) and Solferino (right) for decadal intervals from 1960 (dashed line) to 2010 (solid heavy line). At Kantunilkin, these projections are based on the decreasing minimum temperatures since 1961 during the growing season, which includes June, July, August, and September (see text for details). At Solferino, these projections are based on the increasing minimum temperatures since 1971 in March, April, May, October, and November (see text for details).

Peninsula, encompassing Kantunilkin, whereas Solferino has remained green (NASA 2001). Reports indicate that the forest largely remains intact at Solferino, whereas the landscape surrounding Kantunilkin has been increasingly deforested for agricultural production. These observations correspond to the areas that have become agricultural during the past few decades, as well as to increasing secondary forest vegetation. As discussed earlier, relative humidity (and, thus, dew point) is highly dependent not only on the moist air from the ocean, but also increasingly from the forest vegetation itself. This would be especially apparent during the peak of the growing season when the stomata are wide open.

These results are crucial to the global climate scenarios and for regional impacts. Rising CO_2 concentrations mean more water, rising sea levels, and increased chances of flooding. Recent research has shown that the forests in this hemisphere (and especially in North America) are critical CO_2 sinks. We do not know all of the details (Malhi & Grace 2000), but much of the increasing carbon goes below ground and is associated with mycorrhizal fungi in a manner that may be similar to what we have found in temperate regions (Rillig et al. 1999). Just as important, deforestation changes the sequestration of carbon both by directly eliminating the forest, but also likely by the changes in soil organisms in response to the ecosystem adjustments to perturbation.

Both agricultural and vegetation maps show dramatic increases in agricultural area (fig. 2.6) and secondary forest (see vegetation maps of Gonzalez-Iturbe and colleagues, in Olmstead 1999). These will reduce the

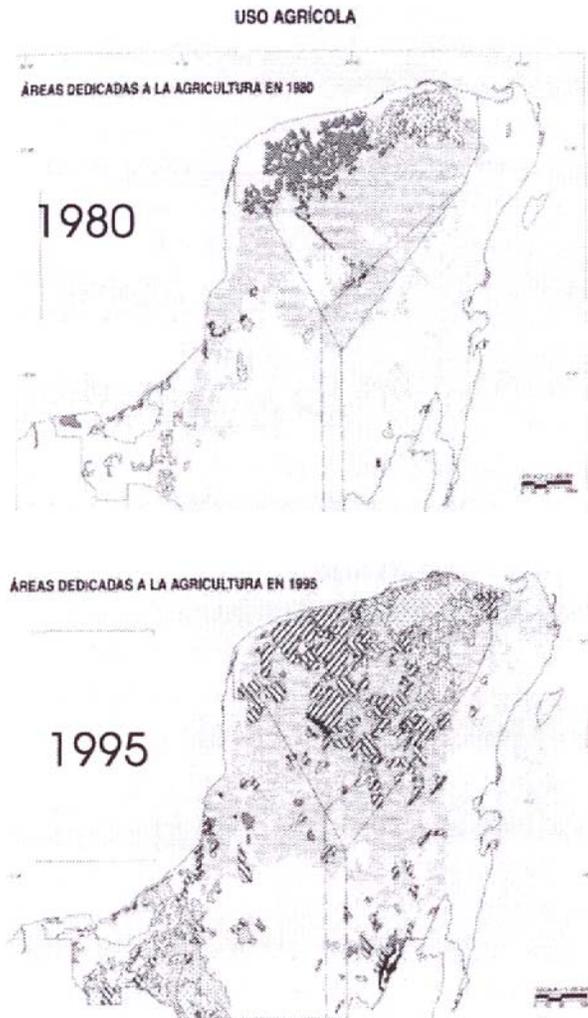


FIGURE 2.6. Changing plant cover in northeastern Yucatan Peninsula, showing changes in agricultural lands between 1980 and 1995. The striped regions are permanent or rotational agriculture. For other finer resolution, see original reference. (Source: Redrawn from Gilberto XIX AKE' 1999).

carbon sink strength. The dramatic increases in protected areas are just as important, however, because they protect the carbon-sequestration capacity of the region. Careful agricultural, wildland, and forest management practices (demonstrable in the Yucatán as nowhere else) have the potential to make observable inroads, or at least reductions, in our degrading global environment.

The global environment may be critical for developing scenarios of climate change for the Yucatán Peninsula (Kerr 2001). El Niño signals can be found in the fossil records and suggest that this phenomenon may be sensitive to the changing global environment. To our knowledge, there are

no signals known for La Niña patterns. There is some speculation, however, that La Niña may be increasing in strength and frequency as the Pacific gyre changes. Hurricane frequency is expected to increase with increasing La Niña activity, and intensity is expected to increase with the rising global sea surface temperatures. Based on these projections, we can expect more frequent and intense hurricane activity, increasing disturbance by flooding and wind, and rising sea levels.

CONCLUSION

Past climates have dramatically affected human activities in the lowland Maya regions. The Maya civilization arose during one climate regime, expanded and flourished during a second climatic shift, and then retracted and changed over a third. Characteristics changed dramatically with severe drought, and the recovery in human activities changed forms. Climate is continuing to change. Importantly, the critical shifts today may well be induced by humans—not by the Maya locally, but certainly worldwide—and, in many cases, in ways that the Maya changed their surroundings a millennium ago.

Elevated CO₂ concentrations (through its effects on water-use efficiency and nutrient-use efficiency) and deforestation (through loss of habitat for wildlands, and possible effects on water recycling) could have rather dramatic effects on all natural and agricultural resources of the region. These need to be considered in any land-use planning—both for protection of wildland resources, and for the impacts on agriculture and forestry.

Finally, the region itself may be a critical one for the remainder of the globe. Tropical North America is being recognized as a key sink for elevated CO₂ levels. The large reserves that protect wildlands, forestry, and integrated community activity may hold clues not only to how people in regions around the globe should behave, but also how we are linked around the globe.

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Chapter 3

In the Beginning: Early Events in the Development of Mesoamerica and the Lowland Maya Area

Alan Graham

INTRODUCTION

The purpose of this chapter is to describe early background events and processes that ultimately contributed to the definition of the Maya lowlands. Some of these occurred at the time of origin of the Yucatán Peninsula, while others were in operation when the earliest humans arrived. Those most relevant to the human occupation can be organized around the geologic, climatic, and vegetational history of the region.

GEOLOGIC HISTORY

The Lowland Maya area is noteworthy as the site of two ancient geologic events that are of great importance to the subsequent history of Mesoamerica. One was catastrophic and altered the course of biological evolution, while the other was gradual and determined the ultimate nature of the physical environment.

The catastrophic event occurred at the end of the Cretaceous (65 Ma), when an asteroid 10 ± 4 km in diameter impacted the Yucatán Peninsula and left a crater roughly 180 km in diameter buried beneath Chicxulub in north-coastal Mexico (lat. $89\text{--}90^\circ$ N, long. $21.5\text{--}20.5^\circ$ W; Hildebrand et al. 1995). The asteroid impact was a spectacular occurrence that profoundly affected climates, atmospheric chemistry, and evolutionary patterns. In particular, it removed the dinosaurs as the main predator of the mammals, thereby accelerating mammal diversification and radiation into modern forms. The less dramatic event involved the position and sedimentary history of two

crustal blocks that would shape the landscape morphology and edaphic environment of the peninsula.

The geologic origin of a region significantly influences the environment under which successive communities of organisms exist, and is the basis, in part, for their adaptations to the prevailing physical conditions. In the case of Mesoamerica, its origin involved two blocks or terranes (Figure 3.1).

The Maya (Yucatán) Block is a fragment resulting from the separation of South America from North America and was originally situated near its present position in the Gulf of Mexico (Ross & Scotese 1988). The Maya Block was sutured onto central Mexico during the Cretaceous, and the contact is represented by the Saline Cruz Fault Zone that runs across the Isthmus of Tehuantepec.

The Chortis Block was originally located along the western coast of Mexico in the Mesozoic; it moved southeastward along the Motagua-

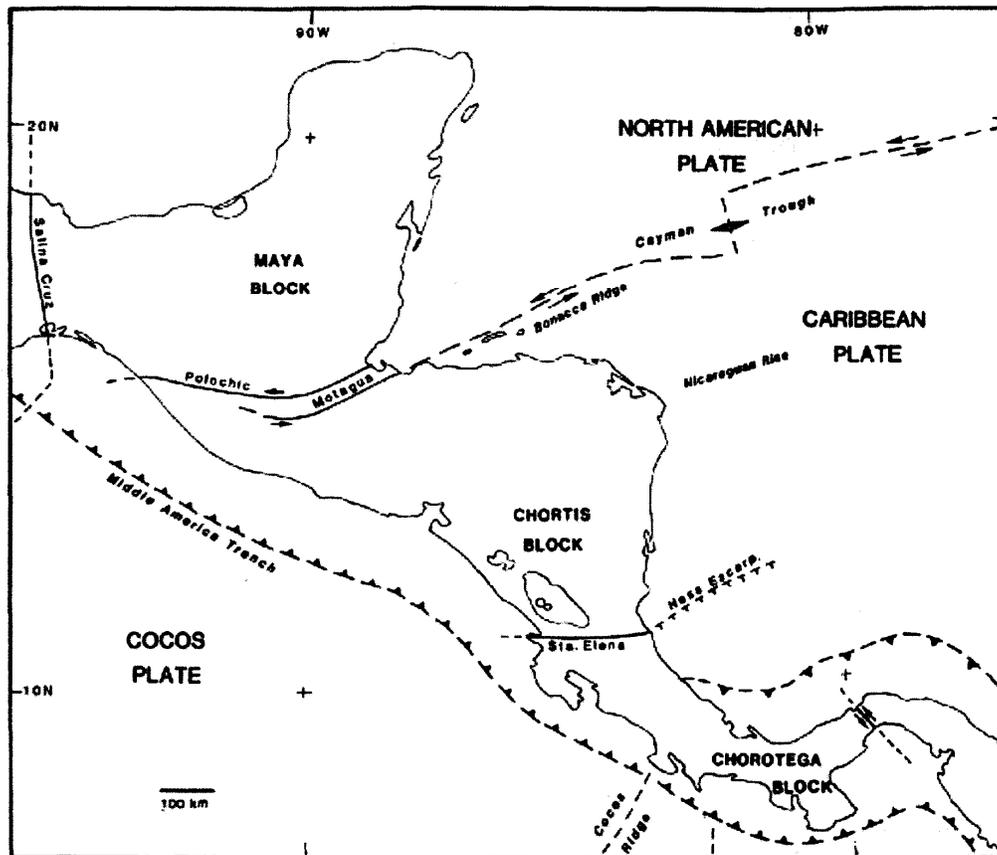


FIGURE 3.1. The Maya and Chortis blocks and their boundaries. (Source: From Donnelly et al. (1990). Used with permission of the authors.)

Polochic Fault Zone of northern Guatemala. The Chortis Block also was in place by the end of the Cretaceous, and its northern boundary with the Maya Block represents the contact between the North American and South American plates. Movement along the fault still generates earthquakes that periodically devastate the region (e.g., Guatemala on 4 February 1976) (see Espinosa 1976; Plafker 1976). The southern boundary of the Chortis Block is the Santa Elena fault just south of Lake Nicaragua.

An important geological feature of the Maya Block is that throughout most of its history it was a shallow marine platform (Logan 1969; Driscoll and Diebold 1999, Figures 12, 13; see Figures 3.2, 3.3 in this chapter). A sequence of mangrove-bearing lignites—extending from Malpaso, Chiapas, near the Veracruz border southeast to San Cristobal—identify the shoreline in the Oligo-Miocene as being approximately 90 km inland from its present position (Frost & Langenheim, Jr. 1974). The carbonate sediments and coral reef material that accumulated in this depositional setting formed limestone;

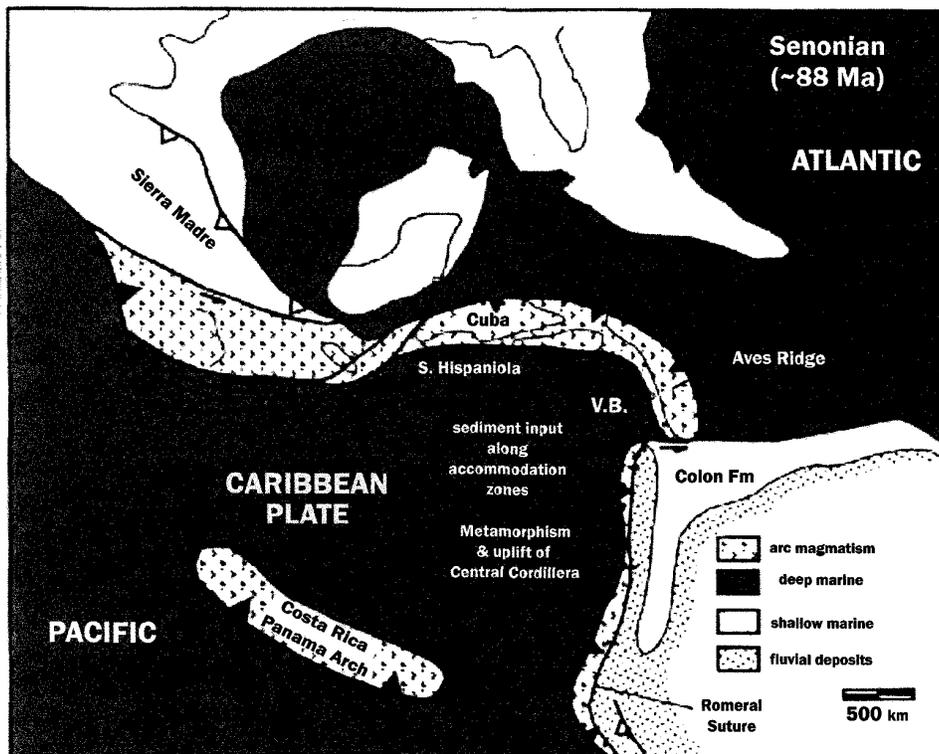


FIGURE 3.2. Location of the Yucatán sedimentary platform in the Senonian (~88 Ma). Note deposition in shallow marine waters. (Source: Reprinted from N.W. Driscoll and J.B. Diebold, 1999, Tectonic and stratigraphic development of the eastern Caribbean: New constraints from multichannel seismic data, in *Caribbean Basins*, p. 616, with permission from Elsevier Science.)

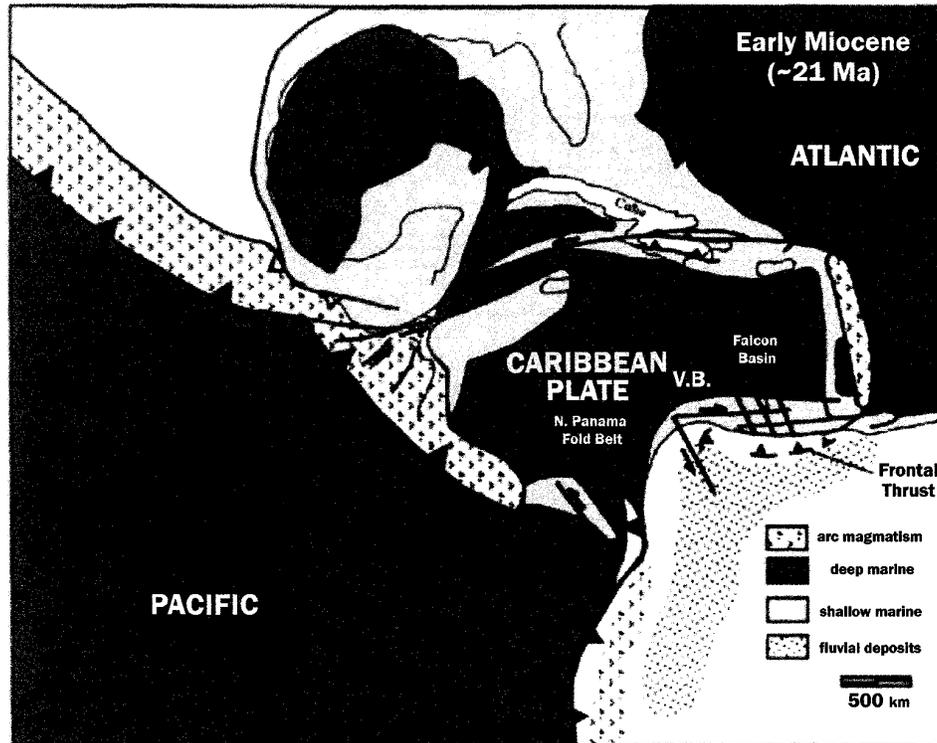


Figure 3.3. Location of the Yucatán sedimentary platform in the early Miocene (~21 Ma). Note continued deposition in shallow marine waters. (Source: Reprinted from N.W. Driscoll and J.B. Diebold, 1999, Tectonic and stratigraphic development of the eastern Caribbean: New constraints from multichannel seismic data, in *Caribbean Basins*, p. 619, with permission from Elsevier Science.)

with subsequent tectonic movement, combined with sea-level fluctuations, these depositions became emergent and weathered into the karst topography that now characterizes the region. (A karst topography is one that results from the subaerial erosion of limestone to produce a rough porous surface, numerous aquifers, and little surface drainage.)

The legacy of this geologic origin is apparent in the present biota. The mean annual precipitation (MAP) is plentiful; at Cozumel, for example, the MAP is 61 inches. Yet the vegetation is a dry deciduous forest resulting from the rapid percolation of water through the porous substrate. The impact on the human population that settled in this environment is reflected in the numerous studies focused on methods of water conservation, as well as the necessity of coping with water shortages in the midst of plentiful rainfall. Examples of these studies include Maya lowland hydraulic systems (Matheny 1976), Maya impact on a tropical karst environment (Deevey et al. 1979), water storage among the ancient Maya (Adams 1991), and

water storage adaptation in the Maya lowlands (Scarborough & Gallopín 1991).

CLIMATIC HISTORY

Our concepts of the climatic history of the tropics have undergone three significant changes within the past few decades. Earlier it was believed that while Quaternary climates fluctuated widely in the high latitudes, those in the low latitudes were comparatively stable. For example, mean annual temperature (MAT) in the polar regions was estimated at 12 to 14°C colder than at present at the latest glacial maximum 18 Kyr, while in the tropics it was placed at only 0 to 2°C colder. This view was based on results of the Climate Long-Range Investigation and Mapping Program (CLIMAP 1976), which was concerned with the climates of the last glacial and interglacial interval, and the Cooperative Holocene Mapping Project (COHMAP 1988), which attempted to reconstruct northern hemisphere climates at selected time intervals of the Holocene (i.e., the past 11 Kyr).

Information was slowly accumulating, however, that suggested climates were not as uniform in the tropics during the late Cenozoic as the CLIMAP and COHMAP data suggested. The early work of van der Hammen (e.g., van der Hammen, Absy, & Gonzalez 1960) indicated that the MAT was about 8°C colder at glacial maximum at 2,560-meter (m) elevation in the Sabana de Bogotá, Colombia; subsequent work established that significant temperature variations had occurred at high elevations throughout the tropics (e.g., Hooghiemstra 1984).

It was uncertain, however, whether these variations extended into the tropical lowlands. The Haffer model of biological diversification assumed that they did (Haffer 1969), and there was supporting evidence for this assumption (Prance 1982). Some version of the model still appears valid (see review in Burnham and Graham 1999); its mechanism depends on cool and dry climates during glacial intervals, which alternate with warmer and wetter periods during Amazonia interglacials. During the former intervals, the dry caatingas-cerrado vegetation from the surrounding uplands would move onto the lowlands, and geographically and reproductively isolate the rainforest into refugia where moist conditions would be maintained during drying cycles, such as at the confluency of major rivers or at the base of mountain slopes. During the latter intervals, the rainforest would expand from these refugia, coalesce into the nearly continuous cover as at present (thereby facilitating hybridization), and the caatingas-cerrado vegetation would move back onto the drier slopes.

Direct evidence from the Amazon lowlands is emerging now based on noble gases ($5.4^{\circ} \pm 0.6^{\circ}\text{C}$ cooler; Stute et al. 1995), pollen diagrams (van

der Hammen and Absy 1994), and speciation patterns among arboreal echimyid rodents derived from mitochondrial DNA (mtDNA) analyses (de Silva & Patton 1993). In addition, strontium-calcium ratios in corals from Barbados (lat. 13° N) suggest temperatures were 5°C cooler at 19 Kyr (Guilderson, Fairbanks, & Rubenstone 1994). Thus, an important revision in our concept of tropical climates is the increasing acceptance that temperature fluctuations in the range of 4–6°C likely affected terrestrial lowland populations throughout the late Cenozoic.

A second development is realizing how the rapid pace of these changes compared with the older four-stage model, which depicted a more leisurely rate of climatic and glacial fluctuations. According to the four-stage model there were four glacial advances separated by three interglacials, each of ~175,000 years duration, in addition to the present interglacial (Holocene) that began at approximately 11 Kyr. Data from the Ocean Drilling Program, the Deep Sea Drilling Project, the Greenland Ice Core Project, and the Greenland Ice Sheet Program II now show that, for the past ~800,000 years, northern hemisphere glaciations have followed the 100,000-year Milankovitch eccentricity cycle. [This cycle is based on the fact that Earth's orbit around the Sun is not a perfect circle, but an ellipse. Furthermore, there is a patterned variation in the shape of the ellipse (eccentricity), so that at times Earth is closer to the Sun (the perihelion) or farther away (the aphelion), and this variation observes a 100,000-year cycle.] Oxygen isotope studies from deep-sea cores and other evidence reveal nine glacial cycles within the past ~800,000 years, with glacial intervals lasting ~90,000 years and interglacial intervals lasting only ~10–11,000 years (Johnson 1982; see review in Graham 1999a, 40, 274–280).

Superimposed on these longer cycles are shorter ones of a few thousand years (known as Heinrich events) and of a few hundred years or less in duration [called Dansgaard-Oeschger (D-O) events]. The pace of these fluctuations is quite rapid: “in the period from 40 to 8 Kyr there were sudden changes of 5–10°C that sometimes lasted less than 5 years, and in the past 8 ky [thousand years] changes of up to 10–12°C were recorded in a few decades and lasted as little as 70 years” (Graham 1999a, 40). These data were derived from the high latitudes; the question was whether they were expressed further south and affected the terrestrial biota. Some evidence is emerging that they did.

Lake Tulane in Avon Park, south-central Florida, occupies a limestone sinkhole; an 18.5-m core provided pollen and spores that reflected vegetational changes for the past 50,000 years (Grimm et al. 1993; Watts and Hansen 1994). Of special interest are peaks in the amount of *Pinus* (pine) pollen for periods 14–16, 21–23, 26–28, 30–33, 36–37, and 48–51 Kyr. All but the 30–33 Kyr interval correspond with Heinrich events (Figure 3.4). This suggests that the rapid climatic changes, documented in North Atlantic

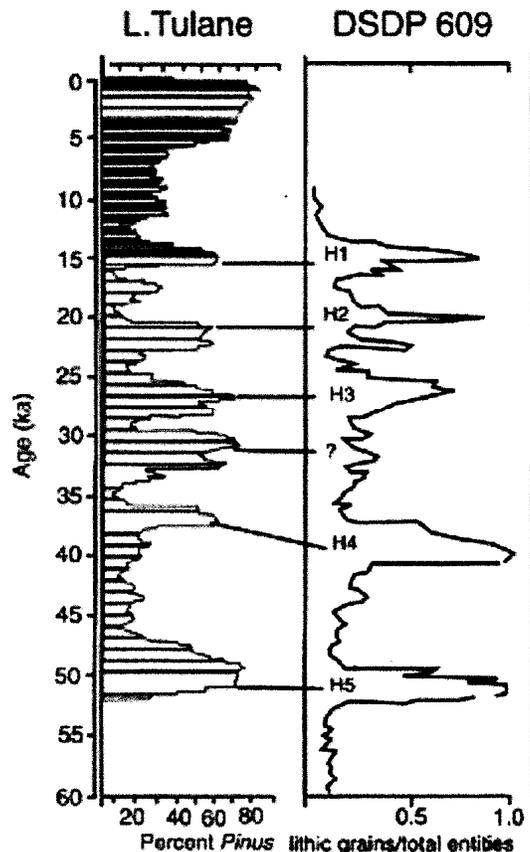


FIGURE 3.4. Pollen profile from Lake Tulane, Avon Park, Florida, showing pine pollen peaks, and DSDP (Deep Sea Drilling Project) site 609 (north Atlantic) Heinrich events 1-5. (Source: Reprinted from *Palaeography, Palaeoclimatology*, Vol. 109, Watts and Hansen, "Pre-Holocene and Holocene pollen records of vegetation history from the Florida Peninsula and their climatic implication," pp. 163-176. Copyright 1994 with permission from Elsevier Science.)

marine sediments, affected lowland terrestrial communities at least as far south as lat. 27.5°N . It is further known that the most tumultuous times are at the glacial-interglacial interface.

A third aspect of climate to emerge recently is the correlation between El Niño–Southern Oscillation (ENSO) events and a myriad of global temperature and precipitation patterns. An El Niño is a warming of equatorial Pacific Ocean waters with consequent atmospheric disturbance and redistribution of rainfall. During El Niño years there is a weakening of the northeast trade winds, and few hurricanes form in the Gulf of Mexico and the Caribbean Sea. In non–El Niño years, hurricanes increase by tenfold and bring immense amounts of water suddenly and unpredictably into the region. Notable examples are "the Great Hurricane" of 1831 that killed over

1,500 people on Barbados; Hurricane Floyd of 1999, which was one of the fiercest atmospheric disturbances ever recorded in the Atlantic Ocean; and, particularly noteworthy, Hurricane Gilbert, with recorded windspeeds up to 280 km/hr. (175 mi/hr.) that devastated the Yucatán Peninsula in 1988. During these disturbances, unrelenting torrents of rain can strike areas marginal to the path of the hurricane, such as those that fell for weeks across central Mexico in October 1999.

There is an imprecise cycle to ENSO events, but they generally occur every three and seven years and persist for three or more seasons, with the strongest effects often lasting one to two years. The sequence of some strong ENSO events for the nineteenth and twentieth centuries is given in Box 3.1. There is evidence from lake sediments in New England (17,000 years old; Rittenour, Brigham-Grette, & Mann 2000) and from corals (100,000 years old; Hughen, Schrag, & Jacobson 1999) that El Niños are a long-established feature of global climates. One of the many significant contributions of modern climatological research has been to provide a chronology for ENSO events and to demonstrate the extent of their effect on regional precipitation patterns, including those of the Maya lowlands.

VEGETATIONAL HISTORY

The nature of the mid- to late-Cenozoic vegetation leading up to the modern communities of Mesoamerica is recorded in a sequence of Oligo-Miocene palynofloras from mangrove-bearing lignites along the Front Ranges and High Plateaus physiographic province of Chiapas (Langenheim, Hackner, and Bartlett 1967; Tomassini-Ortiz and Martínez-Hernández 1984; Martínez-Hernández 1992; Palacios and Rzedowski 1993; Graham 1999b), in Mio-Pliocene upland swamp deposits of northern Guatemala

BOX 3.1. Strong (S) to very strong (VS) ENSO events in the nineteenth and twentieth centuries.

1803–1804 (S+)	1877–1878 (VS)	1925–1926 (VS)
1814 (S)	1884 (S+)	1932 (S)
1828 (VS)	1891 (VS)	1940–42 (S)
1844–1845 (S+)	1899–1900 (S)	1957–1958 (S)
1864 (S)	1911–1912 (S)	1972–1973 (S)
1871 (S+)	1917 (S)	1982–1983 (VS)

Source: Graham 1999a, 32, and references cited.

(Graham 1998), and in mangrove-bearing lignites of the middle Pliocene Paraje Solo palynoflora near Coatzacoalcos in Veracruz, Mexico (Graham 1976). An interesting pattern evident in these floras is that the older Oligo-Miocene assemblages contain little or no pollen of northern temperate elements [e.g., *Abies* (fir), *Picea* (spruce), *Juglans* (hickory), *Liquidambar* (sweetgum), *Quercus* (oak), *Ulmus* (elm), and others], while pollen is present in Miocene and younger floras. The event that correlates with their gradual introduction into the northern Latin American biota is the global temperature decline that began near the end of the early Miocene (Graham 1999a, 86–92; 1999c). By the middle Pliocene (as shown by the Paraje Solo flora), the principal components of the modern vegetation were in place—with one exception—and final modernization was accomplished during the climatically turbulent events of the Quaternary.

The exception was the absence (or poor development) of the lowland neotropical rain forest near its present northern limits in Veracruz. The dominants of the modern community include *Bernoullia*, *Brosimum*, *Calophyllum*, *Dialium*, *Ficus*, *Pseudolmedia*, and *Terminalia*. None of these were recovered from the middle Pliocene Paraje Solo Formation of coastal southeastern Veracruz. Rather, the prominent paleocommunities represented by pollen were coastal mangrove, upland deciduous and pine-oak forest, and even the high-altitude bosque de oyamel [*Abies* (fir) and *Picea* (spruce)]; the latter no longer grow this far south in Mexico].

Although the middle Pliocene was globally a warm interval (Cronin and Dowsett 1991; Wrenn, Suc, and Leroy 1999), upwelling of cold bottom waters, intensified by the closure of the Isthmus of Panama 3.5 Ma, was likely a factor in cooling coastal temperatures. The effects were disruption of the rain forest; lowering of ecotones, thereby bringing the deciduous forest, pine-oak forest, and high-altitude conifer forest into closer proximity to the lowland depositional basin; the appearance of *Picea* far south of its present range; and possibly the introduction of *Quercus oleoides* and *Podocarpus guatemalensis*, primarily upland temperate genera, into the present Veracruz lowlands. If this is the vegetational history in the early stages of the late Cenozoic climatic fluctuations, it is likely that the biota of lowland Mesoamerica was an especially dynamic assemblage in terms of its range and composition during the tumultuous Quaternary.

Another aspect of late Tertiary vegetation relevant to its subsequent modernization is that even though there were no extensive dry communities evident in the Pliocene flora, there were dry elements growing in the region. These included *Acacia*, *Bursera*, *Casearia*, *Celtis*, *Cupania*, *Eugenia*(?), and *Mimosa*. They probably grew in drier habitats afforded by slope, exposure, and edaphic conditions, or in local communities such as the

current *Nolina-Hechtia-Agave* desert in the limestone hills west of Perote on the Veracruz-Puebla border (Gómez-Pompa 1973). These restricted communities and preadapted forms of the Pliocene were representative of taxa that were available to coalesce and expand into dry deciduous forest and related vegetation types as dry conditions developed during intervals of the Quaternary.

There is a general relationship between cool climates and reduced precipitation because, with lower temperatures, less water evaporates from the ocean surface into the atmosphere. This system operated in the Maya lowlands during the Quaternary as demonstrated by pollen profiles from lakes in Guatemala (Leyden 1984, 1987; Leyden et al. 1993, 1994). Marine isotopic data indicate that temperatures were cooler by 4.7 to 6.5°C approximately 36 to 24 Kyr, and pollen profiles from Late Quexil provide proxy data from the vegetation that precipitation was somewhat less than at present.

Approximately 24 to 12 Kyr, temperatures were lower by 6.5 to 8.0°C, and conditions were arid as indicated by the vegetation, lower lake levels, and an increase in charred particles. When this pattern is combined with recent evidence for the rapidity of climatic change, and the increasing documentation that these changes affected the terrestrial biota in the lower latitudes (e.g., Figure 3.3), the dynamic nature of the environment is evident. The response of the vegetation to these changes is reflected in several additional spore and pollen profiles and other evidence from the region (Cowgill et al. 1966; Tsukada & Deevey 1967; Wiseman 1978, 1983; Covich 1978; Miksicek et al. 1981; Folan & Hyde 1985; Hansen 1990; Hodell, Curtis, & Brenner 1995; Jauregui 1997).

CONCLUSION

Events that shape the conditions under which civilizations must live include those of ancient geologic origin that determine the structure, topography, and substrate of the physical environment. These features of the lowland Maya region were set in the Cretaceous with the formation of a submerged carbonate platform that gave rise to a karst topography, creating the need for innovative water conservation practices and devices, and with the asteroid impact that led to the development of cenotes. Subsequent climatic trends favored the development of a seasonally dry vegetation and subjected the region to fluctuating periods of cool/dry and warm/moist conditions. These cycles are a long-term feature of Mesoamerica, and the most rapid changes occur at glacial-interglacial boundaries as climates adjust to new thresholds. With these geologic, climatic, and biotic components of the lowland Mesoamerica ecosystem in operation, the region

was now to experience a novel interaction with human occupants that would begin a new phase in its environmental history.

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Chapter 4

Paleolimnological Approaches for Inferring Past Climate Change in the Maya Region: Recent Advances and Methodological Limitations

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INTRODUCTION

The past two decades have witnessed renewed interest in exploring the climatic context in which lowland Maya culture arose, developed, and collapsed. During the early part of the twentieth century, it was generally assumed that neotropical climate had remained relatively stable throughout the Holocene. That myth persists today, in part because isotope studies from Greenland ice cores indicated minimal temperature change at high latitudes over the last 11,500 years (Oldfield 2000). With respect to Mesoamerica, it was thought that recent instrumental measurements of temperature and rainfall on the Yucatán Peninsula were no different from climate conditions that prevailed during the period of ancient Maya florescence. As approaches to reconstructing past climate became more sophisticated and began to focus on low-latitude sites, it was apparent that tropical climate conditions following the Pleistocene were not static, but varied considerably, especially with respect to moisture availability (e.g., Street and Grove 1976; Abbott et al. 1997; Bridgwater, Heaton, and O'Hara 1999; Verschuren, Laird, and Cumming 2000; deMenocal et al. 2000). Scientists working at sites around the globe inferred past climate changes using numerous sources of

information, including marine and freshwater sediments, pollen analysis, tree ring data, tree-line migration, shifting lake stages, and glacial advances and retreats. Soon, there was ample evidence of worldwide Holocene climate fluctuations on millennial and centennial timescales, and terms such as “hypsihermal,” “Medieval Warm Epoch,” and “Little Ice Age” became established in the paleoclimatology lexicon.

In the Maya lowlands, archaeologists were also beginning to uncover evidence of long-term climatic instability. At El Mirador, in Petén, Guatemala, Terminal Preclassic housemound groups were discovered in bajos that are presently subject to seasonal inundation. It is unlikely that considerable labor would have been invested for construction in areas prone to annual flooding (Dahlin 1983). At Lake Cobá, in Quintana Roo, Mexico, Maya-constructed walkways on the lakeshore are presently underwater, suggesting that they were built during a drier period when the lake stage was lower (Folan et al. 1983).

A reliable water source is essential for both human physiological requirements and agriculture. Given the high seasonality and low total annual rainfall across much of the Yucatán Peninsula, combined with the scarcity of accessible surface water and groundwater, the Maya took special steps to obtain sufficient water in some localities. Archaeologists have long noted the proximity of some Maya archaeological sites (e.g., Dzibilchaltún, Chichén-Itzá, Yaxhá, and Ceibal), to available water source including wetlands, cenotes, lakes, and rivers (e.g., Wilson 1984; Adams 1980; Rice and Rice 1990). Where surface water and groundwater were not readily available, the Maya built water storage facilities such as *aguadas* and reservoirs (Matheny 1976; Scarborough and Gallopín 1991; Back 1995; Scarborough 1993). The importance of water to the Maya is clearly evident in their mythology, art, and architecture (Back 1981).

Because much of the Yucatán Peninsula lies in a zone that is climatically marginal for agriculture, small changes in precipitation income can have devastating effects on crop yields. The importance of the annual hydrologic cycle in the Maya lowlands has always been acknowledged. Once it became apparent that late Holocene climate was variable, archaeologists began to address how changes in moisture availability affected prehistoric Maya settlement distributions and cultural development (Folan et al. 1983; Gill 2000; Messenger 1990). It was suggested that long-term climate changes influenced the human population at Dzibilchaltún directly by limiting access to water in Cenote Xlacáh, and indirectly by affecting the local flora and fauna (Folan 1985).

Evidence for climate change during the Maya epoch was emerging from the archaeological record (Dahlin 1983; Folan 1985; Folan et al. 1983). Independently, researchers began to explore the paleoclimate of the Maya area using global circulation models (GCMs), and hindcasting climate on the

Yucatán Peninsula by correlation with long-term temperature records from distant sites. Gunn and Adams (1981) proposed that precipitation in southern Mexico was correlated with temperature in the northern hemisphere. They showed that cold northern hemisphere temperatures produce wetter weather on the Yucatán Peninsula, and warmer temperatures are associated with drier conditions due to a reduction in midwinter rainfall. By correlation with glacial advances and retreats in Alaska and Sweden, Gunn and Adams (1981) inferred shifts in available moisture for the Maya lowlands during the latter Holocene, and speculated that reduced precipitation around A.D. 900 (1150 ¹⁴C yr. B.P.) negatively impacted both Maya trade and agriculture.

More recently, Gunn, Folan, and Robichaux (1995) used an alternative approach to retrodict moisture availability in the Maya region. They first correlated mean global temperature with seasonal discharge from the Candelaria River, Mexico, for the years 1958 to 1990; this analysis convinced them to reverse their earlier ideas, and to conclude that global warm periods are associated with wetter climate in the Maya lowlands. They discovered that warm temperatures preclude a local dry season, interfering with milpa production by preventing burning of felled vegetation. Cold global temperatures postpone the onset of the seasonal rains and delay planting. Gunn, Folan, and Robichaux (1995) argued that intermediate temperatures promote the wet-dry seasonality that is most conducive to successful swidden agriculture. They inferred past mean global temperature using a combination of October orbital precession, an index of volcanism, and solar energy output. Next, they reconstructed discharge of the Candelaria River—that is, past climate conditions on the Yucatán Peninsula—for the period of Maya occupation (approximately the last three thousand years), and related river runoff to several key developments in Maya prehistory. According to their model, the ninth century A.D. Maya Collapse occurred during a period of global cold temperatures and drought conditions in the Maya lowlands.

Paleoclimatological studies were also undertaken using variables found in lake and wetland sediment cores collected at sites throughout the Maya lowlands. Because direct measurements of past climate conditions cannot be made, “proxy” variables such as pollen, diatoms, and invertebrate remains are used to reconstruct past climate. Pollen analysis provided reliable information about the Pleistocene/Holocene climate transition in the southern Maya lowlands (Leyden 1984; Leyden et al. 1993; Leyden et al. 1994), but proved to be of little utility for inferring climate conditions in the later Holocene because watersheds in Petén, Guatemala, were densely populated (Rice and Puleston 1981; Rice, Rice, and Deevey 1985; Rice and Rice 1990), and regional, human-mediated deforestation over the last 3,000 to four 4,000 years overwhelmed any climate signal (Bradbury et al. 1990; Deevey 1978; Deevey et al. 1979; Vaughan, Deevey, and Garrett-Jones 1985;

Brenner, Leyden, and Binford 1990; Leyden 1987; Hansen 1990; Brenner 1994; Islebe et al. 1996; Curtis et al. 1998).

Alternatively, paleoclimate inferences have been based on paleosalinity changes in water bodies, using assemblages of sedimented microfossils from groups of organisms with known salt tolerances. For instance, salinity changes over the past 7,000 years were inferred at Cobweb Swamp, northern Belize, based on subfossil communities of gastropod mollusks (snails) and small crustaceans called ostracods (Alcala-Herrera et al. 1994). Shifts in the salt content of the wetland were initially driven by sea-level rise. The last 3,500 years of the record is thought to have been influenced principally by climate change. Long-term lake level trends (i.e., moisture availability) were also inferred based on salinity preferences of diatom assemblages from lake sediment cores collected along a transect from Cenote San José Chulchacá, in the dry area west of Mérida, to Lake Cobá, in the wetter area of eastern Quintana Roo (Figure 4.1) (Whitmore et al. 1996). Each diatom taxon has specific ecological requirements and possesses a distinctive, identifiable siliceous “skeleton” or frustule that is preserved in lake sediments.

There are advantages and disadvantages to the various paleoenvironmental approaches that have been used to address late Holocene climate change in the Maya area. Modeling efforts did not require collection of new data, but relied on data from remote sites and assumed that modern correlations between climate variables in Yucatán (e.g., rainfall), and temperature in high-latitude sites, for example, could be projected back in time over millennia. Paleolimnological data from the Yucatán Peninsula have the advantage of coming from the region of interest, but there are limitations, nonetheless, to their use. As mentioned previously, human disturbance over the last three to four millennia had such a dramatic impact on regional vegetation that the pollen record could not be employed to decipher late Holocene climate change in the region. Inferences based on stratigraphic shifts in community assemblages of ostracods, gastropods, and diatoms require knowledge about the ecology of the enumerated taxa. There are, however, few ecological studies of the contemporary plankton and benthos in the Maya lowlands, and regional calibration data sets have not been developed that quantitatively relate water column chemistry to the relative abundance of various taxa. Furthermore, studies of stratigraphic shifts in subfossil communities require specialized sample preparations, identification of numerous taxa, and enumeration of large numbers of individuals.

As early as the 1970s, a new technology was being applied to the question of Maya paleoclimate—that is, reconstruction of past moisture conditions based on stratigraphic measurement of the oxygen isotope signal in the sedimented carbonate shells of aquatic invertebrates (Covich and Stuiver 1974). By the 1990s, advances in stable isotope mass spectrometry had facilitated the use of small sample sizes and permitted rapid analysis,

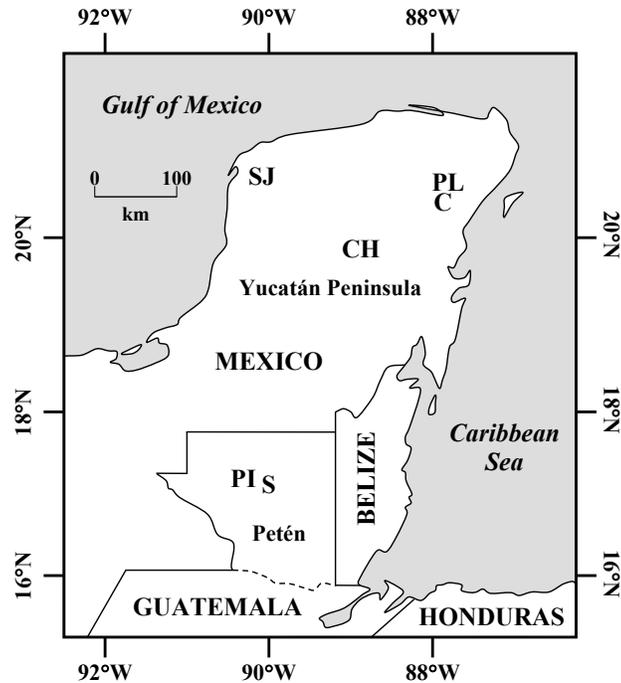


FIGURE 4.1 Map of the Maya lowlands. Coring sites referred to in the text include Cenote San José Chulucacá (SJ), Lake Punta Laguna (PL), Lake Cobá (C), and Lake Chichancanab (CH) in the northern Yucatan Peninsula, and Lake Petén-Itza (PI) and Lake Salpetén (S) in the Central Petén Lake District, Guatemala.

making this technique ideal for generating high-resolution reconstructions of past changes in moisture availability. In this chapter, the theoretical basis for using stable isotope geochemistry to address Maya paleoclimate is explained. The selection of appropriate study lakes is discussed as are the advantages and limitations of applying isotope-based methods for climatic inferences. Results and interpretations from recent investigations in the Maya lowlands are also summarized.

THEORETICAL BASIS FOR ISOTOPE-BASED PALEOCLIMATE STUDIES

There are three naturally occurring stable isotopes of oxygen: ^{16}O , ^{17}O , and ^{18}O . The lightest isotope (^{16}O) is most common, representing 99.7630 percent of the isotope pool. ^{17}O is the rarest, representing only 0.0375 percent of the total, while ^{18}O accounts for 0.1995 percent. Because of their different masses, the isotopes behave differently when they enter into physical, chemical, and biological processes in the environment. It is the differential behavior of the heaviest (^{18}O) and lightest (^{16}O) isotopes, referred to as

fractionation, and their changing relative abundance in the environment, that is exploited for paleoclimate reconstructions. The isotopic signature, or $\delta^{18}\text{O}$ of environmental samples, can be measured by isotope ratio mass spectrometry; results are presented in standard delta (δ) notation. This is an expression of the $^{18}\text{O}/^{16}\text{O}$ ratio in a sample relative to the ratio in the Vienna Pee Dee Belemnite (VPDB) standard, expressed on a per mil (‰) basis:

$$\delta^{18}\text{O} = \frac{(^{18}\text{O}/^{16}\text{O})_{\text{sample}} - (^{18}\text{O}/^{16}\text{O})_{\text{VPDB}}}{(^{18}\text{O}/^{16}\text{O})_{\text{VPDB}}} \times 10^3 \text{ ‰}$$

Talbot (1990), Chivas et al. (1993), Curtis and Hodell (1993), Holmes (1996), and others have presented the rationale for using the stable isotope ($\delta^{18}\text{O}$) signal in sedimented freshwater carbonate shells to reconstruct past climate conditions. The isotope ratio ($^{18}\text{O}/^{16}\text{O}$) in sedimented shell material is governed by the isotope ratio in the lakewater at the time the organism lived, the temperature at which carbonate precipitation occurred, and biological fractionation by the organism (von Grafenstein, Erlernkeuser, and Trimborn 1999). Because there is little evidence for major excursions in the mean temperature of the tropics during the Holocene, the changing $\delta^{18}\text{O}$ of lakewater over the last 10,000 years has been the major determinant of the $\delta^{18}\text{O}$ in shell carbonate. The $^{18}\text{O}/^{16}\text{O}$ ratio of lakewater has, in turn, been controlled by hydrologic variables. Assuming that the $\delta^{18}\text{O}$ of regional rainfall has remained fairly constant during the Holocene, relative changes in hydrologic inputs (precipitation and runoff) and outputs (evaporation and outflow) govern the in-lake oxygen isotopic ratio (Figure 4.2).

In tropical, closed-basin lakes (i.e., those that lack significant overland outflows), the factor that most influences the waterbody's hydrologic budget is the relationship between evaporation (E) and precipitation (P) (Fontes and Gonfiantini 1967; Gasse et al. 1990; Lister et al. 1991). During dry periods (high E/P), ^{18}O becomes relatively concentrated in the lake water because H_2^{16}O , with its higher vapor pressure, is preferentially lost to evaporation. Conversely, during moist periods (low E/P), the water column is relatively depleted of ^{18}O (Figure 4.2). Measurements of the $\delta^{18}\text{O}$ signature of rainfall and lake water in the Maya lowlands demonstrate that ^{18}O is concentrated in regional lakes due to evaporation (Figure 4.3).

Short-lived aquatic organisms that form calcium carbonate shells preserve a record of the E/P ratio that prevailed during their lifetimes (von Grafenstein, Erlernkeuser, and Trimborn 1999). When they die, their remains are buried in sediments on the lake bottom, thereby preserving an archive of past climate change (Figure 4.4). The stratigraphic paleoclimate record can be deciphered by mass spectrometric measurement of the $\delta^{18}\text{O}$ of sedimented shells. More positive $\delta^{18}\text{O}$ values generally indicate higher E/P

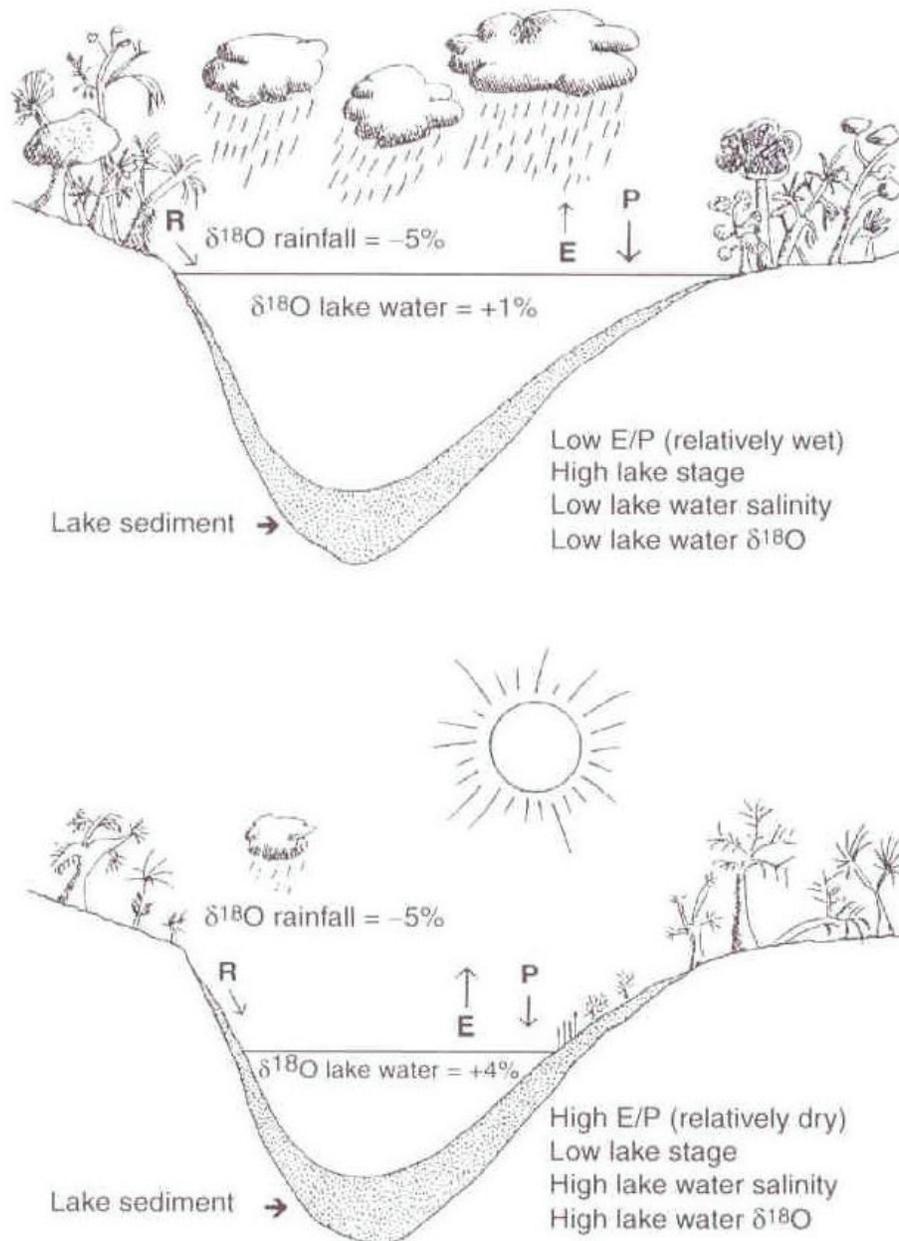


FIGURE 4.2. Cross section of a hypothetical closed-basin lake in the Maya lowlands, showing differences with respect to lake stage, lake water salinity, and lake water $\delta^{18}\text{O}$ during relatively wet (top) versus relatively dry (bottom) Holocene periods. Note that the $\delta^{18}\text{O}$ signal of input (rainwater) is assumed to have remained constant during wet and dry Holocene periods. In watersheds with negligible surface outflow, changes in lake volume are a function of the shifting relation between evaporation (E) and precipitation (P) over the lake and surface runoff (R).

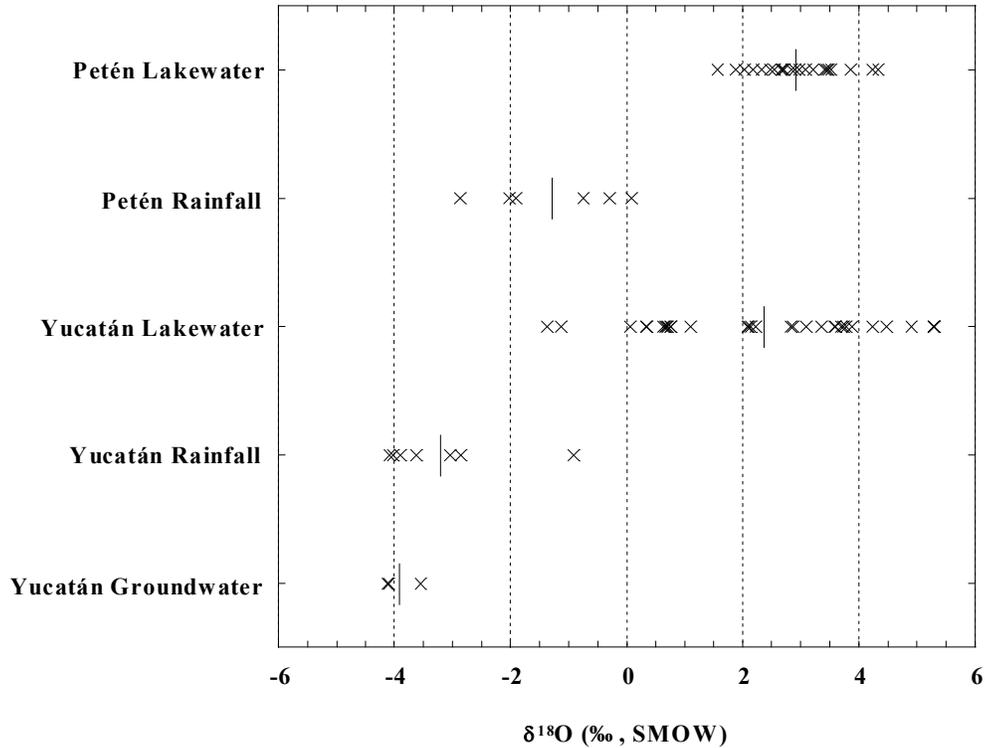


FIGURE 4.3. Oxygen isotope ($\delta^{18}\text{O}$) signatures of lake water, rainwater, and groundwater collected at sites in the Central Petén Lake District, Guatemala, and northern Yucatán Peninsula, Mexico. The $\delta^{18}\text{O}$ of samples is expressed relative to Standard Mean Ocean Water (SMOW). Individual sample results are indicated by the symbol x, and the mean value for samples is shown as a vertical line. For Petén, 22 lake water and 6 rainwater samples were analyzed. In the Yucatán Peninsula, the number of samples analyzed from lake water, rainwater, and groundwater were 32, 7 and 3, respectively. Differences between values for lake water and rainwater illustrate that ^{18}O is concentrated in lakes as a consequence of evaporation. In the long term, weighted mean $\delta^{18}\text{O}$ values for rainwater collected at other low-elevation, circum-Caribbean sites range from -5.65‰ to -4.01‰ . (Source: Rozanski, Araguás-Araguás, and Gonfiantini 1993.)

(drier) conditions and/or decreased surface and groundwater inflow, whereas more negative values indicate relatively lower E/P (moister) conditions and/or increased inflow at the time the organism lived.

CHOOSING A STUDY SITE

The two taxonomic groups that are commonly employed for isotope-based climate reconstructions are the ostracods, which form bivalve shells of calcite, and the gastropods (snails), which are mollusks that make

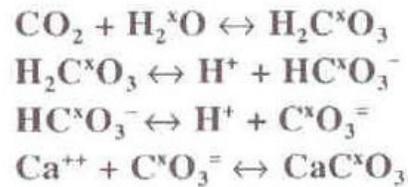
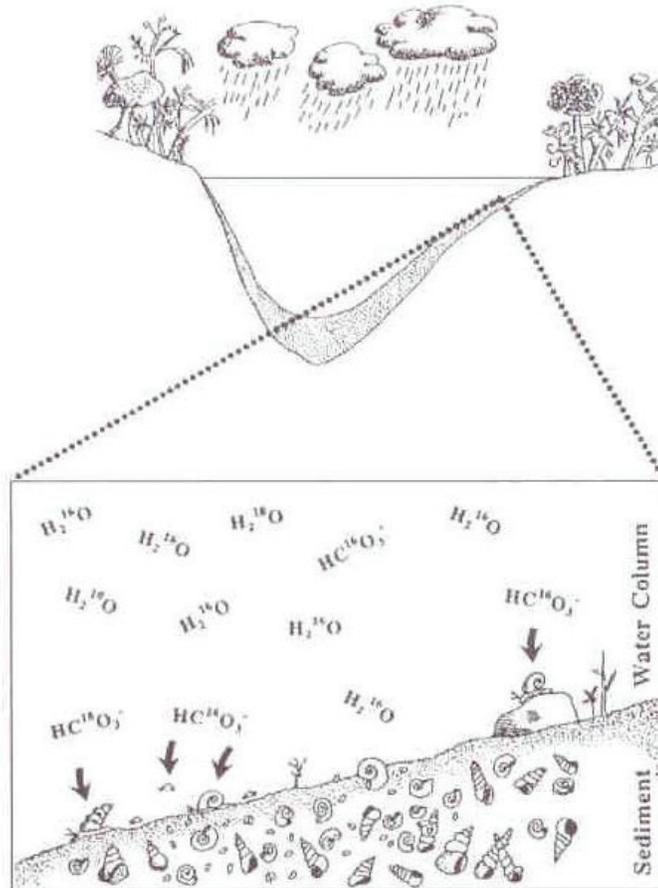


FIGURE 4.4. Cross section of a hypothetical, closed-basin lake in the Maya lowlands (top), with a close-up of the sediment-water interface (bottom). The carbonate equilibrium equation is included below the diagram. Note that the isotopic signature of the water molecule (H_2^xO) in the equation, denoted by x , is reflected in the precipitated calcium carbonate (CaC^xO_3). Water and bicarbonate ions (HC^xO_3^-) contain $^{18}\text{O}/^{16}\text{O}$ ratios that reflect climate (E/P) conditions (see Figure 4.2). Ostracods and gastropods living above the sediment surface make calcium carbonate (CaCO_3) shells that reflect the $^{18}\text{O}/^{16}\text{O}$ ratio of the lake water in which they live. When they die, their remains are incorporated into the lake sediment, thereby preserving a record of past climate change (E/P) that can be interpreted through mass spectrometric measurement of the $\delta^{18}\text{O}$ of the sedimented shells.

aragonite shells. The first step in undertaking a study of oxygen isotope changes through time is collection of a sediment core from an appropriate lake. Not all waterbodies, however, yield satisfactory material for inferring past climate, and certain conditions must be met to increase the probability of generating an interpretable paleoclimate record (Table 4.1). First, the lake should lie within the geographic region of interest. Extrapolation of findings from distant sites is problematic because of spatial climate variability and differences in “boundary” conditions between the area of interest and the sediment study locality.

Second, the selected study lake should be relatively “closed” hydrologically, with most water lost to evaporation, rather than via overland outflow or seepage. Third, morphometrically, the lake must be sufficiently deep and have enough volume that it does not desiccate during periods of low rainfall. Drying at the core site can cause discontinuities (hiatuses) in sedimentation, and may lead to the erosion of sediments that were deposited previously. On the other hand, lakes that are too large and deep may display negligible isotope shifts in response to modest changes in E/P, because they lose or gain only a small fraction of their total volume when E/P changes occur. In general, tropical lakes with maximum depths of about 15 to 25 meters (m) yield acceptable records.

All factors that alter the hydrologic regime of a waterbody can potentially influence its volume, as well as the salinity and stable isotope signature of its water (see Figure 4.2). For lakes lacking outflows, shifts in precipitation and runoff (input) and evaporation (output) are probably of paramount importance to the hydrologic budget. Nevertheless, processes that change runoff (input) may also influence the lake hydrology. For instance, massive deforestation in a drainage basin can alter watershed transpiration and soil moisture storage (Bosch and Hewlett 1982; Bruijnzeel 1990; Stednick 1996), perhaps enhancing delivery of relatively ^{18}O -depleted rainfall and groundwater to the lake (Rosenmeier, Hodell, Brener, Curtis, Martin, et al. 2002).

The chemistry of the lakewater is crucial in that it must have sufficient dissolved inorganic carbon [e.g., carbonate (CO_3^{-2}) and bicarbonate (HCO_3^{-1})] to enable invertebrate shell formation. Furthermore, the lake sediments should be rich in shell remains (Figure 4.5).

Those remains must also be well preserved, because isotopic signatures can be altered by diagenesis (i.e., postdepositional changes such as dissolution and re-precipitation of shell carbonate). Sediment cores should possess remains of adult organisms from at least one taxon at all sediment depths throughout the entire record because some species may precipitate calcium carbonate (CaCO_3) out of isotopic equilibrium with the lakewater. Species-specific isotopic fractionation during shell formation is referred to as “vital effects.” If a single species is not encountered throughout the entire record,

TABLE 4.1. Criteria for lakes used in isotope-based ($\delta^{18}\text{O}$) reconstructions of Maya paleoclimate

Lake Variable	Requirements
Location	The lake should be located near the archaeological site or region of interest. The Maya lowlands are spatially variable with respect to moisture availability, making it difficult to extrapolate paleoclimate results over great distances.
Hydrology	The basin should be fairly closed with respect to hydrologic outputs, losing most of its water to evaporation (E).
Depth	The lake should be sufficiently deep that the core site will not desiccate during dry periods.
Volume	Excessively large, deep lakes may be unresponsive to climate changes as they gain or lose a small proportion of their total water volume due to changes in E/P. There must be a balance between sufficient depth and appropriate volume (V).
Water chemistry	Lake water must be sufficiently hard (i.e., have high enough bicarbonate [HCO_3^{-1}]) to permit shell formation and preservation.
Microfossil abundance	Well-preserved ostracod and snail shells should be abundant throughout the sediment core
Microfossil taxonomy	Multiple individuals of a single taxon should be measured at each sampling level throughout the profile to control for "vital effects." Preferably, several taxa with differing ecologies should be analyzed to assess consistency of the long-term E/P signal.
Chronology	Chronology in karst are as should be based on AMS- ^{14}C dating of terrestrial organic matter (e.g., seeds, stems, leaves, or pollen grains) to avoid hard-water-lake error. Lacking abundant terrestrial remains, steps can be taken to correct ages obtained from aquatic remains such as ostracods or snails.
Sedimentation rate	Sedimentation rates should be sufficiently high to permit paleoclimate reconstruction on a scale with high temporal resolution. Contiguous 1 cm sampling yields decadal resolution in lakes with mean sediment accumulation of 0.1 cm yr^{-1} . Excessively high sedimentation rates, especially those due to soil erosion, may dilute carbonate fossils.
Watershed	Factors that alter drainage basin hydrology (e.g., deforestation) may confound interpretation of $\delta^{18}\text{O}$ records.
Alternate proxies	Ideally, isotope-based E/P reconstructions should be supported by additional proxies such as sediment geochemistry (e.g., precipitated salts or trace metal ratios), or microfossils such as diatoms.

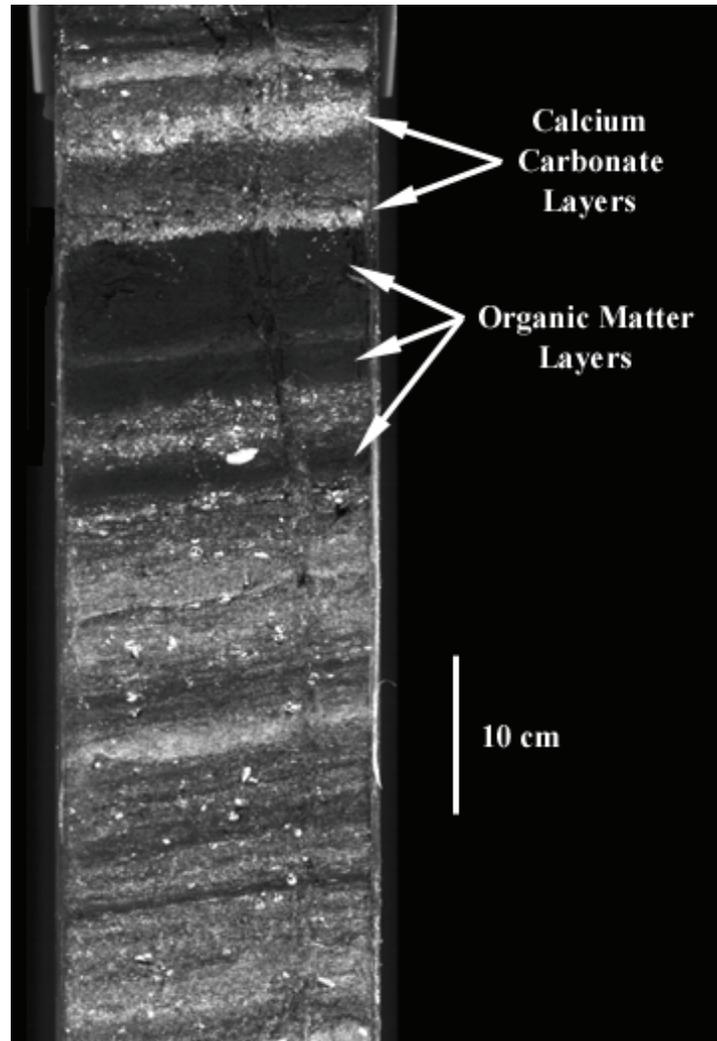


FIGURE 4.5. Section of a sediment core from Lake Punta Laguna in the Maya lowlands, showing finely laminated sediment consisting of organic matter (dark bands) and calcium carbonate (light bands). Note the high density of gastropods (white dots). Sampling intervals of 1 cm generally represent 5 to 20 years of sediment accumulation.

multiple species can be used, but their isotope signatures should be compared where they are found in the same stratigraphic levels to assess isotopic offset due to “vital effects.” Ideally, several taxa found throughout the profile should be analyzed separately so that multiple isotope records can be generated using organisms that occupy different ecological niches. In each stratigraphic level, multiple individuals of a given taxon will constitute a sample, and sample measurement yields the mean $\delta^{18}\text{O}$ for the sedimented assemblage.

Prior to collecting and subsampling a core, it is impossible to determine whether all the above criteria will be met. Nevertheless, the lake shoreline can be inspected for the presence of abundant small shells, and surface sediments throughout the lake can be sampled quickly with a dredge to establish the likelihood of collecting cores rich in carbonate remains.

The lake sediment core should have a continuous, datable record that covers the time period of interest. One analytical conundrum that has arisen in the Maya lowlands is the difficulty of generating reliable sediment chronologies. Lakes in karst country almost invariably have high bicarbonate (HCO_3^{-1}) concentrations in the water column that permit shell formation. It is, however, these same high bicarbonate concentrations that confound radiocarbon dates on organic matter and inorganic carbon (i.e., shells) of aquatic origin. This problem is called hard-water-lake error (HWLE) (Deevey and Stuiver 1964) and stems from the fact that some of the carbon in the carbon dioxide (CO_2) and bicarbonate (HCO_3^{-1}) used for photosynthesis by aquatic algae and other plants comes not from the atmosphere, but rather from the dissolution of ancient (e.g., Cretaceous, in the case of Petén, Guatemala), ^{14}C -depleted rocks in the watershed.

Similarly, snails and ostracods that form their shells from dissolved bicarbonate in such systems may incorporate ^{14}C -depleted carbon into their calcium carbonate shells. These processes lead to violation of a key assumption of radiocarbon dating—namely, that plants or shelled organisms fix ^{14}C from a carbon pool in equilibrium with the atmospheric ^{14}C concentration. This disequilibrium, which can make radiocarbon ages on aquatic organisms from karst lakes artificially old, can be transferred up the lacustrine food web, affecting dates on all materials of aquatic origin. The advent of accelerator mass spectrometry (AMS)- ^{14}C dating has remedied this problem to some degree by enabling the analysis of small pieces of terrestrial organic matter identified in lake cores. The most reliable chronologies are thus based on AMS- ^{14}C dating of terrestrial seeds, twigs, leaves, and even pollen grains. Paired dates (i.e., from the same core depths) on terrestrial (e.g., wood) and aquatic (e.g., shell) material from a core can provide an estimate of the magnitude of HWLE. These paired dates can sometimes be used to adjust, or correct, a chronology based largely on abundant shell remains.

The sediment accumulation rate at the coring site should be high enough to permit sufficient sampling resolution, but not so high that microfossils are diluted. Very high rates of sediment accumulation may permit high sampling resolution, but may also preclude recovery of a long record if the corer cannot penetrate the entire sediment lens. A rough rule of thumb is that average, long-term Holocene sedimentation rates in Maya-area lakes are on the order of 0.1 centimeters per year (cm yr^{-1}), so that contiguous 1-cm sampling intervals yield roughly decadal resolution on environmental changes.

Once again, it is difficult to evaluate the sedimentation rate at a core site prior to collection and dating of the profile.

High-resolution seismic surveying can help to assess sediment geometry and sediment distribution in the lake's subsurface (Figure 4.6). The reflections seen on seismic profiles usually image the bedding surfaces, and thus show stratigraphic horizons in the sediment record. By mapping geometric unconformities and units with characteristic seismic facies, one can establish a seismic stratigraphy, which partitions the sediment succession into seismic sequences. Mapping unconformities is particularly important, because it documents periods of non-deposition and/or erosion and can be used to reconstruct lake level changes. Thinning or thickening of seismic units also documents lateral changes in sedimentation rate. Seismic profiles can yield crucial information to identify appropriate coring sites for acquiring long, reliable sediment records of Holocene climate change that span the period of Maya occupation. Depending on the study objectives, seismic stratigraphies can be used to help choose the best coring sites to yield cores with high temporal resolution (high sedimentation rate, continuous sedimentation), long time sequences (low sedimentation rate, continuous sedimentation), or evidence of specific environmental changes (e.g., lake level fluctuations, or unconformities).

Recent studies in Lake Salpetén, Guatemala, illustrate the utility of using seismic surveys to choose coring locations. A north-south profile across the width of the lake (Figure 4.6) shows a steep, fault-controlled northern shore that leads to the deepest part of the basin (maximum depth = 32 m). In contrast, the slope of the southern shore is gentle. Intense sediment focusing has led to the deposition of a thick sediment package in the deepest part of the basin.

It is possible to correlate the seismic profile to Salpetén (SP) core 80-1, and identify lithologic changes associated with prominent reflectors, as well as determine the age of these reflectors using radiocarbon dating. Near the base of the sequence is a sharp reflector that coincides with the contact between gypsum and organic-rich, laminated gyttja, which marks the Pleistocene/Holocene boundary. The gyttja is overlain by a thick "Maya Clay" unit, which is an erosional deposit that has been equated with human-induced deforestation of the catchment. The base of the "Maya Clay" in SP core 80-1 was dated to 3160 ^{14}C yr. B.P. (about 1400 B.C.), by AMS- ^{14}C analysis of terrestrial material, suggesting that the Petén environment had already sustained Maya impact by the beginning of the middle Preclassic Period (about 1000 B.C.). The Maya clay is overlain by another organic-rich gyttja that was deposited following the Classic Collapse and subsequent reforestation of the watershed. Ongoing studies involve using the seismic profiles to map the three-dimensional distribution of the "Maya Clay" in the

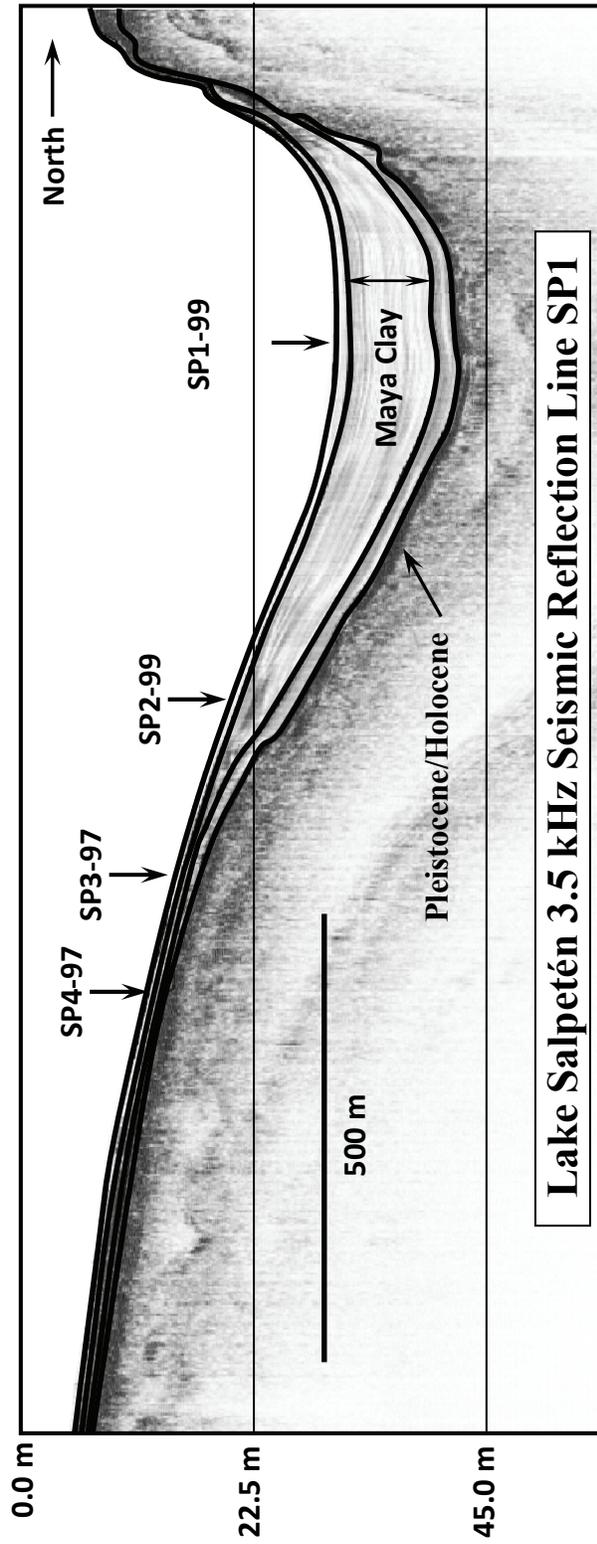


FIGURE 4.6 Single-channel, high-resolution seismic reflection profile from Lake Salpetén. Profile was recorded in digital format using a 3.5 kHz pinger source and GPS navigation. Note lateral variability in thickness of the sediment strata as well as several unconformities, in particular at shallow water depths. The profile for Lake Salpetén shows the sediment stratigraphy along the coring transects. Vertical arrows indicate approximate core locations. The seismic profile suggests the two cores from shallower water display discontinuities in sediment accumulation. Sub-bot-tom profiling, though not attainable in all lakes, can be enormously helpful for choosing core site.

basin and to estimate changing rates of erosion as a consequence of human impact on the environment.

COMPLEMENTARY SEDIMENT PROXIES

Study lakes should ideally contain additional sediment proxies that can be used to support isotope-based paleoclimate inferences. For instance, measurement of other geochemical variables in sedimented shell material, including their strontium/calcium ratio (Sr/Ca) and magnesium/calcium ratio (Mg/Ca), can be helpful for testing isotope-based paleoclimate interpretations (Chivas, De Dekker, and Shelley 1986; Chivas et al. 1993; Curtis and Hodell 1993; Holmes 1996). Diatoms have proven to be sensitive biological indicators of lakewater salinity, which in turn reflects local changes in moisture availability (Fritz et al. 1999). In waterbodies with high concentrations of dissolved ions, salts such as calcium sulfate (CaSO_4 = gypsum) or sodium chloride (NaCl) may precipitate during periods of low lake level and high salinity (Hodell, Curtis, and Brenner 1995). In addition to their utility as subjects for isotopic study, ostracod species assemblages reflect salt concentrations in a waterbody (Bridgwater, Heaton, and O'Hara 1999; Bridgwater, Holmes, and O'Hara 2000).

RESULTS AND DISCUSSION

Isotope records from the northern Yucatán Peninsula

The earliest effort to develop an isotope-based climatic reconstruction for the Yucatán Peninsula was undertaken by Covich and Stuiver (1974) at Lake Chichancanab. They retrieved a 12-m core of which approximately the topmost 9 m represented Holocene deposition. The oldest Holocene radiocarbon age in the core was 7380 ^{14}C yr. B.P. (6230 B.C.), and $\delta^{18}\text{O}$ measurements were run on *Pyrgophorus* snail shells at 17 Holocene stratigraphic levels, yielding an average sampling interval of about 500 years. Today, improvements in mass spectrometry enable rapid $\delta^{18}\text{O}$ analysis of very small samples, permitting the generation of continuous, high-resolution isotope stratigraphies. Whereas Covich and Stuiver (1974) had to amass sample weights of about 50 milligrams (mg), modern instruments are capable of measuring isotope ratios in samples weighing as little as 20 μg (micrograms).

In the 1990s, lake sites on the northern Yucatán Peninsula were re-cored to obtain high-resolution paleoclimate records that span the period of Maya occupation. To date, the most reliable isotope-based reconstructions of past E/P have come from Lake Chichancanab (19°50' N, 88°45' W) and Lake

Punta Laguna (20°38' N, 87°37' W). A 4.9 m core was collected from 6.9 m of water in Lake Chichancanab (Figure 4.7) and 1 cm sectioning of the profile yielded a mean sampling resolution of about nineteen years. The section terminated on a paleosol that contained terrestrial gastropods (Hodell, Curtis, and Brenner 1995). The lake first filled with water about 8200 ¹⁴C yr. B.P. (7250 B.C.); the early lacustrine deposits are characterized by high concentrations of gypsum (CaSO₄), relatively high δ¹⁸O values for gastropod and ostracod shells, and large numbers of *Ammonia beccarii*, a benthic foraminifer. *Ammonia beccarii* can tolerate a wide range of temperatures (10–35° C) and salinities [7–67 grams per liter (g.L⁻¹)], but reproduces only at salt concentrations between 13 and 40 g L⁻¹ (Bradshaw 1957). High E/P (i.e., dry climate) is inferred for this part of the early Holocene record based on biological and geochemical indicators that point to low lake level and high salinity.

Lake Chichancanab filled rapidly after about 7200 ¹⁴C yr. B.P. (6000 B.C.) and carbonate, rather than gypsum, began to precipitate. The stable isotope signatures of shells declined and *A. beccarii* was no longer present. These proxies all indicate relatively moister mid-Holocene conditions that persisted until about 3000 ¹⁴C yr. B.P. (1250 B.C.) (Figure 4.7). The moist conditions at Chichancanab reversed at about 3000 ¹⁴C yr. B.P. (1250 B.C.), and a drying trend is inferred from increased sulfur (gypsum) deposition and higher δ¹⁸O values for gastropod and ostracod shells (Figure 4.7).

Late Holocene drying has also been documented in lake sediment cores from other sites around the Caribbean, including Haiti (Hodell et al. 1991) and northern Venezuela (Bradbury et al. 1981; Leyden 1985). Within chronologic uncertainty, the oxygen isotopic signal from Lake Miragoane, Haiti, agrees remarkably well with the geochemical records from Lake Chichancanab (Figure 4.8). Both indicate a trend toward drier climate in the late Holocene beginning at about 3000 ¹⁴C yr. B.P. (1250 B.C.) and intensifying at 2500 ¹⁴C yr. B.P. (750 B.C.) This climatic event coincides with the base of the “Maya Clay” unit in Lake Salpetén (Figure 4.6), raising the question to what extent vegetation and erosional changes at this time were due to climate and/or Maya deforestation.

According to the Lake Chichancanab and Lake Miragoane isotope records, swidden agriculture developed in the lowlands coincident with a climatic drying trend. The timing of cutting, burning, and planting was critical to successful agricultural harvests, especially under increasingly dry conditions in this region where rainfall is highly seasonal. The slash-and-burn cycle was no doubt administered by Maya leaders using calendars based on astronomic observations (Milbrath 1999). The importance of the timing and quantity of precipitation to Maya agriculture is evident in the widespread portrayal of the rain god Chac on architectural structures in the northern part of the peninsula.

Lake Chichancanab, Mexico

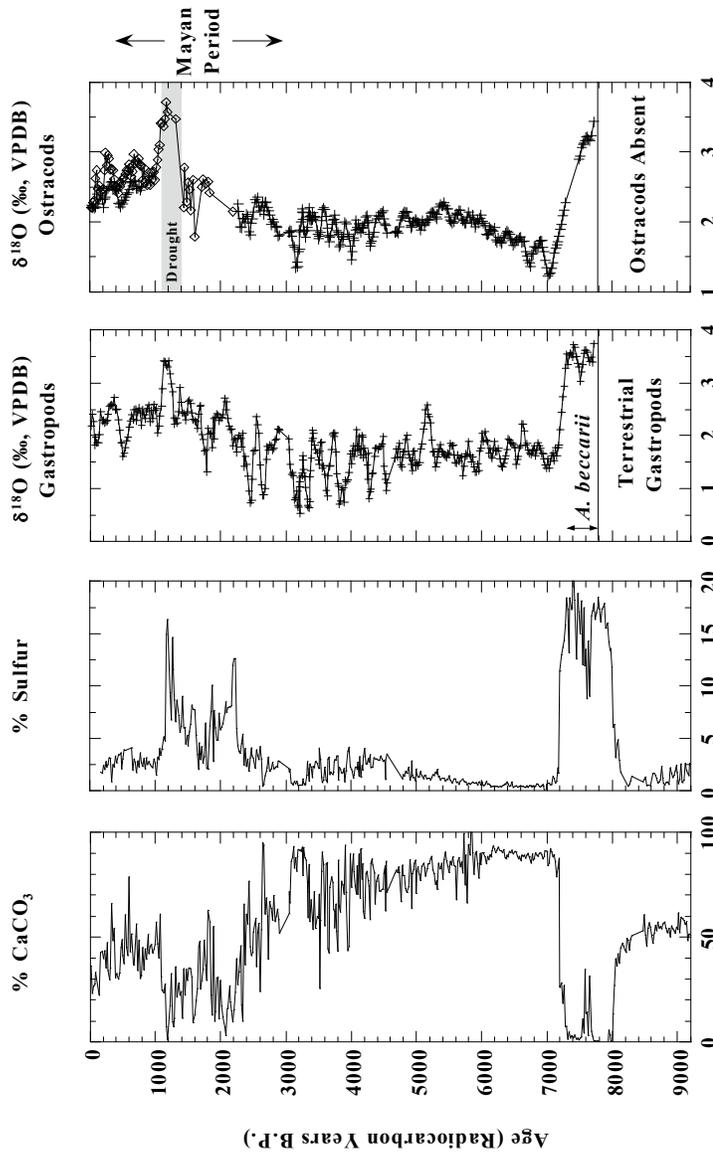


FIGURE 4.7. Paleoclimate record from Lake Chichancanab (Hodell, Curtis, and Brenner 1995) showing percent CaCO_3 , percent sulfur (gypsum), $\delta^{18}\text{O}$ of gastropod shells (*Pyrgophorus coronatus*), and $\delta^{18}\text{O}$ in ostracod shells *Physocypria* sp. (+) and *Cyprinotus* cf. *salinus* (\diamond), based on sampling at 1-cm intervals. Values are plotted against time, with the major period of Maya occupation (between about 3000 and 400 ^{14}C yr. B.P., or 1250 B.C. to A.D. 1450) indicated to the right of the plot. Oxygen isotopic results are 3-point running means. The foraminifer *A. beccarii* was found between about 7800 and 7300 ^{14}C yr. B.P. (6570 and 6150 B.C.). The gray line in the ostracod plot indicates the Late Classic drought dated at 1140 ± 35 ^{14}C yr. B.P. (A.D. 920 \pm 35 yr.). (Source: Reprinted with permission from D.A. Hodell, J.H. Curtis, and M. Brenner, 1995, Possible role of climate in the collapse of Classic Maya civilization, *Nature*, 375, pp. 391-394. Copyright 1995 Nature.)

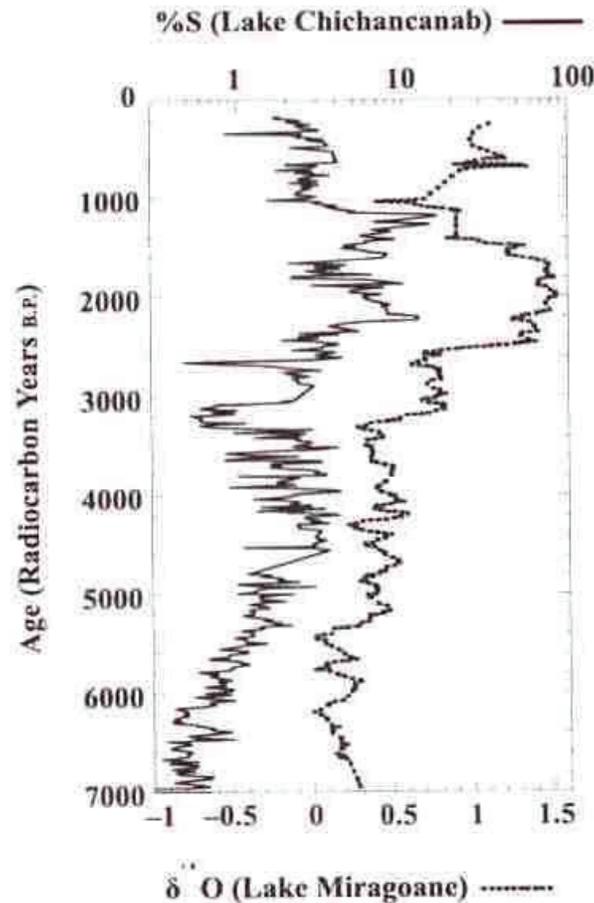


FIGURE 4.8. Weight percent sulfur (%S) record from Lake Chichancanab (plotted on a logarithmic scale) and a five-point running mean of the $\delta^{18}\text{O}$ record if the ostracod *Candona* sp. from Lake Miragoane, Haiti (Hodell et al. 1991; 1995). Note the general similarity of the records in the Holocene, especially the increase beginning at ~ 3000 ^{14}C yr B.P. (1250 B.C.), the abrupt increase at ~ 2500 ^{14}C yr B.P. (750 B.C.), and the decline at ~ 1000 ^{14}C yr B.P. (A.D. 1010.). (Copyright 1995 *Nature*.)

Early Maya farmers dealt not only with interannual variations in the timing and amount of rainfall, as they do today, but also with pronounced decade-to-century shifts in available moisture between about 3000 ^{14}C yr. B.P. (1250 B.C.) and about 1050 ^{14}C yr. B.P. (A.D. 1000). In the Chichancanab core, samples from about 65 cm depth contain high concentrations of gypsum and high $\delta^{18}\text{O}$ values, indicating very dry (high E/P) climate conditions. The proxies suggest this was one of the driest periods of the Holocene since the initial filling of the lake (Figure 4.7). The culmination of this dry episode occurred at 1140 ^{14}C yr. B.P. (A.D. 920), as determined by an AMS- ^{14}C date on a terrestrial seed at 65 cm. It is probable that terrestrial vegetation grew close to the coring site during this period when the lake volume was

shrinking. The timing of this very dry episode coincides closely with the Classic Maya Collapse (Hodell, Curtis, and Brenner 1995).

A 6.3 m core was collected from just over 6 m of water in Lake Punta Laguna (Figure 4.9). The basal age on the section is only 3500 ^{14}C yr. B.P. (1820 B.C.), indicating that the mean sediment accumulation rate at the site was high (0.18 cm yr^{-1}). The core was sampled at 1 cm intervals, yielding an average sampling resolution of about six years. Long-term variability in E/P is evident in the high-resolution, isotope-based paleoclimate record. Although there are dramatic fluctuations in the 3.5-millennia record, mean conditions between ~ 1740 and 920 ^{14}C yr. B.P. (A.D. 300–1100) were nevertheless drier than mean conditions before or after (Figure 4.9). The $\delta^{18}\text{O}$ peak at 1210 ^{14}C yr. B.P. (A.D. 860) in the Punta Laguna section corresponds closely to the dated drought at Chichancanab (1140 ^{14}C yr. B.P., or A.D. 920).

The isotope records from Lake Chichancanab and Lake Punta Laguna indicate that the Classic Collapse occurred during a drought episode. The two study lakes lie in the dry, northern part of the Maya lowlands, which was apparently least affected by the cultural decline (Lowe 1985). Depopulation during the ninth century A.D. was more characteristic of sites in the wetter, southern lowlands. If the drought were indeed widespread, one might expect the northern area to have been more impacted. Nevertheless, groundwater is more accessible in the north, because the shallow water table lies just below the land surface. Farther south, groundwater is largely inaccessible and lies at considerable depth.

Compared with settlements on the northern part of the peninsula, sites in the southern lowlands may have been more dependent on surface water in lakes, *bajos*, artificial reservoirs, and *aguadas*. As shallow depressions and reservoirs began to dry, increasing pressure would have been brought to bear on the lands and communities surrounding deeper lakes in central Petén. Archaeological surveys and test excavations in Petén show that many watersheds saw a dramatic population decline by the Terminal Classic (about A.D. 900). Whereas Late Classic Maya population (A.D. 550–800) densities in the drainage basins typically exceeded 200 persons per square kilometer (km^{-2}) (Rice and Rice 1990), densities dropped to less than 100 persons km^{-2} by the Terminal Classic. By the Late Postclassic (A.D. 1500), many watersheds were virtually abandoned, and there is evidence that local soils were stabilized as forests recolonized riparian areas. If drought played a role in the demographic decline in the southern lowlands, then paleoclimatic evidence should be found in Petén lake cores.

Isotope records from Petén, Guatemala

The early work of Covich and Stuiver (1974) suggested that Lake Chichancanab would be a good study site. Covich's published and unpublished

Lake Punta Laguna, Mexico

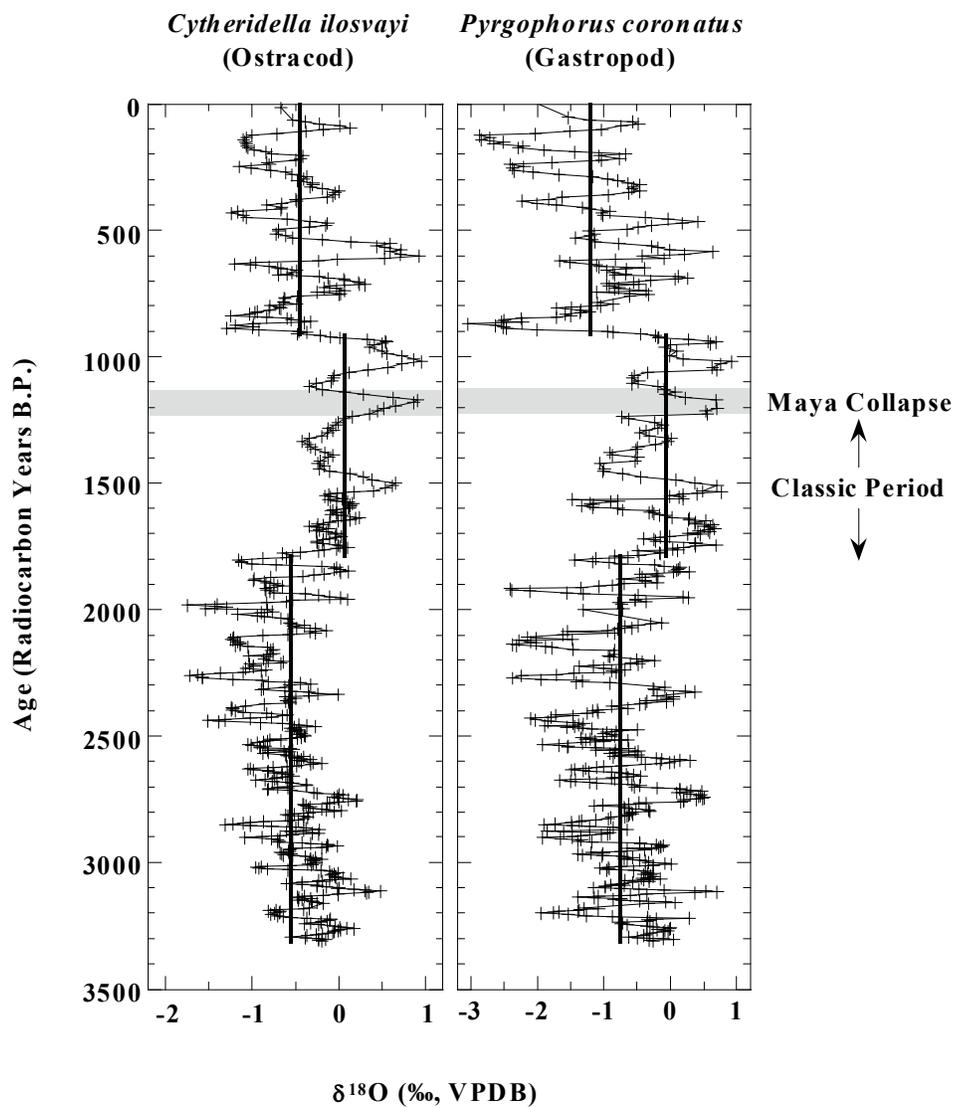


FIGURE 4.9. Oxygen isotope ($\delta^{18}\text{O}$) records based on the ostracod *Cytheridella ilosvayi* and gastropod *Pyrgophorus coronatus* from Lake Punta Laguna. Records represent five-point running means and span the last 3500 ^{14}C yr B.P. Note that the Classic Period is relatively dry compared to periods before or after. Also note the decadal to centennial variability in the record that presumably would have created difficulties for Maya agriculturalists. One of the driest episodes is dated to 1180 ^{14}C yr B.P. (A.D. 860), corresponding to the Maya collapse. (Source: Reprinted with permission from J.H. Curtis, D.A. Hodell, and M. Brenner 1996, Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implication for Maya cultural evolution, *Quaternary Research*, 46, pp. 37-47. Copyright 1996 Academic Press.)

work was also used to prioritize study sites in Petén, Guatemala. His study of the subfossil mollusk communities in Lake Petén-Itzá sediments (Covich 1976) suggested that cores from this large water body (99 km²) would yield plentiful material for isotope work. In 1993, a 5.45 m core was collected in 7.6 m of water from the southern basin of Lake Petén-Itzá, east of Flores (Curtis et al. 1998). A piece of wood at 527-cm depth had a radiocarbon age of 8840 ¹⁴C yr. B.P. (7930 B.C.), suggesting that each 1 cm sample represented, on average, about 19 years of sediment accumulation. Two isotope profiles were generated using the gastropods *Cochliopina* sp. and *Pyrgophorus* sp., and a composite ostracod record was completed using *Cytheridella ilosvayi* and *Candona* sp. (Figure 4.10). High isotope values in the early Holocene suggest persistent dry conditions following the arid late Pleistocene (Leyden 1984; Leyden et al. 1993; Leyden et al. 1994). The onset of moister conditions appears to have been postponed until about 6800 ¹⁴C yr. B.P. (5700 B.C.), after which there is a rather steady, 2,000-year decline in $\delta^{18}\text{O}$ values.

In contrast to the isotope-based inference for dry early Holocene conditions, the early Holocene pollen assemblage from Lake Petén-Itzá is characterized by high forest taxa that indicate moist climatic conditions were established by 8500 ¹⁴C yr. B.P. (7550 B.C.) (Islebe et al. 1996; Curtis et al. 1998). The presence of aquatic microfossils in sediments deposited after about 9000 ¹⁴C yr. B.P. (8240 B.C.) provides evidence that conditions were certainly moister than in the arid late Pleistocene, when there was no lacustrine deposition at the site. High isotope signatures in the bottom 1.5 m of the core may reflect the fact that, during the early Holocene, a large proportion of lakewater volume was lost each year to evaporation. Alternatively, dense vegetation cover in the early Holocene may have influenced watershed hydrology by increasing evaporation and soil water moisture storage (Rosenmeier, Hodell, Brenner, Curtis, Martin, et al. 2000).

After Lake Petén-Itzá attained a new isotopic equilibrium about 5000 ¹⁴C yr. B.P. (3770 B.C.), it demonstrated little fluctuation about the mean condition. Unlike the drying trend that characterized the last three thousand years of the records from the northern Yucatán Peninsula, Haiti, and northern Venezuela, there is no evidence for drying in the Lake Petén-Itzá isotope record. Although the Lake Petén-Itzá isotope results may reflect climatic stasis during the latter half of the Holocene, it is also possible that the lake was unresponsive to all but the most dramatic changes in E/P due to its extremely large volume. Seismic reflection studies, completed in summer of 1999, revealed that Lake Petén-Itzá is a cryptodepression with a maximum depth of approximately 160 m (Anselmetti et al. 1999). The deepest part of the lake lies some 50 m below sea level. Even lake stage excursions of several meters represent a gain or loss of only a small fraction of the lake

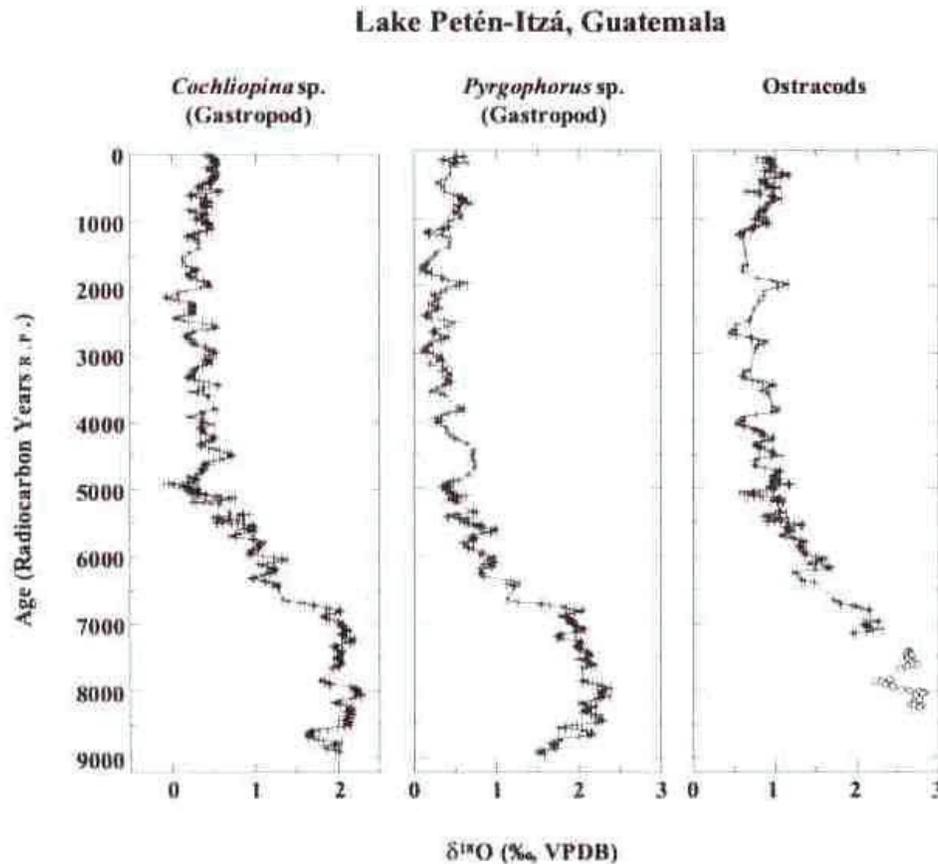


FIGURE 4.10. Oxygen isotope ($\delta^{18}\text{O}$) records from the Lake Petén-Itzá core, Petén, Guatemala (Curtis et al. 1998). Values are five-point running means plotted against ^{14}C yr. B.P., and are based on gastropods (*Cochliopina* sp. and *Pyrgophorus* sp.) and ostracods (*Cytheridella ilosvayi* [solid line] and *Candona* sp. [open circles]). Note the fairly constant values after ~ 5000 ^{14}C yr. B.P. (3770 B.C.), which probably reflect the unresponsive nature of this very deep (~ 160 m) and large (99 km^2) lake. (Source: Reprinted from J.H. Curtis, M. Brenner, D.A. Hodell, R.A. Balsler, G.A. Islebe, and H. Hooghiemstra 1998, A multi-proxi study of Holocene environmental change in the Maya Lowlands of Petén, Guatemala; Figure 10, *Journal of Paleolimnology*, 19, pp. 139-159, with kind permission of Kluwer Academic Publishers.)

volume, and are unlikely to have significantly altered the $\delta^{18}\text{O}$ signature of the water column.

Recent research was done at Lake Salpetén ($16^{\circ}58'$ N and $89^{\circ}40'$ W), a small ($A = 2.6 \text{ km}^2$) water body that lies just east of Lake Petén-Itzá, near El Remate. The lake is 104 m a.s.l. (above sea level), has a maximum depth of 32 m (Brezonik and Fox 1974), and is similar in its chemistry to Lake Chichancanab. Lake Salpetén is saturated with respect to sulfate (3000 mg L^{-1}), contains high concentrations of total dissolved solids (4500 mg L^{-1} TDS),

and has a conductivity of about $3600 \mu\text{S}\cdot\text{cm}^{-1}$. The lake is prone to stage fluctuations; during the regression episode of the late 1990s, gypsum was precipitated on the stumps of drowned trees in the littoral zone. Cores were collected along a transect in Lake Salpetén in 1997 and 1999, at water depths of 9.2, 14.0, 16.3, and 23.2 m (see Figure 4.6). Abundant gastropod shells were evident in the profiles. Radiocarbon dates on cores from the two shallower sites suggest a sedimentation hiatus prior to $910 \text{ }^{14}\text{C}$ yr. B.P. (A.D. 1150), but its duration could not be determined because some sediment deposited prior to that time may have been lost during the low stand. Discontinuities in the sediment record were confirmed by the seismic reflection profile (see Figure 4.6).

Oxygen isotope ($\delta^{18}\text{O}$) profiles from several cores have yielded consistent results (Figure 4.11; Rosenmeier, Hodell, Brenner, Curtis, and Guilderson 2002). Human alteration of watershed hydrology confounds interpretation of $\delta^{18}\text{O}$ as a proxy of changing E/P. Lower $\delta^{18}\text{O}$ values may represent decreased E/P (wetter climate) and/or greater surface runoff and groundwater inflow to the lake caused by human-induced deforestation. For example, declining $\delta^{18}\text{O}$ values between 1300 and 400 B.C. (3050–2340 ^{14}C yr. B.P.) coincided with palynologically documented forest loss that may have led to increased inflow. Minimum $\delta^{18}\text{O}$ values occurred in the Middle and Late Preclassic Periods between 400 B.C. and A.D. 150 (2340–1860 ^{14}C yr. B.P.) (Figure 4.11).

High lake stands are also documented at this time by radiocarbon dates on aquatic gastropods retrieved from pits dug into subaerial soils (i.e., lake sediments) located about 1 m to 7.5 m above the present (1999) lake stage (Rosenmeier, Hodell, Brenner, Curtis, Martin 2002). Following the period of minimum $\delta^{18}\text{O}$ values (400 B.C. to A.D. 150, or 2340–1860 ^{14}C yr. B.P.), the signal increases in a series of steps at A.D. 150, 550, 850, and 1300 (1860, 1540, 1190, and 660 ^{14}C yr. B.P.). These $\delta^{18}\text{O}$ increases may reflect a series of aridity increases and/or decreased hydrologic inputs as a consequence of forest recovery associated with population declines (Rosenmeier, Hodell, Brenner, Curtis, and Guilderson 2002). Within error associated with the sediment chronology, most of these steps in the $\delta^{18}\text{O}$ signal correspond with discontinuities in Maya cultural evolution: Preclassic abandonment (A.D. 150–200), Maya Hiatus (A.D. 500–550), and Terminal Classic Collapse (A.D. 800–950). Whether this coincidence represents a response of culture to climate change, or a response of environment to human disturbance is not known.

Oxygen isotope studies from lakes in Petén have thus far yielded ambiguous results. The $\delta^{18}\text{O}$ records from Lake Petén-Itzá indicate little change for the past five thousand years (see fig. 10), whereas those from Lake Salpetén show a series of stepped changes in the $\delta^{18}\text{O}$ equilibrium value of lakewater. Contradictory results among Petén lakes may be due to anthropogenic vegetation changes that altered hydrologic budgets of individual

Lake Salpetén, Guatemala

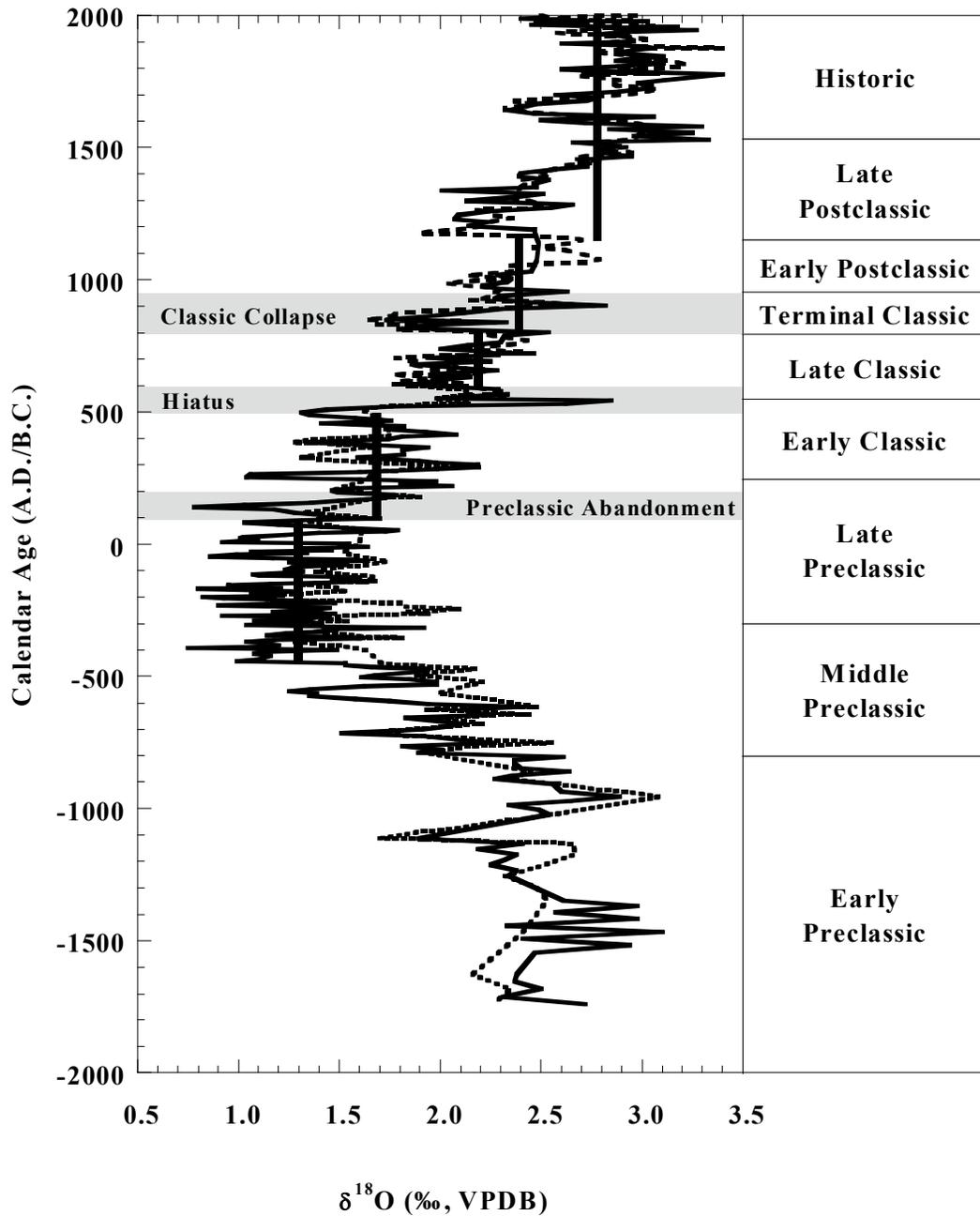


FIGURE 4.11. Oxygen isotope ($\delta^{18}\text{O}$) composition of ostracod valves (*Physocypria globula*) from cores taken in Lake Salpetén, Petén, Guatemala (Rosenmeier, Hodell, Brenner, Curtis, and Guilderson 2002). Note the shifts in the heavy black lines that delineate mean $\delta^{18}\text{O}$ values for each period. Isotope results are compared to major subdivisions of Maya Cultural evolution.

lakes and produced different $\delta^{18}\text{O}$ patterns. In contrast, lakes in northern Yucatán yield consistent $\delta^{18}\text{O}$ patterns reflecting climatic variations (E/P). Hydrology in Petén watersheds may have been more subject to human impacts because the southern lowlands receive more rainfall, forest stature is greater, and local topography is steeper.

***Objectives of Future Paleoclimate Research
in the Maya Lowlands***

Oxygen isotope records from Lake Chichancanab and Lake Punta Laguna have provide tantalizing evidence of a link between the Classic Maya Collapse and declining moisture availability in the ninth and tenth centuries A.D. Lake Petén-Itzá and Lake Salpetén in the Petén lowlands yielded ambiguous results, most probably because of human disturbance of individual watershed hydrology. High-resolution paleoclimate records from other sites throughout the Maya lowlands are required to further address the hypothetical causal relationship between drought and cultural demise. The next challenge is to identify additional, appropriate lakes for isotopic study.

The best paleoclimate records from the southern lowlands will likely be found in lakes whose drainage basins were not densely settled, and those with low watershed/lake ratios. Archaeologists can help identify these optimal study lakes. Deciphering the paleoclimatic record from the Maya lowlands will involve collaboration between archaeologists and paleoenvironmental scientists. A better understanding of the long-term relationship between climate and Maya culture will not only have bearing on the interpretation of the archaeological record, but should be informative about the future prospects for sustainable agriculture in a region that is once again becoming densely populated.

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Chapter 5

Rhythms of Precipitation in the Yucatán Peninsula

Lorrain Giddings
Margarita Soto

INTRODUCTION

The distribution of rain in Mexico is a vital issue. There are extensive arid areas where non-irrigated agriculture is virtually impossible, just as there are equally extensive areas where it is only marginally practical. In the Yucatán Peninsula, however, non-irrigated agriculture is normally possible the year-round. Still, even there, the timing and distribution of rainfall are critical, and periods of drought have vitally affected agriculture.

Only recently have sufficiently detailed meteorological records become available for studying changes in precipitation over time. This paper will compare some of the precipitation tendencies in the Yucatán Peninsula and show how they are different from the rest of Mexico.

EXPERIMENTAL DETAILS

Data

Most data have been taken from the ERIC II (2000) CD-ROM, a recompilation of daily and monthly Mexican meteorological data from 5,330 meteorological stations from 1940 to 1997 (Quintas 2000). The data are still quite incomplete; nevertheless, they furnish the first publicly available set of statistics dense enough to examine meteorological details for the whole country. The compilers of ERIC II are actively working to add more data, as well as to correct existing data—a manual process made especially difficult because data are dispersed throughout the country in local handwritten

records. Deficiencies in ERIC II data are especially notable for the Yucatán Peninsula, the Sonora Desert, and the Chihuahua Desert.

ERIC II data were supplemented by the GHCN (Global Historical Climatology Network) data set (Wallis, Lettenmaier, and Wood [1991] 1998), which has only 351 Mexican stations but uses longer time series for many of the same stations covered by ERIC II. GHCN data for Belize, Guatemala, and U.S. border states were included to ensure control in border areas. Unfortunately, only the Yucatán Peninsula data lacks external control for extrapolations, and even Belize and Guatemala data are missing after 1990. Still, some peninsular records are available through 1997.

Quantitative information on El Niño events was derived from databases accessible through the Internet. At this time, data are available through a specific URL (NINO3), as well as through other sources.

Standardized precipitation index

McKee's Standardized Precipitation Index, or SPI (Edwards and McKee 1997), was used because it allows station comparisons without regard to individual differences in normal rainfall. The SPI is a statistical index that measures the standard deviations above and below the midpoint of the long-term precipitation statistics for a station. The numeric calculation of SPI for various intervals was made possible through modification of a FORTRAN source program available over the Internet (Edwards 1997).

Calculation of the SPI was based on a minor modification of the program for more convenient input and output of data. Only SPI-12 was used here—that is, SPI values for the previous 12 months. Shorter and longer periods were also calculated, but SPI-12 was the most convenient for examining the long-term variation of precipitation without the possibility of seasonal variations.

The average SPI value for any station is zero. Negative values show a deficit of precipitation, while positive values represent an excess of precipitation. Most researchers consider values between -1 and $+1$ to indicate normal conditions. Values below -1 indicate dryness, and, in most circumstances, values below -2 are formally considered to indicate droughts. Values above $+1$ are wet, and values above $+2$ are severely wet.

Procedure

Original data were formatted for use in the SPI program using ASCII editors. Once processed, the SPI values were combined in Microsoft Excel work sheets and processed in Microsoft Access, which allow only 256 total columns for data. Because there were about 700 columns (i.e., months) for approximately 6,000 stations, the data had to be handled in three batches:

1940–1960, 1960–1980, and 1980–1998. Quattro Pro worksheets were then used for archival storage of data sets because these worksheets have no column limitations.

Surfer grids of data were prepared by using the Surfer 7 program (Golden Software 1999), which utilizes a Kriging algorithm in a macro programmed in Visual Basic for Applications. Stations with problematic data were identified by analysis of residuals, and removed; their surfer grids were then recalculated, converted to SPI contour maps, and exported as GIF images. These maps were also converted to IDRISI images (Clark Labs 1999) for more convenient manipulation as time series. Once in IDRISI, it was practical to derive other products from the images, such as SPI profiles.

Because of the standard method of calculation and representation of results, the SPI-12 images conventionally refer to conditions for the 12 months previous to the formal image date. For example, an SPI-12 image dated September 1955 uses the precipitation total for October 1954 through September 1955, with the average centered around March through April 1955.

The series of about 700 monthly images allows examination in various forms, including video presentations. Due to the limitations of a print publication, only a sampling of SPI-12 images will be presented to illustrate the accompanying discussion.

NORMAL CONDITIONS FOR THE YUCATÁN PENINSULA

Mosiño and García (1974) divided Mexico into eight precipitation zones (Figure 5.1). The Yucatán Peninsula forms a separate zone. It is different from most of the rest of Mexico, in that it is relatively free of droughts during the summer and characterized by moderate rainfall throughout the year. They also classified parts of the Mexican states of Tamaulipas, Oaxaca, Michoacan, as well as other states in the same zone.

The zonation shown in Figure 5.1 illustrates only some of the previous research in this area. The basis for defining these precipitation zones is quite different from the SPI zones studied here. No other areas appear to form part of the Yucatán SPI zone.

According to García's (1981) modification of the Köppen classification system for climates, most of the Yucatán Peninsula can be classified as Aw (hot subhumid). There is a gradient, with the eastern part of the peninsula more humid (Aw_2), the central part intermediate (Aw_1), and the western part drier (Aw_0). The northern part is considered semiarid (BS_1), with a small portion near the town of Puerto de Progreso even more arid (BS_0).

Precipitation arises principally from convection of humid winds from the east. For this reason, eastern precipitation is usually substantial, averaging from 1,200 to 1,500 millimeters (mm) per year. In the central part of the

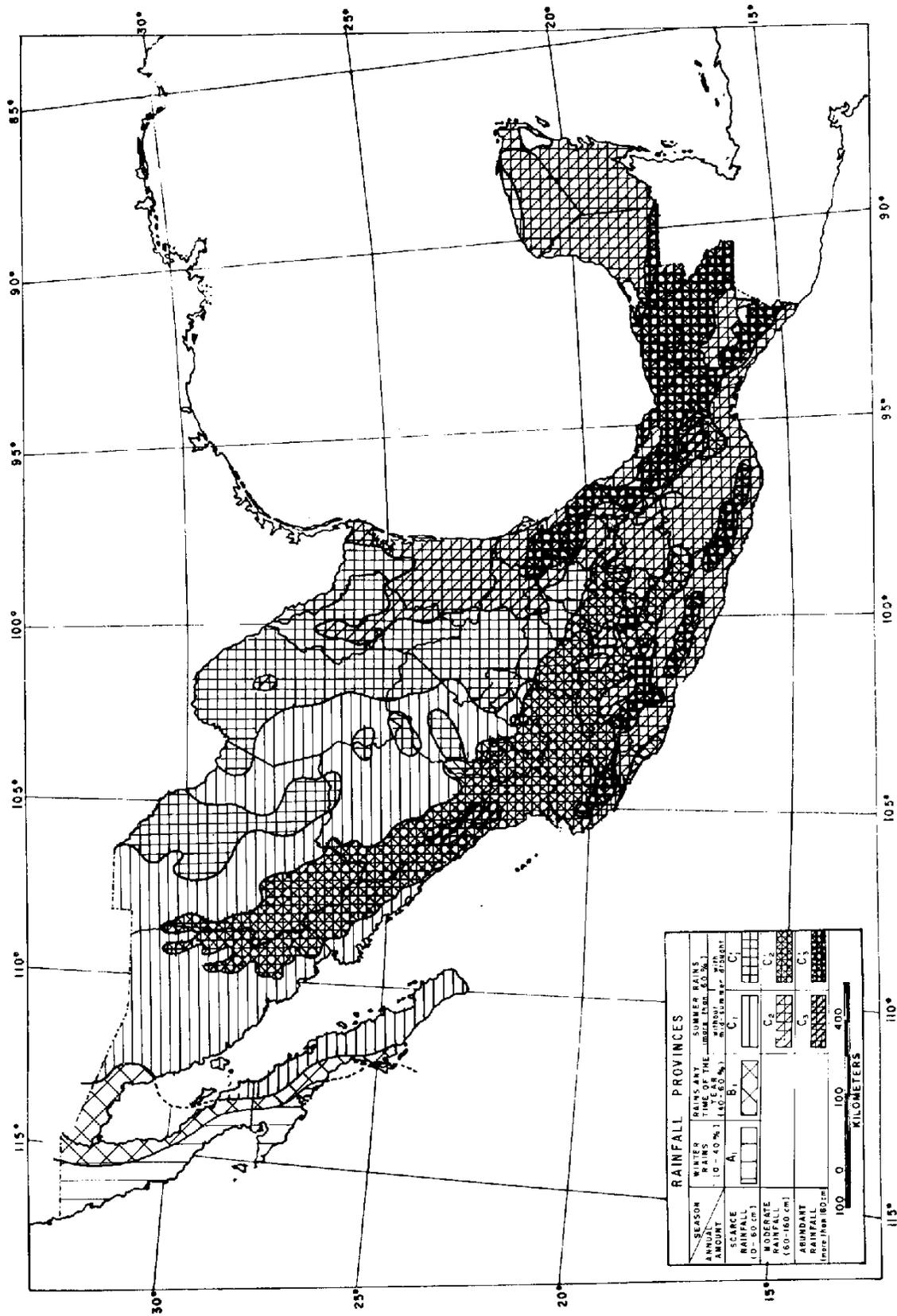


FIGURE 5.1. The distribution of Mexico's eight precipitation zones, as proposed by Mosiño and Garcia. (Source: Reprinted from P.A. Mosiño and E. Garcia, Figure 18, Rainfall provinces, in *The Climates of North America*, *World Survey of Climatology*, 1973, with permission of Elsevier Science.)

peninsula, annual precipitation is less than 1,100 mm, and parts of the western portion have less than 1,000 mm of total rainfall. Precipitation also decreases to the north of the peninsula, falling as low as 500 mm near Puerto de Progreso.

The Yucatán Peninsula has some of the highest annual temperatures in all of Mexico and is normally classified into two zones. The hotter zone, with an average annual temperature greater than 26°C, is located in the central and western part of the peninsula. The cooler zone, with an average annual temperature between 24°C and 26°C, is located in the north of the peninsula and includes the Caribbean coast and the coast of the Gulf of Mexico.

Nevertheless, it must be remembered that natural phenomena such as tropical storms and hurricanes (as well as events such as El Niño) can complicate the picture drastically.

YUCATÁN IN THE CONTEXT OF SPI-12 OF ALL MEXICO

Figure 5.2 compares a SPI-12 profile of mainland Mexico (top curve, which excludes Baja California and the Yucatán Peninsula) with a SPI-12 profile for the Yucatán Peninsula (second curve). In examining both curves, it can be seen that there is no obvious relationship between the two profiles. One might expect that critical points—whether peaks or valleys—would coincide, but this happens very rarely. Even with excessive smoothing, there are few coincidences and no apparent similarities.

It is interesting to note that although apparent deficits in Yucatán precipitation are prominent, excesses are much less evident. The maximum SPI-12 that appears (1.28) is not extreme, whereas the minimum SPI-12 (−1.96) is quite extreme. This implies that deficits (droughts) are less frequent than excesses (perhaps leading to floods), but when deficits occur they are more extreme. This coincides with the popular perception of Yucatán droughts as rather rare events compared with normal rainy weather.

PERIODICITY

The annual precipitation pattern in the Yucatán Peninsula is evidently periodic, but the causes of this periodicity are unknown. When SPI data for the peninsula are analyzed with the *FREQ* program (CoDebris 1995), the following harmonic components are evident:

The first six harmonic components yield the smooth curve (i.e., the third curve) in fig. 2. Although much of the general curve shape is reproduced, there are severe variations. Using all 12 harmonic components improves the fit; it would also be possible to obtain a better fit for the curve by using many more components, but this would be a meaningless exercise.

<u>Period Months</u>	<u>Amplitude SPI Units</u>	<u>Phase Degrees</u>	<u>% of Mean Square Error</u>
74	0.2559	038.3	11.59
17	0.2602	344.7	9.68
62	0.2060	317.8	6.74
48	0.2090	046.3	5.37
39	0.1908	111.2	5.77
291	0.1810	187.3	5.04
29	0.1645	148.9	4.46
54	0.1610	278.5	4.21
32	0.1490	135.0	3.55
85	0.1434	117.0	3.20
26	0.1292	237.8	2.75
117	0.1044	243.8	1.72

Still, the existing curve reveals some tendencies that might be useful for a rough prediction of future humidity; the extension to 2006 is based on data for the first six harmonic components.

Figure 5.2. also includes the values of NINO3 (i.e., the “Niño 3 anomaly”), which includes deviations from the average of monthly Pacific Ocean sea surface temperatures in the sector bordered by long 90° W to 150° W and lat 5° N to 5° S. Although it is evident that El Niño events affect precipitation patterns over the country by various means, including the movement of natural atmospheric zones (including the jet stream), there is obviously no simple correlation with precipitation patterns in the Yucatán Peninsula.

TYPICAL PATTERNS

Figure 5.3 to 5.6 show SPI-12 patterns for all of Mexico, which can be correlated with the profiles shown in Figure 5.2. It should be remembered that the average of each image is centered about five and six months before the nominal date of the image.

Figure 5.3 shows the SPI-12 pattern during October 1982, the driest of months for mainland Mexico. Yucatán was nearly normal at this time, as was the northern part of Baja California.

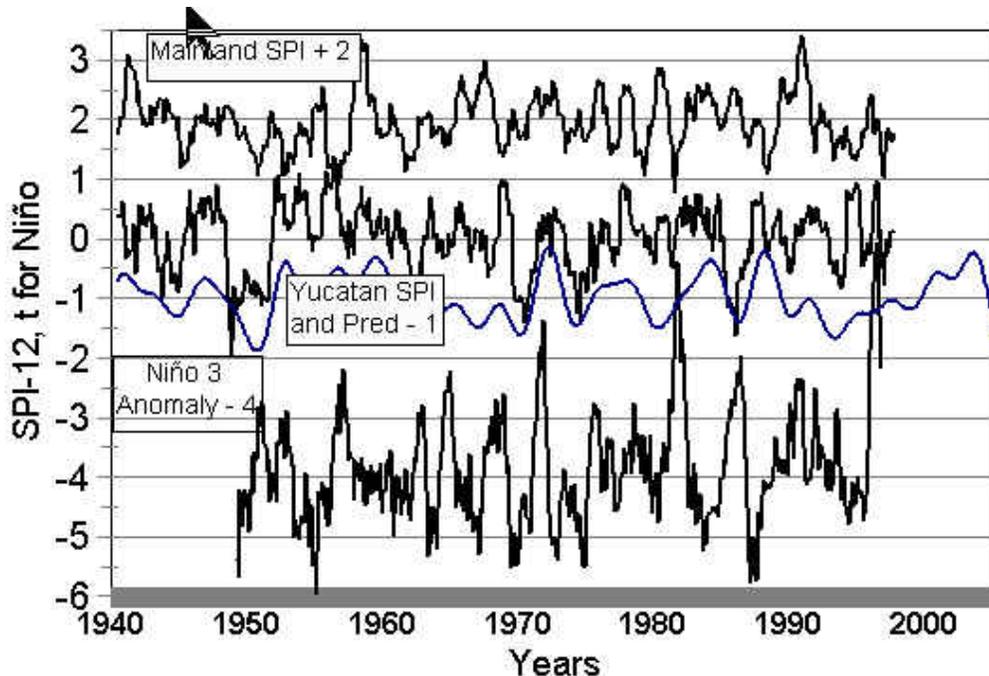


FIGURE 5.2. Periodicity of SPI-12. The top curve shows the SPI-12 profile for mainland Mexico (excluding Yucatán and Baja California), and the second curve shows the SPI-12 profile for the Yucatán Peninsula. The third curve shows an approximation to the Yucatán profile based on six harmonic components. For comparison, the bottom curve presents the NINO3 Anomaly.

By contrast, Figure 5.4 shows the SPI-12 pattern from May 1987. At this time, the north-central part of Mexico was much wetter than normal, while Yucatán was enduring its driest period. (Of course, the actual precipitation values would give a different picture because SPI compares current values in a statistical way with historical values, and does not present their actual values. Precipitation in a wet period in a desert may well be less than precipitation in a wetter area's dry period.)

When Yucatán was wettest (image from April 1957), north-central Mexico was very dry, as can be seen in Figure 5.5. When mainland Mexico was wettest (image from December 1958), Yucatán was only slightly wet, while precipitation in northern Baja California was normal, as can be seen in Figure 5.6.

Some researchers have postulated a direct correlation between precipitation patterns and the occurrence of El Niño. Fig. 7–10 display the precipitation patterns around four separate El Niño events. The SPI-12 images, however, are quite varied and do not suggest any direct correlation.

Around the intense El Niño event of 1983 (Figure 5.7), there was severe drought in the central part of Mexico and wet episodes in Yucatán, the northwest portion of Mexico, and the U.S. state of California. This suggested

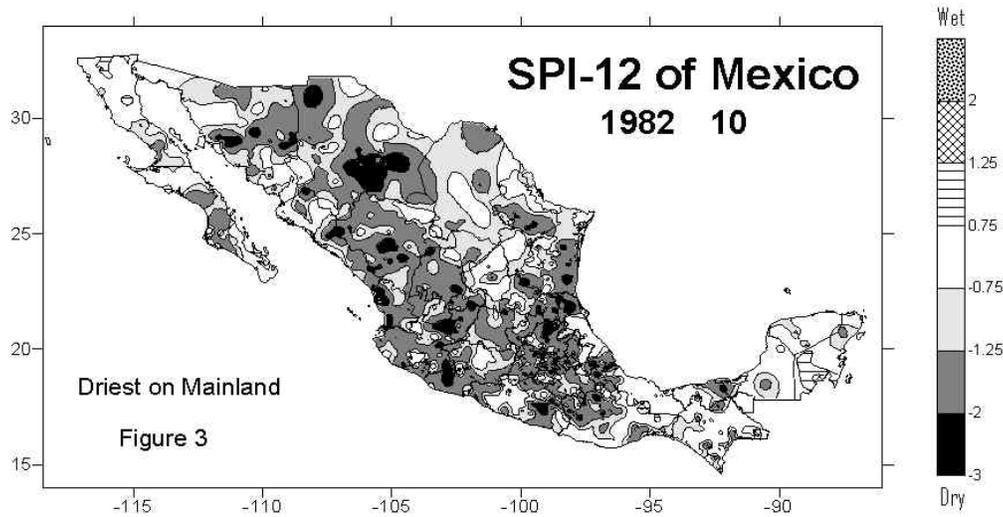


FIGURE 5.3. SPI-12 pattern for October 1982. The driest period on the mainland corresponded with nearly normal conditions in Yucatán and in the northern part of Baja California.

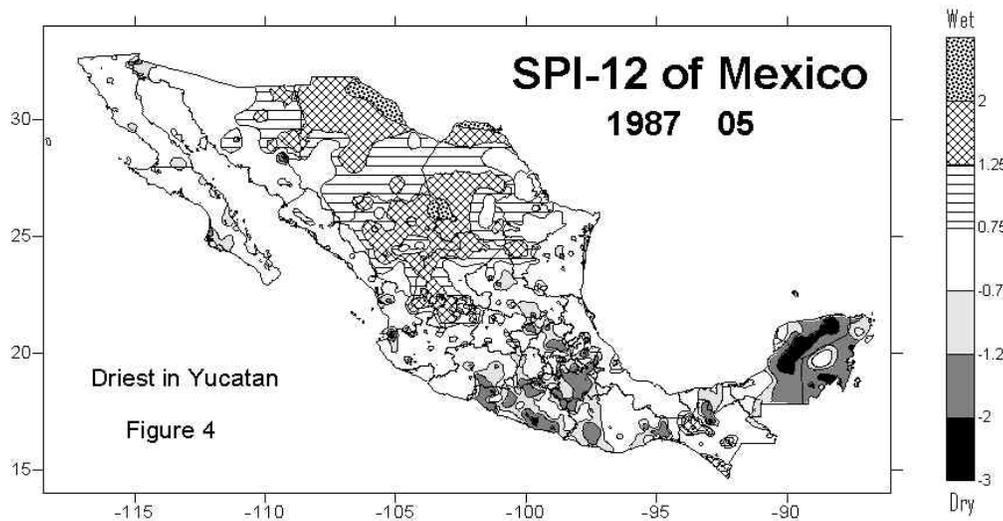


FIGURE 5.4. SPI-12 pattern for May 1987. The driest period in Yucatán contrasts with a wet period in north-central Mexico.

to many that there was a direct correlation between El Niño events and precipitation patterns in Mexico. On the other hand, wet and dry patterns were considerably different around the 1988 El Niño event (Figure 5.8).

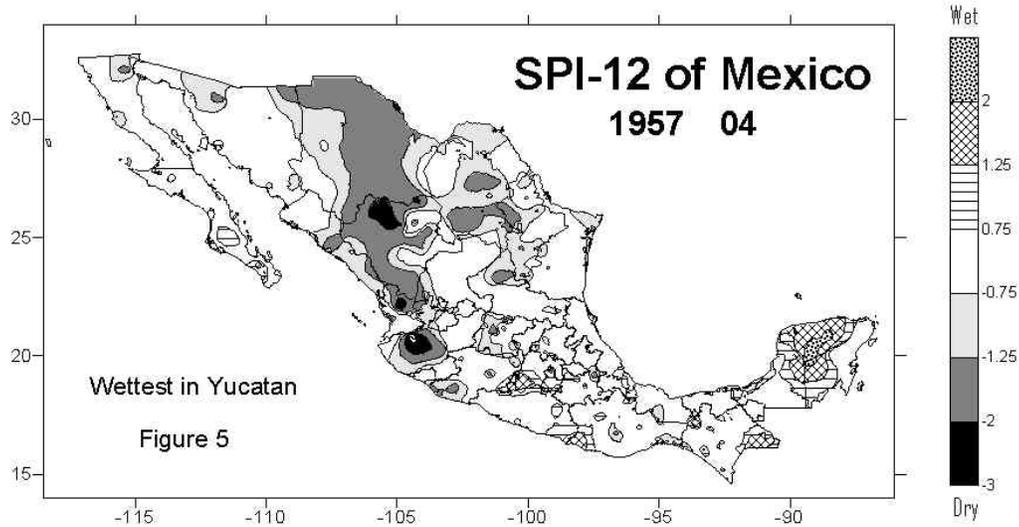


FIGURE 5.5. SPI-12 pattern for April 1957. When Yucatán was wettest, north-central Mexico was very dry.

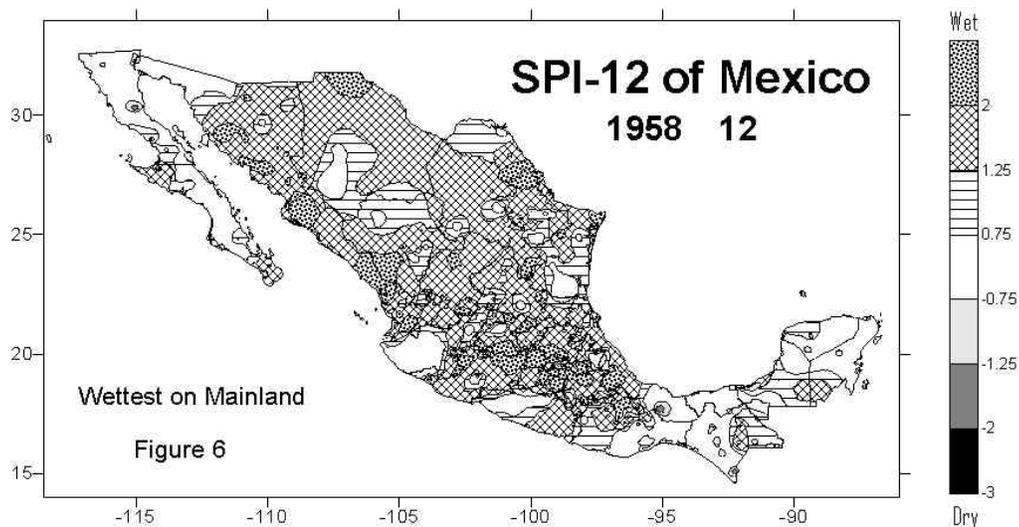


FIGURE 5.6. SPI-12 pattern for December 1958. The mainland was quite wet, but Yucatán and Baja California were nearly normal.

Although conditions in the northwest of Mexico were wet around the 1973 El Niño (Figure 5.9), the rest of Mexico was fairly normal. Around the 1966 El Niño (Figure 5.10), conditions were quite different from other events.

It is evident that there is no clear pattern of precipitation accompanying El Niño events in Mexico. Although there appears to be a certain tendency for precipitation events to occur in California and northern Baja California, there are no clear tendencies throughout the rest of Mexico.

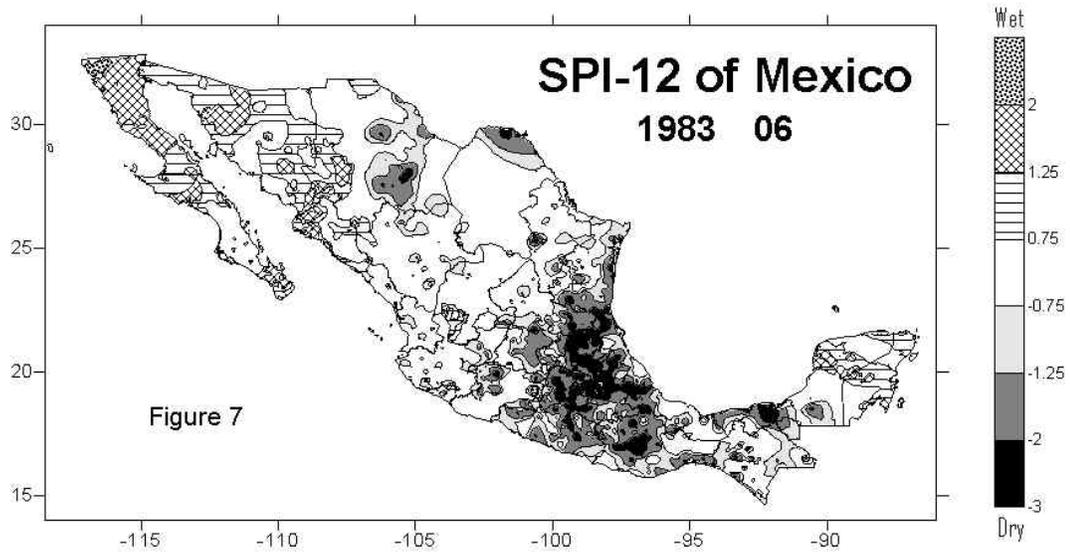


FIGURE 5.7. SPI-12 pattern for the El Niño event of June 1983. The central portion of Mexico underwent a severe drought, while neighboring areas experienced wet episodes.

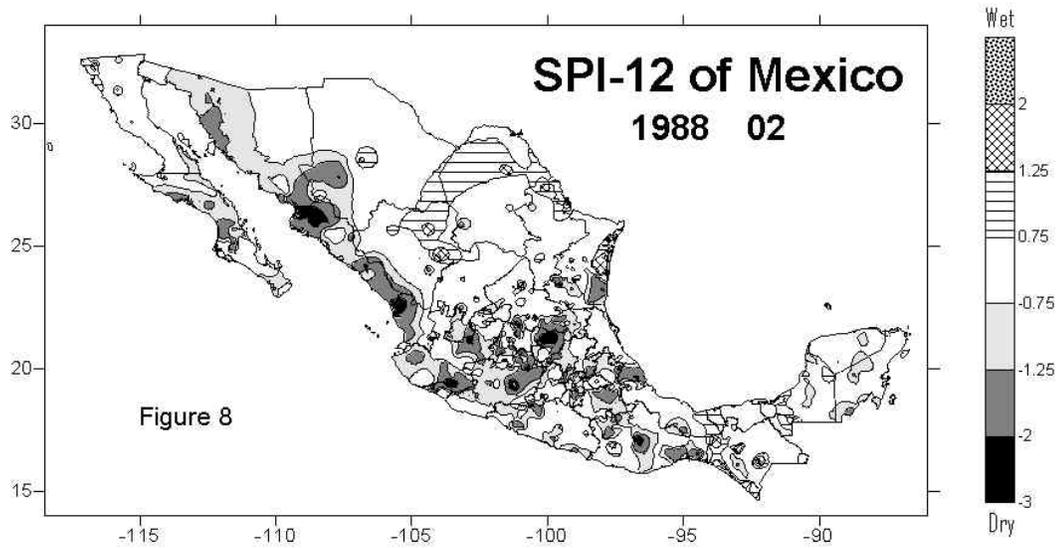


FIGURE 5.8. SPI-12 pattern for the El Niño event of February 1988. Wet and dry conditions were quite different around the El Niño event of 1988.

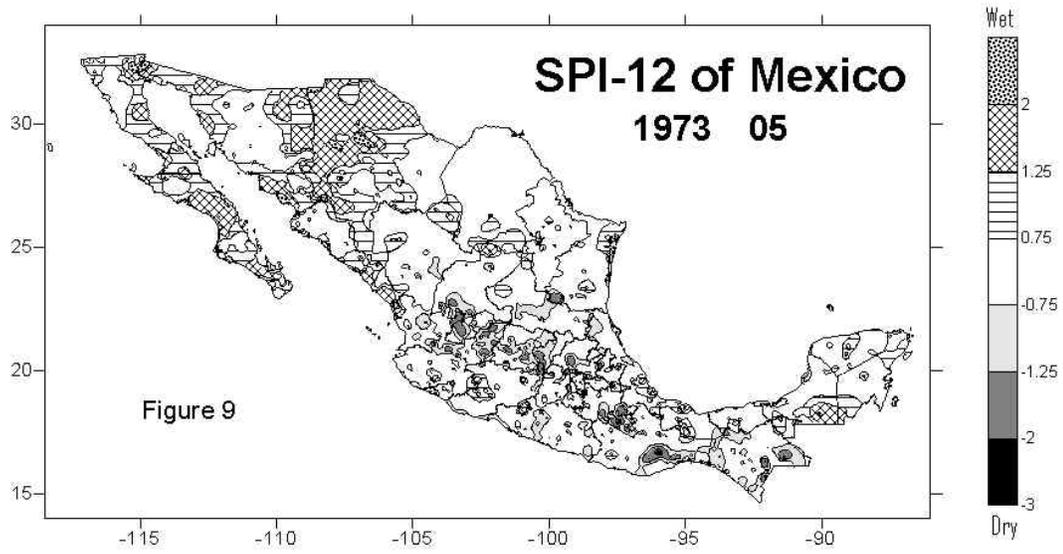


FIGURE 5.9. SPI-12 pattern for the El Niño event of May 1973. While the northwest portion of Mexico was wet, the rest of the country experienced nearly normal conditions.

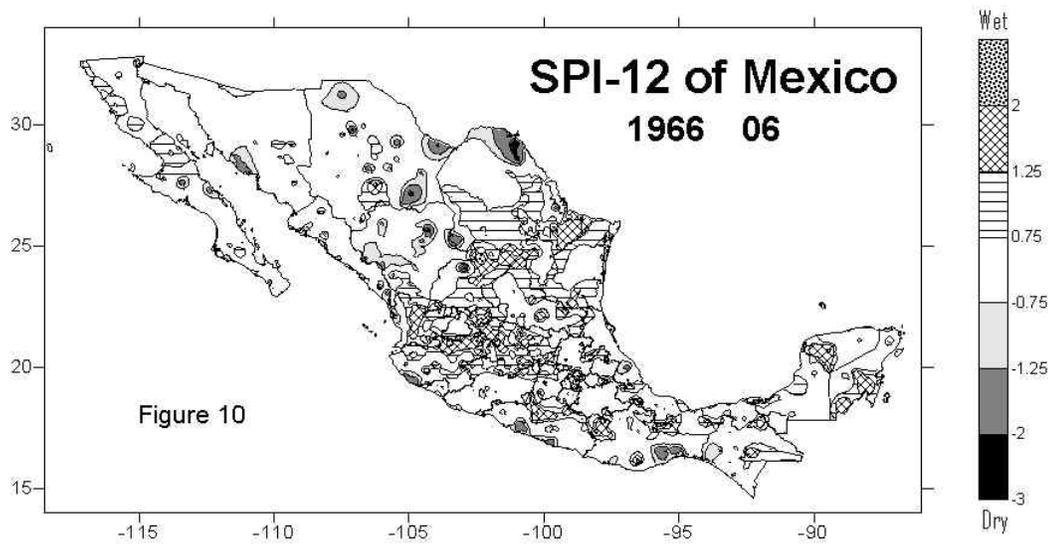


FIGURE 5.10. SPI-12 pattern for the El Niño event of June 1966. Wet and dry conditions were also different around the El Niño event of 1966.

CONCLUSION

The Yucatán Peninsula constitutes a precipitation zone distinct from the other precipitation zones in Mexico. Detailed studies of rainfall as a function of time have recently become possible through the use of databases that have compiled daily and monthly Mexican meteorological data from more than 5,000 meteorological stations over a nearly 60-year period.

Although the Yucatán Peninsula is probably the part of Mexico most deficient in historical meteorological data, the annual precipitation in the peninsula was periodic from 1940 to 1997, but still quite different from that of mainland Mexico over the same time interval. Droughts on the peninsula are much rarer and tend to be more severe than wet periods. Precipitation on the peninsula has also been shown not to have a simple relation to the El Niño disturbances. Inasmuch as the timing and distribution of rainfall is critical for agricultural interests, further studies on changes in precipitation over time remain to be done.

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Chapter 6

Structure and Diversity of the Forests at the El Edén Ecological Reserve

Gillian P. Schultz

INTRODUCTION

The Yucatán Peninsula of Mexico is an excellent laboratory for studying the biological diversity and ecosystem processes of an area that has been under constant human disturbance for several thousand years. In recent years, the field of ecology has embraced a new paradigm—that humans are an integral part of the earth's ecosystems, and that human impacts upon ecosystems, both positive and negative, are in need of study (Turner 1990; Turner and Butzer 1992). Some believe that the nature we see around us today is a remnant of ecosystems shaped and created by humans in the past (Gómez-Pompa, Flores, and Sosa 1987; Gómez-Pompa 1987; Gómez-Pompa and Kaus 1998; Murphy and Lugo 1995; Rico-Gray and García-Franco 1991).

The vegetation of the Yucatán Peninsula is a mosaic of successional forests resulting from at least 3,000 years of human manipulation, including agriculture, logging, and (more recently) urbanization, as well as natural disturbances such as climate change, fires, and hurricanes. Although it would be difficult to determine the direct long-term effects of human

I would like to thank Dr. Arturo Gómez-Pompa for introducing me to the Yucatan Peninsula and providing me with the opportunity to study at El Eden. Thanks to A. Sanders, G. Carnevali, P. Sima, R. Duran and R. Liesner for assistance with plant identifications. T. Bannister, R. Palestina, W. Law, A. Lemas and many other volunteers for their assistance in the field. This work was supported by grants from UCMEXUS and the graduate student research award of the Torrey Botanical Society. I also thank J. Holt and R. Minnich, A. Conover and C. Schultz for helpful comments on earlier drafts of this chapter.

disturbance as distinguished from those resulting from natural disturbances, detailed vegetation studies would offer insights into the nature of the dynamics and composition of the vegetation across gradients of space and time. While there have been many general studies on the vegetation of Yucatán (Flores and Espejel 1994; Lundell 1934; Miranda 1958; Rzedowski 1978) few have examined how the species are distributed across vegetation types and how the different communities differ from each other in terms of diversity and floristic composition.

Understanding basic aspects of the diversity, structure, and floristics of a forest is necessary to study forest dynamics, plant-animal interactions, and nutrient cycling (Nadkarni, Matelson, and Haber 1995). From a conservation standpoint, knowing the major components of an ecosystem can provide a basis for management and restoration decisions. Until the last 20 years, the northeastern portion of the Yucatán Peninsula, known as the Yalahau region, was unknown biologically. In the early 1990s, however, the creation of both the Yum Balam Protected Area and the El Edén Ecological Reserve in northeastern Quintana Roo, Mexico, increased interest in quantifying and qualifying the biological richness of the area. Several initial surveys suggest that the region may have relatively high levels of biodiversity and endemism within the peninsula (Lazcano-Barrero et al. 1992; Lee 1980; Snedaker, Clark, and Olmstead 1991).

Dry tropical forests

Most of the earth's biological diversity occurs in the world's tropical regions (Wilson 1992). Much of the research in tropical biodiversity and conservation has focused on wet tropical forests, and little attention has been paid to dry tropical forests. Dry tropical forests, although poorly studied, encompass a greater geographic area than wet tropical forests, with an estimated maximum area of 42% of intratropical vegetation (Murphy and Lugo 1995; Mooney, Bullock, and Medina 1995). The most unifying characteristic of dry tropical forests is the common climatological pattern of several months of severe drought (Mooney, Bullock, and Medina 1995). Holdridge (1967) defines dry tropical forests as those forests that occur in frost-free areas with a mean annual temperature above 17°C, annual rainfall between 250 and 2,000 mm, a ratio of potential evapotranspiration to precipitation greater than 1, and a prolonged dry season of up to six months. Degree of deciduousness is often considered another important characteristic; however, many dry tropical forests remain evergreen throughout the year (cf. Beard 1955, Hartshorn 1988).

Diversity and endemism in dry tropical forests

Overall plant diversity in dry tropical forests is lower than that of wet tropical forests. There is a general belief that species that occur in dry tropical forests represent a subset of species of wet and moist tropical forests (Gentry 1995). However, several studies have shown a seemingly minimal overlap of species between wet and dry forests. Frankie, Baker, and Opler (1974) examined a forest in Costa Rica and found that, of 298 tree species sampled, only 11 species occurred in both wet and dry zones. Gentry (1995), in a general comparison of Neotropical dry and wet tropical forests, found the floras to be quite similar on the family and generic levels, but large differences could be found at the species level.

Endemism, at least on a phytogeographic scale (where endemism is defined as restriction to a specific geographic area), is generally lower in the Neotropical dry tropical forests (Gentry 1995). However, Mexican dry tropical forest sites have unusually high levels in endemism, particularly those in Western Mexico (Chamela) and the Yucatán Peninsula (Sian Ka'an), when compared with sites in Central America (Gentry 1995; Lott, Bullock, and Solis-Magallanes 1987; Rzedowski 1978; Rzedowski and Rzedowski 1989). As mentioned above, the Yalahau region in the northern Yucatán Peninsula may represent another area with relatively high levels of both endemism and general biodiversity.

STUDY AREA

The tropical lowlands of the Yucatán Peninsula are a mosaic of vegetation zones that are located atop a vast limestone platform, formed by shallow marine deposition throughout the Cretaceous period, which slowly emerging from the sea during the Cenozoic era (Tulazyck 1993). The peninsula has a very thin soil layer, made up mostly of limestone derivatives (e.g., kaolinite and montmorillonite). The lowlands are characterized by a number of solution features including depressions, caverns, lakes, and sinkholes (cenotes). Soils are classified as gleysols and rendzinas (Flores and Espejel 1994).

Across the peninsula, factors such as geologic age, topographic relief, forest canopy height, and annual precipitation decrease from south to north. Average temperatures range from 23°C in January to 28°C in May (Back 1985). Yalahau receives an annual rainfall of 1,400 to 2,000 mm, which is a relatively high amount for the region. The high rainfall has contributed to the development of a series of elongated karstic depressions that follow a trending fault zone known as the Holbox Fracture Zone (Ward, Weidie, and Back 1985; Tulazyck 1993). Several types of forests surround these

wetlands, including semideciduous tropical forest and various stages of secondary forest. The area is characterized by a pronounced dry season beginning in December and ending in late May, with a second short dry season in August.

The forests described in this chapter are situated within the El Edén Ecological Reserve (lat 21°12' N, long. 87°11'W), a 1,492-hectare (ha) private ecological reserve that was founded in 1990 for tropical diversity research and conservation (Figure 6.1). The reserve lies on the eastern side of Yalahau and is thought to be representative of regional vegetation, with the exception of marine habitats.

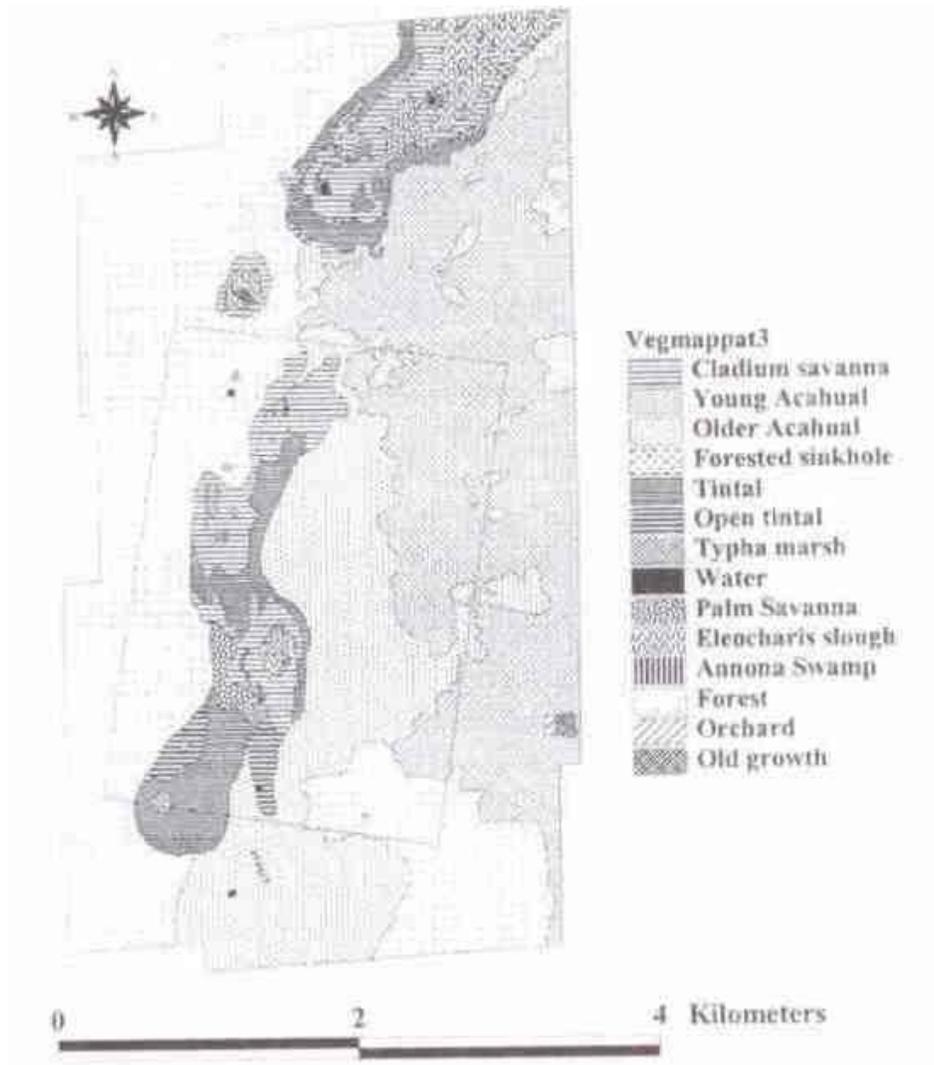


FIGURE 6.1. Vegetation of the El Edén Ecological Reserve and surrounding area (lat 21°12'N, long 87°11'W).

Vegetation

General vegetation descriptions have classified the area as tropical semievergreen forest (Rzedowski and Rzedowski 1989). The vegetation maps of Miranda (1958) and Flores and Espejel (1994) indicate that the area is a transitional zone between medium-statured semideciduous forest and semi-evergreen forest. Investigations using aerial photographs and ground surveys have indicated that the vegetation of El Edén can be broken into five major types: (1) selva mediana (medium-statured, semideciduous forest, 10–15 meters [m] canopy); (2) different age acahuals (here used to refer to secondary semideciduous forest with a 7–10 m canopy); (3) tinal (seasonally inundated forest); (4) savanna (including both palm savanna and sloughs dominated by Cyperaceae); and (5) aquatic vegetation. Forest, acahuals, and wetland systems each cover approximately one-third of the reserve. The present paper will describe the selva mediana (which will be referred to as “forest” throughout the remainder of the paper) and acahual.

El Edén contains evidence of a variety of both human and natural disturbances. Human disturbances include pre-classic Maya settlements, timber extraction (late nineteenth century) and chicle extraction (dates unknown). Aerial photographs reveal extensive fire mosaics, mostly resulting from escaped fires of slash-and-burn agriculture, although some are the result of lightning. More recently, the wetlands of Yalahau have been tapped as a source of fresh water for the tourism center of Cancún, and the consequences of this disturbance are still unknown. The area also has been subject to damage by hurricanes.

METHODS AND MATERIALS

Overall floristic composition

A species list was created for El Edén from extensive field collections. Identifications were made primarily by the author and Andrew Sanders, curator of the Herbarium at the University of California, Riverside (UCR). Some specimens were sent to specialists for identification. Nomenclature follows *Flora Mesoamericana* (Davidse, Sousa, and Knapp, 1994, 1995, <<http://www.mobot.org/MOBOT/fm/welcome.html>>), where possible, and the “Flora of Guatemala” (Standley, Steyermark and Williams 1946-1977). Vouchers are deposited at the (UCR), Herbarium; partial sets have also been left at the herbaria of the Autonomous University of Yucatán (UAY); Center for Scientific Investigations, Yucatán (YUC); and The College of the Southern Frontier (Colegio de la Frontera Sur) Chetumal (ECO). The flora was analyzed for percent endemism

(those species occurring only within the physiogeographic Yucatán Peninsula, as defined by Duran et al. 1998), and percent exotics (those species that are pantropical in distribution and/or known to be introduced).

Structure and diversity

For the structure and diversity study, ten 20 m x 20 m plots were randomly placed in the mature forest and the secondary forest, for a total of twenty plots. All trees over 2.5 cm dbh (diameter at breast height, 1.4 m) were marked with aluminum tags and measured for dbh. In addition, height was estimated. Data for all ten plots in each vegetation type was pooled to provide a composite picture. Trees that could not be identified in the field were sampled and taken to the herbarium at UCR for identification. Those that still could not be identified were classified as morphospecies. Sterile vouchers were deposited at the UCR Herbarium. To determine whether sampling was adequate, species-area curves were constructed in the ordination program PC-ORD for Windows (McCune and Mefford 1999) for forest, acahual and the combined data set. The program calculates the species-area curves with a random sequence of subsamples (up to 500 times).

To compare the structure and diversity within and between the two vegetation types, the following indices and parameters were calculated: structure (frequency and dbh of individuals with dbh > 2.5 cm); the Shannon-Weiner diversity index (H') and Simpson's diversity index (D) (Magurran 1988), evenness (E) and richness (S) of each community of all individuals with dbh>2.5 cm; relative density of species; relative frequency of species; biomass as a measure of relative dominance [(total basal area of species x / total basal area of all species) x 100]; and relative species importance values (R.I.V., defined as "relative density + relative frequency + relative dominance").

Breeding systems

A preliminary investigation of breeding systems of the tree species was done as part of the qualification of vegetation. Trees were classified into three breeding categories following Bawa, Perry, and Beach (1985); Bullock (1985); and Gillespie (1999): (1) hermaphrodite (including monostylous and heterostylous hermaphroditic species); (2) monoecious (including andromonoecious, polygamo-monoecious, and strictly monoecious species); and (3) dioecious (including androdioecious and strictly dioecious species). Each forest type was analyzed for the total number of species in each breeding system, as well as for the relative abundance of the three breeding systems.

RESULTS

Overall floristic composition

The flora of El Edén contains 100 families, 303 genera, and 414 species. Of all species, 40.3% (166/414) are classified as trees (Figure 6.2). The most speciose woody families include Fabaceae, Euphorbiaceae, Rubiaceae, Verbenaceae, and Sapindaceae (Table 6.1). The most speciose herbaceous families are the Asteraceae, Fabaceae, Orchidaceae, Bromeliaceae, Convolvulaceae, and Cyperaceae (Table 6.1). The largest genera at El Edén are (species number in parentheses) *Tillandsia* (7), *Coccoloba* (6), *Eugenia* (6), *Acacia* (5), and *Ficus* (5). *Caesalpinia*, *Croton*, *Eleocharis*, *Ipomeoa*, *Sideroxylon*, and *Solanum* are represented by four species each, while the remainder of the genera are represented by only one or two species each.

Taxonomic richness (total number of species) at El Edén is comparable to other dry tropical forest sites (Table 6.2). Of the total species, 9.5% (39 spp.) are endemics (Table 6.3) to the physiogeographic Yucatán Peninsula. The endemism rate at El Edén is slightly higher than the 7.3% for the peninsula as a whole (Duran et al. 1998). The flora of El Edén represents

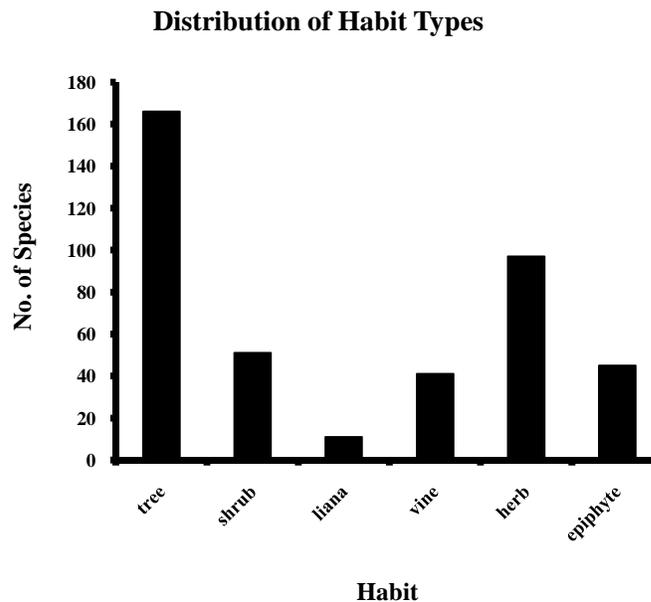


FIGURE 6.2 Distribution of habit types in the flora of El Eden Ecological Reserve.

TABLE 6.1 Most speciose families by habit type in the flora of El Eden Ecological Reserve

	Total	Tree	shrub	liana	vine	herb	epiphyte
<i>Fabaceae</i>	48	29	4	-	10	5	-
Asteraceae	25	-	6	-	2	17	-
Euphorbiaceae	17	10	2	-	-	5	-
Orchidaceae	15	-	-	-	1	-	14
Rubiaceae	14	5	8	-	-	1	-
Verbenaceae	13	6	2	-	1	0	4
Bromeliaceae	11	-	2	-	-	-	9
Sapindaceae	10	6	-	4	-	0	-
Convolvulaceae	10	-	-	-	10	-	-
Cyperaceae	10	-	-	-	-	10	-
Moraceae	9	9	-	-	-	0	-
Polygonaceae	9	8	-	0	-	1	-
Sapotaceae	9	9	-	0	-	-	-
Myrtaceae	8	7	1	0	-	-	-

approximately 18% (411/2300) of the known flora of the Yucatán Peninsula, with endemics at the reserve accounting for about 23 percent (39/168) of the total endemics of the peninsula.

Exotics (i.e., those species described in the primary literature as native to an area other than Mexico) account for only 3.5 percent for the total flora, while 6.3% of the total El Edén flora is pantropical in distribution. The majority of the exotic species are also pantropical in distribution and includes such weedy species as *Leonurus japonicus*, *Rhynchelytrum repens* and *Corchorus siliquosus*.

Structure and composition of woody vegetation

Acahual plots had 110 species and 1,701 individuals in all ten plots. Forest plots had 120 species and 1,286 individuals. Species with relative importance values over 5 percent (Table 6.4) in the forest plots include *Manilkara sapota*, *Metopium brownei*, *Thrinax radiata*, and *Lysiloma latisiliquum*. In the acahual plots, *M. brownei*, *Bursera simaruba*, *Swartzia cubensis*, *L. latisiliquum*, *Vitex gaumeri*, and *Lonchocarpus rugosus* all had RIVs over 10 percent. The forest and acahual data sets are combined, and

TABLE 6.2. Comparison of taxonomic richness of woody species (trees and shrubs > 2.5 cm dbh) among forest sites in the Neotropics in 1,000 m² over 2.5 cm dbh.

Site	# spp.	Forest type	Source
Ometepe (Nicaragua)	26	DRY	Gillespie 1999
Masaya (Nicaragua)	33	DRY	Gillespie 1999
Guanica (Puerto Rico)	34	DRY	Gentry 1999
Cosiguina (Nicaragua)	38	DRY	Gillespie 1999
Chacocente (Nicaragua)	43	DRY	Gillespie 1999
La Flor (Nicaragua)	45	DRY	Gillespie 1999
Palo Verde (Costa Rica)	47	DRY	Gillespie 1999
Guanacaste (upland) (Costa Rica)	47	DRY	Gentry 1995
Guanacaste (gallery) (Costa Rica)	55	DRY	Gentry 1995
Santa Rosa (Costa Rica)	54	DRY	Gillespie 1999
Puerto Morelos (Quintana Roo, Mexico) ^a	55	DRY	Whigham et al. 1991
Calcehtok forest (Yucatan, Mexico) ^b	64	DRY	White & Darwin 1995
Chamela (Jalisco, Mexico)	80	DRY DEC	Lott, Bullock & Sollis-Magallanes 1987
Chamela (Jalisco, Mexico)	83	DRY DEC	Lott, Bullock & Sollis-Magallanes 1987
El Edén (Quintana Roo, Mexico) ^c	82	DRY SEMI	Schultz, this study
La Selva (Costa Rica)	98	WET	Hartshorn & Hammel 1982
Los Tuxtlas (Veracruz, Mexico)	108	MOIST	Lot-Helgueras 1976

DRY=dry tropical forest; DRY DEC = dry deciduous forest; SEMI= semideciduous forest; wet = wet tropical forest; MOIST=moist tropical forest).

^a Data is reported for total area of 4800 m² and individuals > 3 cm dbh. Data is reported from a study area of 1,600 m² and only for species > 10 cm dbh.

^b Data is reported for total area of 4800 m² and individuals > 3 cm dbh.

^c Species richness is extrapolated from a species-area curve for 1000 m² for total plots in this study.

TABLE 6.3. Representation of endemic plant species in El Edén and the Yucatán Peninsula

Location	# Endemic Species	Total Species	% Endemism
Yucatán Peninsula ^a	16 ⁸	2,300	7.3
El Edén	3 ⁹	411	9.5

^a From Duran et al. 1998

certain species that had high R.I.V.s in only one or the other forest type having an overall R.I.V. greater than 5 percent.

The Shannon-Weiner Diversity Index (base 2) ranged from $H' = 2.3 - 3.377$ in the forest plots and $H' = 2.64 - 3.23$ in the acahual plots. The mean values for the two vegetation types differed significantly ($F = 0.0334$), with the overall diversity slightly higher in the forest. Evenness ranged from $E = 0.706 - 0.939$ in the forest and $0.796 - 0.899$ in the acahual, and also differed significantly ($F = 0.029$). Richness varied from $S = 25 - 48$ species in forest plots to $S = 29 - 42$ species in acahual plots, but did not differ significantly overall ($F = 0.218$).

The distribution of dbh classes differed between the two forest types (Figure 6.3). Over half of the individuals in the acahual plots had a dbh less than 5 cm, in the forest plots, the majority of trees had a dbh between 5 and 10 cm. The range of size classes in the acahual was also less than the range of size classes in the forest (2.5 to 40 cm in acahual vs. 2.5 to 55 cm dbh in forest).

There was high concordance of the dominant taxa between size classes, i.e. the dominant taxa of the largest size classes were among the dominant taxa of the smaller size classes in all cases with members of the Fabaceae dominant in both vegetation types as well as in both size classes (Table 6.5). This is interesting because a similar analysis in a moist or wet tropical forest would show the opposite trend, with little concordance of taxa between the size classes (see Nadkarni, Matelson, and Haber 1995). In the larger size class in both forest and acahual, *M. brownei* (16 percent) and *L. latisiliquum* (10 percent) have the highest abundance.

Stem density (calculated on a per-hectare basis) showed that, as expected, the acahual had a much higher density of smaller stems (< 10 cm dbh) than the forest (4,045 trees ha⁻¹ versus 2,252 trees ha⁻¹). The overall stem density of trees > 10 cm dbh also differed, with 200 trees ha⁻¹ in the secondary plots and 938 trees ha⁻¹ in the forest.

The species-area curves indicated that sampling adequately represented the available diversity in the forest, acahual and combined date sets. The

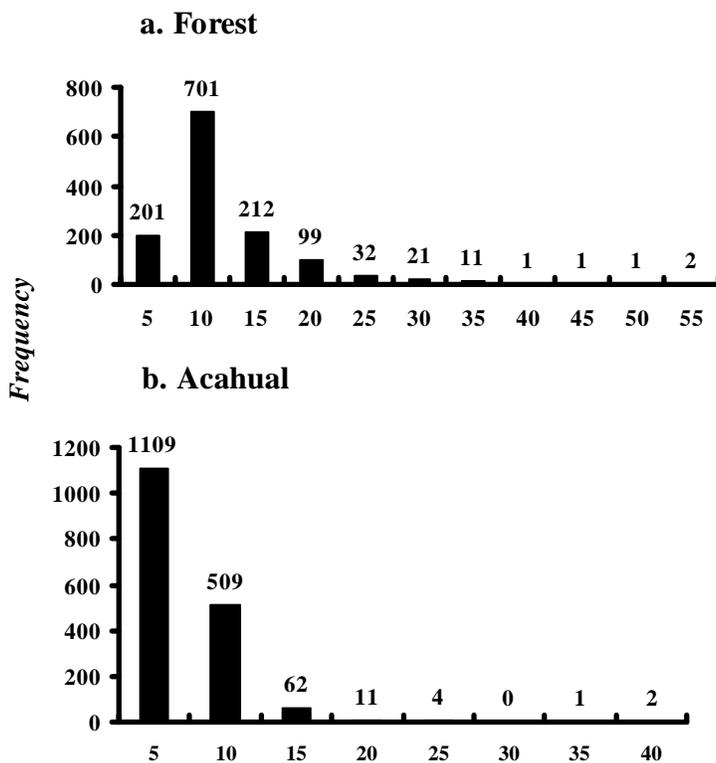


FIGURE 6.3 Frequency distribution of dbh classes in (a) the forest and (b) acahual plots. Numbers represent individuals in each dbh.

slopes of the lines appeared to level off as area increased, thereby indicating that sampling was adequate. In addition, to determine how representative the plots were when compared with the known tree species from the El Edén the checklist, the number of families were tabulated against tree species from the checklist and those that occurred in three or more plots (Table 6.6, after Lott, Bullock, and Solis-Magallanes 1987). Of the potential 116 trees available in those families, 95 trees were sampled (i.e., 82 percent of those available). Some trees in the checklist include trees that occur only in the wetlands (i.e., *Crescentia cujete*) or were planted (*Cordia dodecandra*), which would not otherwise occur in natural forests.

Breeding systems in the woody vegetation

Hermaphroditic plants represent the most common breeding system in the El Edén forest, accounting for 71 percent of all trees at the reserve (Table 6.7). Dioecious tree species account for about 15 percent, and monoecious trees account for 13 percent of the tree species. The frequencies of hermaphrodite and monoecious trees are similar to those found in other dry tropical forests; however, the level of dioecy is somewhat lower.

TABLE 6.4. Relative importance values (R.I.V.) of woody species in forest and acahual plots

Species	Forest + Acahual	Forest	Acahual
<i>Swartzia cubensis</i>	5.23	-	14.39
<i>Nectandra coriacea</i>	5.26	-	7.23
<i>Lonchocarpus rugosus</i>	5.35	-	10.28
<i>Gymnopodium floribundum</i>	7.17	6.79	7.80
<i>Vitex gaumeri</i>	8.63	6.81	11.85
<i>Thrinax radiata</i>	11.10	17.72	-
<i>Bursera simaruba</i>	11.31	6.85	16.49
<i>Lysiloma latisiliquum</i>	15.47	16.25	13.84
<i>Manilkara sapota</i>	17.54	29.34	-
<i>Metopium brownei</i>	20.57	19.78	21.05
<i>Sebastiania adenophora</i>	-	6.25	-
<i>Acacia dolichostachya</i>	-	6.86	-
<i>Piscidia piscipula</i>	-	-	5.20
<i>Lonchocarpus xuul</i>	-	-	5.81
<i>Jatropha gaumeri</i>	-	-	7.23

Floristically, monoecy was represented in 6 families, dioecy was represented in 19 families, and hermaphrodite breeding systems were represented in 32. There were also differences in the distribution of breeding systems between forest and acahual plots: 10% of the trees in acahual plots and 11.4% of the trees in forest plots were monoecious, while 15.4 % of the trees in acahual plots and 9.8% of the trees in forest plots were dioecious.

DISCUSSION

Floristic Representation

Members of the Fabaceae family dominated both the forest and the acahual plots. In addition, Fabaceae is the most dominant family in both the flora of El Edén (45 species in 32 genera) and in the plots (about 19 percent of the total trees). Trees species in the plots represent 92.5 percent of the possible species in the flora. Fabaceae ranks as the most speciose family in 19 out of 25 Neotropical sites and 5 of 6 florulas analyzed by Gentry

TABLE 5. The three taxa with the highest stem density for two size classes (> 10 cm dbh and < 10 cm dbh) in forest and acahual plots

	<u>Forest</u>		<u>Acahual</u>	
	> 10 cm dbh	< 10 cm dbh	> 10 cm dbh	< 10 cm dbh
Family				
	Fabaceae	Fabaceae	Fabaceae	Fabaceae
	Anacardiaceae	Euphorbiaceae	Anacardiaceae	Meliaceae
	Sapotaceae	Sapotaceae	Verbenaceae	Polygonaceae
Genus				
	<i>Lysiloma</i>	<i>Lonchocarpus</i>	<i>Lysiloma</i>	<i>Lonchocarpus</i>
	<i>Metopium</i>	<i>Sebastiana</i>	<i>Metopium</i>	<i>Bursera</i>
	<i>Manilkara</i>	<i>Manilkara</i>	<i>Vitex</i>	<i>Gymnopodium</i>
Species				
	<i>Lysiloma</i>	<i>Lonchocarpus</i>	<i>Lysiloma</i>	<i>Lonchocarpus</i>
	<i>latisiliquum</i>	<i>rugosus</i>	<i>latisiliquum</i>	<i>xuul</i>
	<i>Metopium</i>	<i>Sebastiana</i>	<i>Metopium</i>	<i>Bursera</i>
	<i>brownei</i>	<i>adenophora</i>	<i>brownei</i>	<i>simaruba</i>
	<i>Manilkara</i>	<i>Manilkara sapota</i>	<i>Vitex gaumeri</i>	<i>Gymnopodium</i>
	<i>sapota</i>			<i>floribundum</i>

(1995), so it is generally regarded as the dominant family in Neotropical forests (Lott, Bullock, and Solis-Magallanes 1987).

The Euphorbiaceae ranked second, with 70% of the available species occurring in the plots. The importance of this family at El Edén is interesting as the only other two sites where it has high levels of species are Chamela and the Sian Ka'an Biosphere Reserve—both in Mexico (Gentry 1995). The other families evaluated were all well represented in the plots, with at least 65 percent (and up to 100 percent) of the available species present. Twenty-five of the 28 available endemic tree species occurred in the plots.

The percentage of endemics in the El Edén flora is slightly higher relative to the percentage of endemics in the peninsula. The only other site in the Yucatán Peninsula for which a flora has been completed is the Sian Ka'an Biosphere Reserve (Duran and Olmsted 1990; Villanueva and Cabrera 1990). The total flora of Sian Ka'an has approximately 900 species of which 36 (~5%) are peninsula endemics. El Edén is 1,492 ha, approximately 2% of the size of Sian Ka'an, which is 528,147 ha in extent. El Edén also has less landscape heterogeneity (no marine habitats) than Sian Ka'an. The fact that El Edén is so much smaller, yet has almost half the

TABLE 6.6. Comparison of woody species represented in flora and in three or more plots (forest and acahual)

Family	In flora	In plots
Fabaceae	27	25
Euphorbiaceae	10	7
Sapotaceae	9	6
Moraceae	9	5
Myrtaceae	8	7
Polygonaceae	7	6
Flacourtiaceae	6	4
Rutaceae	6	6
Sapindaceae	6	4
Verbenaceae	6	4
Malpighiaceae	5	4
Rubiaceae	5	5
Ebenaceae	3	3
Erythroxylaceae	3	3
Nyctaginaceae	3	3
Rhamnaceae	3	3

number of species and a higher proportion of plant endemics certainly supports earlier statements of the biological richness of the Yalahau region (Lazcano-Barrero et al. 1992; Lee 1980 Snedaker, Clark and Olmsted 1991).

Breeding systems

Understanding the nature of breeding systems, and the proportion of both total and of dominant species in a tree community, is important for understanding the floristic dynamics of that ecosystem. Opler, Frankie, and Baker (1980) compared percentages of breeding systems in primary and secondary lowland dry forests in Costa Rica and found that the proportion of dioecious species increased with seral age. This paper suggests an opposite trend for the El Edén forests where dioecy decreased with seral age, although this needs further investigation.

Even though the relationships are not always clearly understood, a species' breeding system can often be indicative of self-compatibility. For example, dioecious trees are obligate outcrossers, and many hermaphroditic

TABLE 6.7 Comparison of frequency of breeding systems in trees at several sites in the Neotropics. Polygamous forms are included in monoecy.

Site	Forest Type	Hermaphrodite (%)	Dioecious (%)	Monoecious (%)	Source
El Edén, Quintana Roo, Mexico	dry tropical forest	71	15	13	This study
Guanacaste, Costa Rica	dry tropical forest	68	22	10	Bawa 1974
South Florida	subtropical forest	61	27	12	Tomlinson 1974
La Selva, Costa Rica	tropical forest	65.5	23.1	11.4	Bawa, Perry, & Beach 1985
Chamela, Jalisco, Mexico	dry tropical forest	58	26	15.9	Bullock 1985
Barro Colorado Island, Panama	wet tropical forest	63	8.7	15.2	Croat 1979

trees have variable levels of self-compatibility. Early papers suggested that self-compatibility should be widespread in tropical rainforest trees (Corner 1954; Federov 1966), but more recent studies (Janzen 1971; Bawa 1974) indicate that self-incompatibility is the rule; in fact, many tropical tree species are obligate outcrossers. The nature of breeding systems and levels of self-compatibility in a community are important considerations for understanding species population structure and dynamics. Their importance becomes more pronounced as disturbance levels and resultant patchiness increase in a landscape because, even in large forest extents the majority of tropical tree species are widely dispersed and have low population size. As forest patches become smaller and populations and individuals increasingly isolated, opportunities for outcrossing and dispersal may become increasingly difficult for some species. This should be considered when conservation, management, and restoration decisions are being made.

Comparisons with other studies

When compared with general descriptions of the vegetation in the Yucatán Peninsula, the forests of El Edén represent a subset of species listed as important constituents of tropical subperennial forests. Rzedowski and Rzedowski (1989) list *Brosimum alicastrum*, *Manilkara zapota*, *Metopium brownei*, *Piscidia piscipula*, and *Swartzia cubensis* as abundant species. Flores and Espejel (1994) also list *B. alicastrum*, *M. zapota*, and *M. brownei*, while including *Vitex gaumeri* and *Lysiloma latisiliquum*; Miranda (1958) adds *Thrinax radiata* and *Bursera simaruba*. Site-specific studies seem to indicate that *B. simaruba*, *Gymnopodium floribundum*, *P. piscipula*, and *Thouinia paucidentata* are important components of the forests across the peninsula (Rico-Gray et al. 1988; Thien, Bradburn, and Welden 1982; White and Darwin 1995). With the exceptions of *B. alicastrum* and *T. paucidentata*, all of these species have high R.I.V.s in the forests of El Edén.

However, comparisons with local-scale vegetation studies in the peninsula also show some strong differences between the floristic composition of the El Edén forests and those sites. For example, in their study of two different aged regenerating forests (12 yr and 26 yr since disturbance) in Yucatán state, Perkulis, Prado, and Jiménez-Osornio (1997), found that in the older forest, the species with the highest RIV (over 5 percent) included *Acacia gaumeri*, *P. piscipula*, *Havardia albicans*, *Chiococca alba*, and *Mimosa bahamensis*. In contrast, *L. latisiliquum* only had a 0.5 % RIV, while *M. zapota*, *M. brownei*, *G. floribundum*—all species with high RIVs in the El Edén forests—were not included on their list.

When compared to the 12-year-old stand, the only species with an RIV larger than 5 percent in both El Edén and their site is *B. simaruba*. Perkulis, Prado, and Jiménez-Osornio expected a higher incidence of *L. latisiliquum*, but suggested that its absence may be related to the site's previous land use as a henequen plantation, as well as to reduced intervals between disturbance (Perkulis, Prado, and Jiménez-Osornio 1997).

In a survey of seven sites in north-central Yucatán, White and Darwin (1995), reported that only three species had RIVs comparable to those at El Edén, most notably, *B. simaruba* which had high RIV values (for stems over 3 cm in five of the seven sites). Other species with RIVs over 5% in at least five of the sites included *P. piscipula* and *G. floribundum*. *Lysiloma latisiliquum*, which is so important in the El Edén forests, was comparatively rare, with an R.I.V. over 5% in only two of the seven sites. Other important species at El Edén, *V. gaumeri* and *M. zapota*, were present in two sites each, while *M. brownei* only occurred in one site.

The only other study conducted in northern Quintana Roo (Whigham et al. 1990) lists *M. zapota*, *Talisia olivaeformis*, *Gymnanthes lucida*, *B. alicastrum*, *Drypetes lateriflora*, *Sapindus saponaria*, and *Coccoloba diversifolia* as comprising 64 percent of the trees in their plots. Although all of these species occur within El Edén, *M. zapota* is the only important species shared by both forests studied.

Based on dominance, the only forest descriptions that seem comparable to those in El Edén are those from Campeche, which were described by Orejuela(1980). Quantitative assessments of the forests in Escarcega and Xpuhil show that dominant trees included *L. latisiliquum*, *V. gaumeri*, *B. simaruba*, and *M. zapota*, all important in El Edén.

These large differences in floristic composition across the entire Yucatán Peninsula are in need of further study. Slight gradients in rainfall, soils, and topography may be enough to determine the distribution of some species in the landscape and community composition could differ significantly according to the ecological requirements of its members. The problem with this argument is that many of the tree species in the Yucatán are not only widely distributed in the peninsula itself, but also throughout Central America, e.g. *Bursera simaruba* which is found from Florida to Argentina. Another explanation for the increasing differences in community composition may be related to land-use patterns, which cannot be quantified in most cases due to a lack of long-term aerial photograph and satellite coverage, as well as a lack of reliable land-use records. Several authors have demonstrated that, probably for centuries, the Maya have manipulated and managed their forests through culling and coppicing (Gómez-Pompa and Kaus 1998; Rico-Gray and García-Franco 1992; Peters 2000). As White and Darwin (1995) point out, "a few emergent trees scattered among the canopy cover may be a false indication of old age." (p. 15).

While a complete floristic evaluation comparing the forests described in other studies with those at El Edén has not been conducted, in terms of

general floristic composition, all forests of the Yucatán Peninsula appear similar. Each region draws from the same set of species (i.e., the flora of the peninsula), but large differences exist in the structural and compositional dominance and abundance of those species. My data clearly demonstrate that the forests at El Edén are unique in their composition as related to the dominance and abundance of species with respect to other forests in the Yucatán Peninsula.

Implications

The results of this study demonstrate that, at least when considered floristically, the two forests at El Edén are significantly different. The difference could be explained by succession, with the acahual representing true seral stages of the older forest. Another possibility is that at El Edén, as elsewhere in the peninsula, the shortening of the disturbance interval (especially human-related) is resulting in the loss of the late successional species. These species may not be able to reproduce fast enough to persist; as a result, the community may be undergoing a major change in composition (Rico-Gray and García-Franco 1992).

The northeastern Yucatán Peninsula provides a good place to examine differences between successional forest stands for two reasons. First, there is a lack of obvious environmental differences (e.g., topography, soil types, or rainfall) to consider. Second, the Yalahau region has had comparatively low levels of human disturbance when compared with other areas (e.g., those around major archaeological sites such as Chichén Itzá in the state of Yucatán). Until 30 years ago, the area was largely unoccupied, inaccessible, and unexplored. The creation of Cancún and the associated tourist corridor in the early seventies have led to unchecked growth and an influx of people from around the country seeking work. This combination of low variation in environmental factors and increasing disturbance pressure makes it an ideal place to test hypotheses regarding disturbance and its effect on floristic diversity and composition.

There are two competing hypotheses regarding the nature and composition of vegetation in the Yucatán Peninsula. The first hypothesis suggests that the vegetation has been under constant selection by continuous disturbance, from people as well as by natural sources (Gómez-Pompa 1987; Peters 2000). As a result, the present forests are the product of 3,000 years of manipulation and management (primarily by the Maya), and are thus highly resilient (Gómez-Pompa 1987; Gómez-Pompa and Kaus 1998; Rico-Gray 1991; see also Comiskey and Dallmeier 1998). Additional support for this hypothesis comes from examining the endemic flora of the peninsula. Endemic plants are often rare plants, such as those that are limited by an environmental factor (e.g., edaphic properties). In contrast, the

majority of the endemic plant species in the Yucatán Peninsula—especially the trees—are widespread throughout the peninsula and are classified as secondary species (Gómez-Pompa, personal communication.).

The alternate hypothesis suggests that, while these forests might have some level of resilience, the recent increase in human populations and level of disturbance across the peninsula could be leading to a state of arrested succession, in which the forests will never reach an old growth state. Forests of large trees in the Yucatán Peninsula seem to be limited to protected areas (e.g., archaeological sites, and nature reserves such as Punta Laguna, Quintana Roo). The physical difference between these protected forests and the immediate surrounding areas is quite striking, most notably in that the understory is more open, and many of the trees are quite large (>50 cm dbh and 15 m).

Perhaps both hypotheses are valid. The latter half of the twentieth century has emerged as a time of ecological homogenization; nonnative organisms are having major diversity and structural impacts upon ecosystems (Horvitz et al 1998; Roth 1999; Stohlgren et al 1999). Extinction rates have increased (Myers 1988). Global warming is thought to be negatively affecting animal and plant populations throughout the world (Myers 1988). Until the twentieth century, however, the disturbances in the Yucatán Peninsula were on a smaller scale, and the intervals between disturbances were long enough that the forests could regenerate on their own. Large-scale disturbance resulting in drastic change in community composition has occurred in the peninsula before. The pollen record from several lakes in the central peninsula has shown that dominant vegetation types (based on floristic composition as reflected in the pollen record) have fluctuated due to global climate changes as well as human disturbances (Leyden et al. 1994; Leyden, Brenner, and Dahlin 1998). Now, with the global increases in the movement of exotic organisms, levels of disturbance (Ehrlich 1988), and patchiness of communities (Schelhas and Greenberg 1996), many forests, including those in the Yucatan, may not be able to regenerate on their own.

The intensive disturbance and fragmentation of these forests may reach a point of no return; we may be unable to restore them. It is imperative to gain understanding of their diversity and to initiate restoration experiments and projects now. While this paper's main goal was to describe the floristics and structure of the forests at El Edén, future research should include indepth studies of the sexuality, floral biology, pollination, and dispersal strategies of the flora. As Gillespie (1999) and Janzen (1986) point out, a combination of fragmentation; community turnover that favors species with non-specific pollination (e.g., wind); and dispersal agents can result in the eventual loss of those trees, and other plant species, that have specific pollinators and dispersers.

A better understanding of the dynamics of the Yucatán forests through long-term monitoring of its protected areas. The El Edén Ecological Reserve, and the surrounding areas, provides a good place to do this. The plots used to characterize the vegetation of El Edén were designed to be permanent locations with known floristic composition and structure, and to be used for long-term monitoring of the trees as well as other types of ecological and diversity studies. This research provides a base from which in-depth investigations of the life-history characteristics and ecological roles of the trees in these forests can begin.

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Chapter 7

Hydrogeology of the Yucatán Peninsula

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GENERAL GEOLOGY OF THE NORTHERN YUCATÁN PENINSULA

The northern Yucatán Peninsula, Mexico is a partially emergent carbonate platform with an extensive continental shelf. Mesozoic- and Cenozoic-era limestone, dolomite, and anhydrite overlie deeply buried Paleozoic-era crystalline and sedimentary rocks. The peninsular aquifer system has developed in nearly horizontal, highly-permeable rocks that are dominantly Tertiary period limestones and dolostones. These are thinly covered by Holocene and Pleistocene epoch carbonate rocks and sediments along the coast, as well as by a thin cover of soil inland. Rocks are both porous and permeable, and permeability exists on two scales: cavernous (fracture) and intergranular (porous medium).

Exceptionally permeable zones are developed along faults, perhaps generated by Eocene epoch Caribbean plate movements in the east and, in the northwest, by crustal relaxation and/or basin loading caused by the impact of a large meteorite or comet (Hildebrand et al. 1995). An additional prominent fault, the Ticul Fault Zone (Figure 7.1), whose origin is difficult to assign to a specific tectonic event, is present in the northwest portion of the peninsula. These faults are important as channels for groundwater movement.

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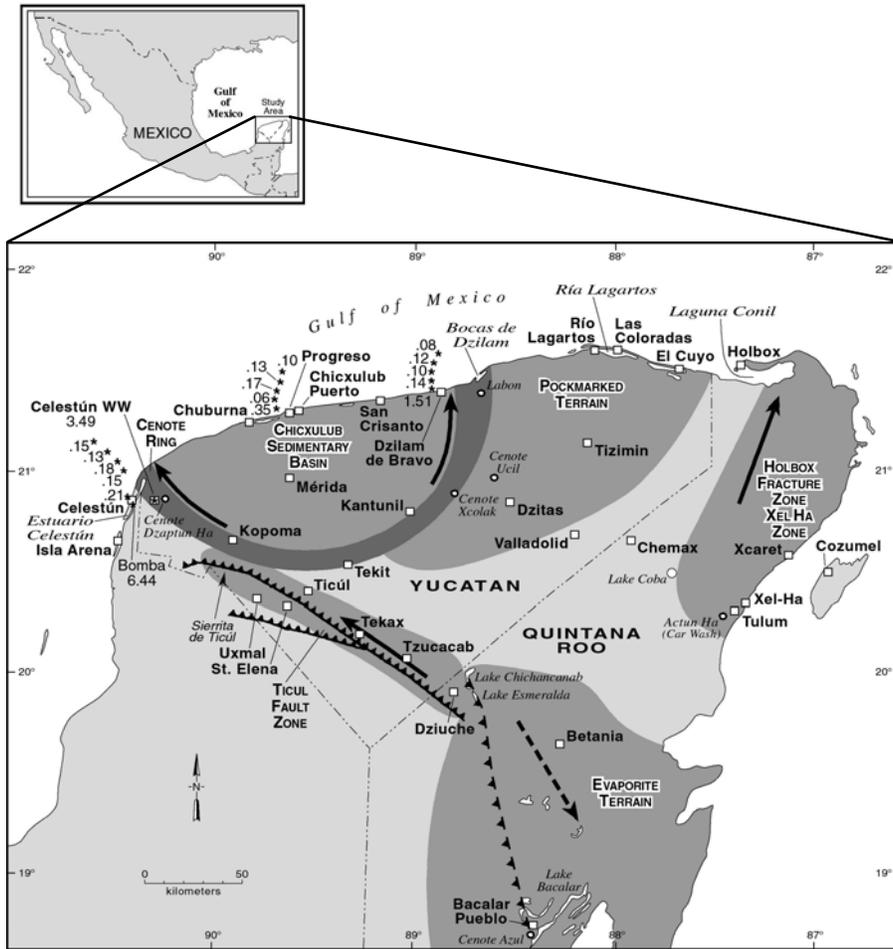


FIGURE 7.1 Map of the northern Yucatán Peninsula showing the major geostructural features and an outline of hydrogeochemical terrains discussed in the text. (Inset map of Mexico shows location of study area). Radium (^{226}Ra) isotope values in dpm/l are shown for three seaward traverses, starting from Celestun, Progreso, and Dzilam de Bravo, and extending 20 km seaward. ^{226}Ra is also plotted for “Bomba” (a coastal spring) and for the Celestun Water Works (WW). Faults are indicated by lines with serrated edges, dashed where uncertain. Groundwater flow directions are indicated by large arrows, dashed where uncertain.

Over almost the entire northern region, a thin freshwater lens is underlain by a marine saline intrusion. North of the Champoton River, in Campeche, there are no permanent streams of more than a few hundred meters length along the west and north coasts. On the east coast of the peninsula, significant streams are not present in Mexico, but do occur in Belize. An extensive aquitard has developed within the surface calcrete layer along the entire north coast from Isla Arena (Campeche) to Holbox

(Quintana Roo); but, with this exception, there are no extensive aquitards beneath the northern peninsula.

The distinctive geology and hydrogeology of the region have had a strong effect on its biota as well as on the culture of its early indigenous inhabitants. Weathering residue of the exceptionally pure carbonate rocks has produced remarkably little soil cover, and may have significantly limited available trace nutrients. Furthermore, even though rainfall is seasonably abundant over much of the peninsula, water is readily available only at specific sites because of the absence of surface streams. Access to water by humans during the pre-colonial period was thus limited to water that could be obtained from sinkholes in limestone [cenotes, after the Maya “dzonot”], from primitive hand-dug wells, or from precipitation collected in various storage devices like those sketched by Frederick Catherwood (Figure 7.2) and described at Uxmal by Stevens ([1843] 1962).

Except for agriculture, the region offers limited natural resources. Easily worked building stone was one factor facilitating monumental pre-Columbian architecture (ambitiously recycled as churches and monasteries after



FIGURE 7.2 Aguada, natural water-filled depression at Uxmal as sketched by Frederick Catherwood. Storage capacity of such natural features was developed and enhanced by Maya hydraulic engineering in the water-starved region south of the Sierrita de Ticul where depth to the water table exceeds 100 m, and cenotes are not present. (Source: From an illustration in Stevens [1843] 1962.)

the Spanish Conquest). Also useful was a distinctive and ubiquitous weathering product of the limestone of the Yucatán Platform—sascab (as follows), which can easily be processed to make building mortar.

Petroleum, which might be expected in the geologic environment of the peninsula, has not been reported. Metals are notably absent. Even flint, which commonly occurs in carbonate rocks, is lacking. It would have been important in a pre-Columbian economy, as evidenced by tiny and delicate imported blades of obsidian found at Maya archaeological sites. The major exportable mineral resource from the area in pre-colonial time was salt, the production of which was aided by the nature of coastal hydrogeologic processes then, as it is now.

SOILS

Distinctive characteristics of the soil and surficial carbonate layers of the Yucatán Peninsula strongly affect evapotranspiration, groundwater infiltration, and recharge. It is ironic that although rock exposure on Yucatán is almost complete in some areas, detailed stratigraphy is not well known, in large part because of the extensive alteration of surface rock. The result of this alteration is a nearly impermeable surface layer of calcrete up to about 3 meters (m) thick that covers much of the northern peninsula. Quiñones and Allende (1974) call this calcrete layer a “carapace” and attribute its formation to recrystallization of aragonite and high-magnesium calcite to form a more stable mineral, low-magnesium calcite. Beneath the carapace is a layer of low magnesium calcite, almost completely lacking in cement, known as “sascab.” Gerstenhauer (1987) notes that the development of these two layers is correlated and attributes sascab development to infiltration of water. Tulaczyk (1993) reports three occurrences of sascab in northern Quintana Roo in which no overlying carapace is present, but which contain “clasts” that could be residues of such a layer destroyed by weathering. These occurrences of what he refers to as diamictic sascab may tentatively support Gerstenhauer’s model in which sascab and calcrete developed together during the Mio-Pliocene epoch under weathering conditions different from those of today.

In many parts of northern Yucatán, the thickness of the soil cover over bedrock is a few centimeters (cm) at most. Rarely is this thickness more than a meter, except in karst depressions such as “aguadas.” The hydrogeologic significance of scarce soil cover is that meteoric precipitation can move quickly from the surface directly into the aquifer through fractures or sinks in the almost ubiquitous calcrete layer. This is a major reason for the absence of surface drainage on the peninsula. Whatever

rainfall is not evaporated or absorbed in the sascab layer moves almost immediately into the aquifer.

Variants of three possible sources exist for the soil that is present in northern Yucatán: (1) residual insoluble material derived from dissolution of carbonate rock, (2) volcanic dust from Central American volcanoes, and (3) dust from more remote sources. Gmitro (1986), who examined the insoluble residue from acid dissolution of several Yucatán carbonate rocks, reported that values close to 0% were most common, and that values seldom exceeded 10 percent.

Pope et al. (1996) have correlated soil maps and geologic maps of the Yucatán Peninsula and report a clear relation between soil type and bedrock age, consistent with persistence of residual soil that is, in some cases, as old as the Eocene. Few analyses of Yucatán soils or argillaceous sediments are available. Schultz et al. (1971) examined three clay beds, used as pottery clays, that are 1–2 m thick and are interbedded with limestone of probable Eocene age. One occurrence is from near Ticul, and the other two occurrences are from the vicinity of Becal, which is about 50 kilometers (km) to the west. These clays, dominated by particles smaller than 0.25 microns (μ), consist predominantly of mixed layered kaolinite-montmorillonite, with quartz as the dominant mineral or dominant additional mineral in the sample fraction greater than 1μ in diameter. The authors presume the deposits to be residual material derived indirectly from airborne pyroclastic material. The insoluble residue left after standard acid leaching of samples of limestone that stratigraphically overlie the clay horizon at Ticul constitutes 0.5–5 percent of the rock mass and is composed of montmorillonite (Schultz et al. 1971).

The slow rate at which soil has accumulated over the Yucatán Peninsula raises the possibility that an appreciable soil component comes from wind-blown dust originating in Africa. The amount of mineral dust from West Africa that is precipitated each year in Miami, Florida, has been estimated to be $1.25 \text{ gm}\cdot\text{m}^{-2}\text{yr}^{-1}$ (based on measurements during 1982–1983; see Prospero 1999). Dominant minerals in West African dust are illite and kaolinite, with lesser amounts of smectite, montmorillonite, and chlorite. Relative percentage of these minerals varies with latitude, with kaolinite dominating at low latitudes; because the West African dust plume extends over Yucatán, the Miami measurements may be relevant to the rate and source of dust deposition in Yucatán. Oxygen isotope analysis of the quartz fraction of soils, and of insoluble residues from carbonate rocks of the Yucatán Peninsula, could, perhaps, distinguish between these sources (Rex et al. 1969).

REGIONAL HYDROGEOLOGY

Porous, permeable karst carbonate of the Yucatán Peninsula contains a fresh groundwater lens underlain by a saline intrusion whose depth is defined approximately by the Ghyben-Herzberg relation

$$d_i = 40 \cdot d_x,$$

where d_x = elevation above mean sea level (msl) and d_i = depth of interface between fresh and saline water [density 1.025 grams per cubic centimeter ($\text{gm} \cdot \text{cm}^{-3}$)]. The nearly flat water table (gradient 2 centimeters per kilometer [cm/km]) is controlled by sea level and, to a lesser extent, by recharge from the annual precipitation of 500 to 1500 millimeters (mm) (Chavez-Guillen 1986, 1988). Ion content of the groundwater comes primarily from mixing with the seawater intrusion and from dissolution of minerals.

Water for human use is accessible where cenotes developed along geologic structures (Cenote Ring, Holbox Fracture Zone), near the coast where the water table is near the surface, and in north-central Yucatán where weathering has resulted in extensive karstification. The depth of the water table increases inland, from greater than 20 m in Ticul to deeper than 100 m in the Puuc region south of the Sierrita de Ticul.

The terminal Cretaceous Chicxulub Impact Crater, centered approximately on Chicxulub Puerto (lat. 21°20' N, long. 89°35' W), has influenced hydrogeology by producing a basin of subsidence that has partially escaped erosion and karstification (Hildebrand et al. 1995; McClain 1997; Perry et al. 1995; Pope et al. 1996). Geologic structures that influence groundwater movement (see Figure 7.1) include the Cenote Ring (or “Ring of Cenotes”), a permeable zone surrounding the Chicxulub Sedimentary Basin; the Ticul Fault Zone (delineated by the Sierrita de Ticul); and the Holbox Fracture Zone in northeastern Quintana Roo (Tulaczyk et al. 1993; Southworth 1985).

Other notable geomorphic/hydrogeologic features are (1) the north coast, characterized by a shallow ramp, nearly-continuous dune ridge, cienaga (saline swamp), and exposed rock (tsekel); (2) the fault-bounded east coast; (3) the north-central plain with strongly developed karst features (“Pockmarked Terrain”); (4) a region of poljes—large, flat enclosed basins whose geologic origin is uncertain—south of the Sierrita de Ticul; and (5) the zone of high-sulfate groundwater, located south and east of Lake Chichancanab in Quintana Roo. Aspects of regional hydrogeology are presented in papers by Back and Hanshaw (1970); Marin et al. (1990); Moore, Stoessell, and Easley (1992); Perry et al. (1989, 1995); Pope, Rejmankova, and Paris (2001); Reeve and Perry (1994); Stoessell et al. (1989); and Stoessell (1995).

**EVAPORITES/BRECCIA AS A SOURCE
OF GEOCHEMICAL TRACERS**

Chemical tracers are proving useful in understanding groundwater movement and rock-water interaction in the Yucatán aquifer. These include, in particular, the major ions calcium (Ca^{2+}), magnesium (Mg^{2+}), sulfate (SO_4^{2-}), bicarbonate (HCO_3^-), and chloride (Cl^-), as well as the minor ion strontium (Sr^{2+}). Analyses have been presented by Perry et al. (1995); Stoessell et al. (1989); Moore, Stoessell, and Easley (1992); and Velazquez-Oliman (1995). The brief summary presented here is based on about 60 major element analyses and 65 additional $\text{SO}_4^{2-}/\text{Cl}^-$ ratios of ours that have not yet been published. Several isotopes also provide useful hydrogeologic information. These include oxygen ($\delta^{18}\text{O}$)–hydrogen ($\delta^2\text{H}$) composition of groundwater, surface water, and precipitation; $\delta^{34}\text{S}$ composition of sulfides and sulfate (SO_4^{2-}); $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in rocks and water; and various isotopes of radium (e.g., ^{226}Ra).

Almost all fresh groundwater of the Yucatán platform is at (or near) saturation equilibrium with calcite and (depending on the value assumed for the solubility product constant, K_{sp}) with dolomite. This is expected in an aquifer system dominated by carbonate rocks.

As reported by Perry et al. (1995), ratios of $\text{SO}_4^{2-}/\text{Cl}^-$ (or $\text{Cl}^-/\text{SO}_4^{2-}$) have helped determine mixing and flow patterns of Yucatán groundwater. The ratio $100 \cdot \text{SO}_4^{2-}/\text{Cl}^-$, expressed in chemical equivalents, is 10.3 for seawater; ratios close to this are observed in much of the northern part of the peninsula. This implies two things:

1. Over much of the peninsula, a major source of ions in the fresh groundwater lens comes from mixing with the underlying saline intrusion, which has been determined to be present as far inland as St. Elena (about 100 km; see Figure 7.1).
2. In most cases, SO_4^{2-} behaves as a conservative ion. Exceptions to the latter observation, to be discussed subsequently, are
 - a. unusual cases in which oxidation–reduction (REDOX) reactions have converted SO_4^{2-} to H_2S and HS^- , and
 - b. the case of Lake Chichancanab, a few kilometers from the southeast border of Yucatán (see Figure 7.1), which is in saturation equilibrium with gypsum; thus, the SO_4^{2-} concentration in this lake is governed by gypsum solubility.

The evaporite beds that produce high-sulfate water in Lake Chichancanab also affect the groundwater geochemistry of a considerable area in central Yucatán, with consequences for tracing groundwater movement; for rock diagenesis; and, in practical terms, for agricultural productivity. Two

possible SO_4^{2-} sources are present in the area. Eocene gypsum-bearing evaporite has been reported in Quintana Roo (Lopez Ramos 1973), and gypsum and anhydrite are also abundant in impact breccia from the Chicxulub Crater (Rebolledo-Viera et al. 2000; Ward et al. 1995). Either of these could be the source of the 2,600 parts per million (ppm) SO_4^{2-} that has found in water of Lake Chichancanab and of high SO_4^{2-} values in groundwater of what is labeled the Evaporite Terrain in Figure 7.1. Gypsum is regularly precipitated around the lake bank, and celestite (SrSO_4) is in saturation equilibrium in the lake water. It is reasonable to postulate that the steep eastern bank of Lake Chichancanab is a fault—upthrust to the east—and that this fault exposes K/T breccia to dissolution by shallow groundwater. A reconnaissance study of groundwater south and east of Lake Chichancanab indicates an apparent lineament of water of high and variable $\text{SO}_4^{2-}/\text{Cl}^-$ ratio extending from Lake Chichancanab to Cenote Azul on the southeast coast of Quintana Roo, near Bacalar Pueblo.

$\text{SO}_4^{2-}/\text{Cl}^-$ ratios show that groundwater from the vicinity of Lake Chichancanab moves northwestward through the Ticul Fault Zone (see Figure 7.1), then northward through the western arm of the Cenote Ring into Estuario Celestun (Velazquez-Oliman 1995; Perry et al. 1995). It is also possible that one or more additional sources of shallow evaporite-bearing rock is present as a SO_4^{2-} source for groundwater south of Lake Chichancanab in the Evaporite Terrain.

The Cenote Ring is a major channel for groundwater movement in northern Yucatán. This is confirmed by $\text{SO}_4^{2-}/\text{Cl}^-$ determinations of groundwater and by groundwater table elevations that were reported by Marin (1990) and Marin et al. (1990). Subsequent unpublished measurements by Perry and Zhang (based on first-order INEGI benchmarks) indicate that multiple groundwater divides exist in the system (cf Steinich et al. 1996), and that the highest groundwater elevation on the northern peninsula occurs approximately at Lake Chichancanab (4 m above msl), indicating the flow directions shown in Figure. 7.1.

COASTAL REGION

The hydrogeology and many of the physical and geochemical characteristics of the coastal area can best be understood with reference to two features. First, water arrives at this coast exclusively as groundwater, and much of this groundwater is channeled into specific zones in response to structural features such as faults or lineaments. This explains the presence of three of the important north coast freshwater discharge zones: Estuario Celestun, Bocas de Dzilam, and Laguna Conil. Second, a coastal aquitard has produced a sort of groundwater “sandwich” along the north coast.

Where fully developed, as at Celestun, the persistent sand dune that overlies this coastal aquitard has the following hydrologic components (from the uppermost downward; see Figure 7. 3):

- A. a thin layer of freshwater produced by local precipitation;
- B. a thin layer of saline water in direct contact with seawater;
- C. the calcrete aquitard upon which the dune rests; the aquitard prevents vertical water movement.

Beneath it, the multilayer hydrogeologic “sandwich” is completed by

- D. the coastal edge of an extensive freshwater lens that constitutes the major peninsular aquifer (with a dynamic hydrostatic head that remains higher than sea level);
- E. the dispersion zone, a zone of variable thickness of active mixing between the freshwater lens (D) above and the saline intrusion (F) below; and
- F. the saline intrusion that penetrates many kilometers inland. Here, as elsewhere, the freshwater lens floats on the saline intrusion, but mixing of these two layers may be particularly active beneath the confining aquitard because the whole system responds to tides (Reeve 1990).

Seawater flows inland within the unconfined upper part of the system, and through the coastal dune, in response to solar-induced evaporation in the cienaga (saline swamp) that occurs on the landward side of the dune ridge (Figure 7.3). The development of this coastal system is discussed below.

The distinctive and widespread north-coastal aquitard formed from the coastal portion of the ubiquitous surface calcrete layer of the peninsula in response to several factors (Perry et al. 1989). These include the low gradient of the land surface (measured in cm/km), the steady rise in sea level for the past 17,000 years (Fairbanks 1989; Coke, Perry, and Long 1991), direct control of the groundwater table by sea level, saturation of groundwater with respect to calcite, and tropical climate with high rate of evaporation of surface water. Perry et al. (1989) have incorporated these factors into the following model to explain observed characteristics of the aquitard.

As shown in Figure 7.4, the groundwater table near the north coast intersects the land surface along a broad band where water comes to the surface and evaporates. Land surface at Mérida (35 km inland) is only 8 m above msl—yielding an average land gradient of about 20 cm/km. (East of Progreso [see Figure 7.1], the slope of the land surface is somewhat steeper than 20 cm/km, whereas in the vicinity of Celestun to the west, the gradient is much less.) The slope of the land is so small that seasonal variation of the

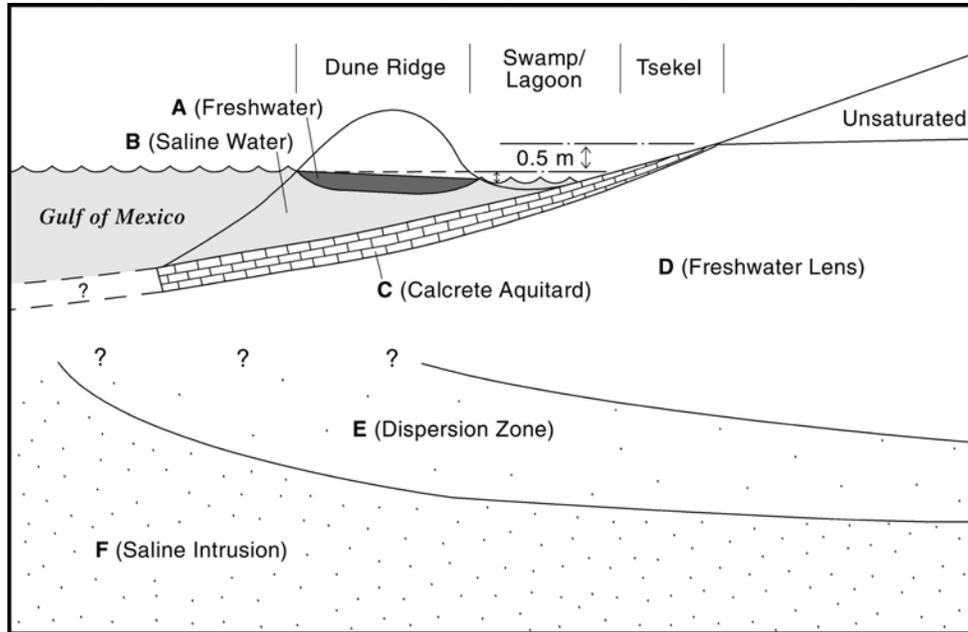


FIGURE 7.3. Schematic cross section of an aquifer system at the coast. A = a thin layer of freshwater produced by local precipitation; C = calcrete aquitard. The flow of salt water through the dune ridge results from the pumping effect of evaporation in the swamp/lagoon (cienega). Other units are labeled as they appear in the text.

water table causes its intersection with the land surface to migrate on the order of 1 km or more during each yearly rainfall cycle (the “transition zone” of Figure 7.4). Because virtually all Yucatán groundwater is saturated with respect to calcite, evaporation of water along this transition zone results in the precipitation of calcite, which fills pore spaces and fractures in the nearly ubiquitous layer of surface calcrete. This has produced a wide swath of impermeable surface calcrete that is almost devoid of soil (the tsekel zone in Figure 7.3 and 7.4) along much of the north coast. Over time, slowly rising sea level has propagated the tsekel zone inland and upward to produce the confining layer or aquitard shown in Figure 7.3 and 7.4.

As postulated by Gerstenhauer (1987), and supported by observations of Tulaczyk et al. (1993), the calcrete layer that extends over Yucatán is perhaps millions of years old. Surface water can penetrate this calcrete layer only through fractures produced by subsurface weathering and collapse. At inland sites where the calcrete layer is well exposed, it is seen to be composed of individual blocks (with an average size of several meters) that are separated from each other by narrow, continuous cracks. Within the tsekel these cracks are filled by calcite, more or less as they form; this

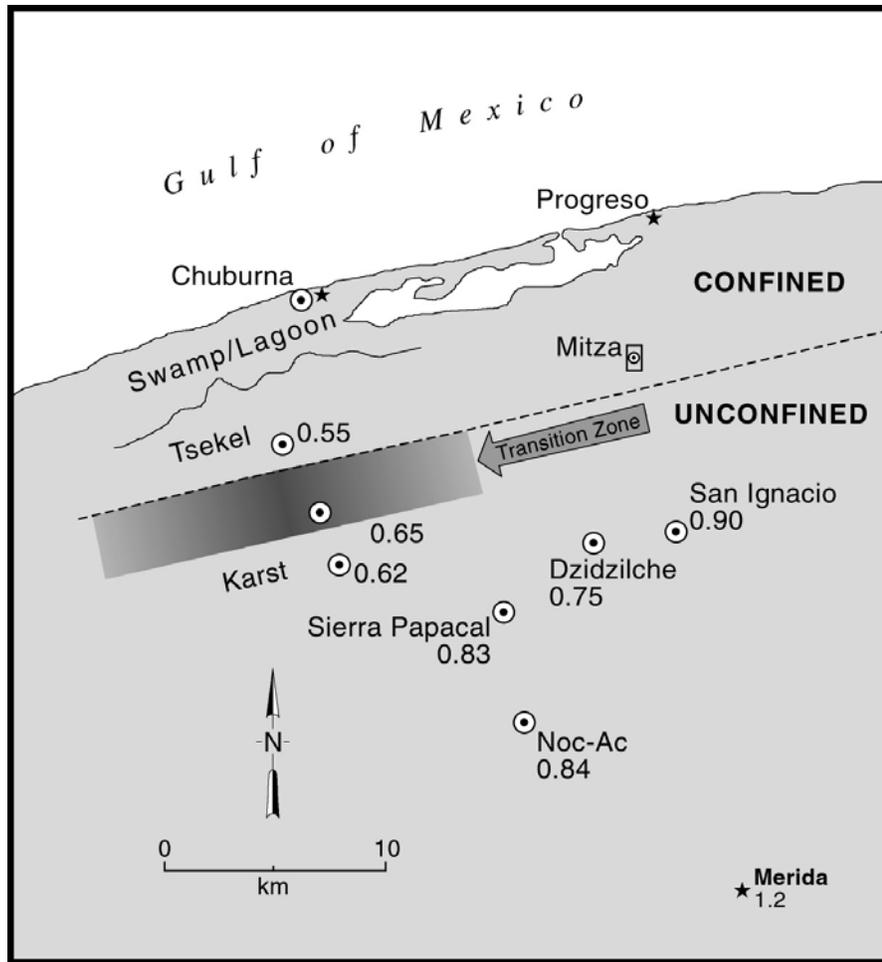


FIGURE 7.4. Detail of the coast showing water table elevations and coastal zones. Groundwater table comes to surface seasonally in the “transition zone”. Numbers are depth to the groundwater table in meters (m). (Source: Perry et al. 1995.)

sealing process, which must be continuous, may be the most important factor in keeping the confining layer intact. Nevertheless, only spaces with widths measured in millimeters can be filled by cementation. Thus, cenotes and large fractures that have become incorporated in the tsekel are not sealed by cementation.

The aquitard formed by filling of voids in the calcrete layer is typically about 0.5-m thick (Sanborn 1991), and it extends into the Gulf of Mexico for an undetermined distance, creating, in effect, a dam that groundwater must flow under or over to reach the gulf. As a consequence, groundwater in the coastal region is under a positive head, which at Chuburna is about 40 cm (Perry et al. 1989).

As noted above, a beach of carbonate sand (consisting in part of high magnesium calcite and aragonite) has developed seaward of the tsekel and above the coastal aquitard. Saltwater from the Gulf of Mexico moves inland

through this dune ridge and forms an evaporative lagoon (or coastal swamp) between the dune ridge and the tselkel (Figure 7.3). Under suitable circumstances, evaporation proceeds to the point at which halite and other evaporite minerals precipitate. This natural process has been enhanced by the construction of evaporating ponds (*charcas*) in Celestun, San Crisanto, El Cuyo, and other places, and is the basis for indigenous salt harvesting that has now been developed on a modern commercial scale at Las Coloradas. (The fact that seawater must move through the coastal dune to produce observed concentrations of halite is an aspect of the coastal system that may have escaped the notice of some people studying the coastal swamp and lagoons, and of those people harvesting salt.)

In cenotes that have, in effect, been moved into the tselkel or coastal swamp by rising sea level, groundwater flow is reversed, and these cenotes become springs of fresh or brackish water. Around some cenotes within the coastal swamp, salinity gradients persist over time and have produced circular bands of vegetation with distinct salinity tolerances. Roots of this vegetation trap organic matter and sediments to form small circular islands (*petenes*) (Febles and Batllori 1995). The aquitard persists for an undetermined distance into the Gulf of Mexico; drowned cenotes, in shallow coastal waters, form submarine springs that are well known to local fishermen (Figure 7.5).

ORIGIN OF THE COASTAL LAGOONS

Before modern coastal development, the north coast of the Yucatán Peninsula consisted of an almost continuous dune ridge, broken only in a few places by largely subterranean outflows of freshwater that created shallow, swampy, brackish-to-saline estuaries. Based on observations of the effects of Hurricane Gilbert, the dune ridge may have been frequently (but temporarily) breached by tropical storms.

Diego de Landa ([1566] 1998) mentioned Ría Lagartos, and Stevens ([1843] 1962) described Bocas de Dzilam. Estuario Celestun is another such system. Estuario Celestun and Bocas de Dzilam are located at the seaward extensions of the Cenote Ring and are fed by groundwater flowing through the fracture system associated with the Chicxulub Impact Crater (Perry et al. 1995; Pope, Rejmankova, and Paris 2001). The most open of these systems is Laguna Conil on the easternmost north coast; there, groundwater (and occasional overland flow) is channeled through the Holbox Fracture Zone (Tulaczyk et al. 1993) extending from Lake Coba to the coast. Groundwater movement to the coast is more diffuse at Ría Lagartos, but aligned wetlands appear south of El Cuyo on the map accompanying Lillo et al. (1999).



FIGURE 7.5. Xbulla, a drowned cenote about 0.5 km seaward from the coast and about 10 km east of Dzilam de Bravo, The vigorous outflow of freshwater from this cenote/spring into the Gulf of Mexico that is apparent in this photograph results from a hydrostatic head of about 0.5 m.

Development of the unusual coastal lagoons of the Yucatán Peninsula is based, in part, on the geochemistry of carbonate rocks and specifically on their behavior in coastal aquifers. Back et al. (1979) demonstrated that “caletas” of the Caribbean coast of the peninsula, such as Xel-Ha, formed (and continued to develop) by solution of solid carbonate rock along fractures intersecting the coast. The dissolution results from the decidedly nonlinear behavior of freshwater and saltwater when they are mixed. As pointed out by Badiozamani (1973), the mixing of two waters, both saturated with respect to calcium carbonate, can form an aggressively unsaturated water.

Back et al. (1979) to demonstrate that the unsaturated mixed water that forms where large freshwater discharges occur on the east coast is responsible for coastal erosion and caletas development along that coast. There, discharges occur through fractures in solid rock, and corrosion of cavern walls and collapse of roof blocks are evident.

In contrast, almost all sites of groundwater discharge along the gently sloping north coast are hidden by sand and silt. Nevertheless, conditions for chemical corrosion are present there as well. Much of the north-coast sand and silt is derived from the shells of marine organisms and is composed of high magnesium calcite and/or aragonite—minerals that are relatively

soluble when compared to low magnesium calcite. Mixing of fresh and saline water can occur anywhere within the plumbing system, including within the sediment column. Although direct evidence is lacking, Perry and Velazquez-Oliman (1996) calculated that a wide range of mixtures of seawater with groundwater from Kopoma (which is typical of the water delivered by the Cenote Ring to Estuario Celestun) is capable of dissolving both calcite and aragonite. Surface water collected from the estuary in the dry month of May was found to be supersaturated with respect to both calcite and aragonite, as was a sample of groundwater taken from a piezometer driven through the mud and silt of the estuary. However, a mixture of roughly equal parts of these two waters produces a water still supersaturated with respect to calcite, but approximately at saturation with respect to the more soluble aragonite.

Perry and Velazquez-Oliman (1996) interpreted this result to mean that groundwater arriving at Estuario Celestun mixes with seawater and dissolves as much of the aragonitic and high magnesium calcite fraction of the carbonate silt and sand as it is capable of before discharging into the Gulf of Mexico. This implies that lagoons of the north coast are maintained by a balance between the supply of carbonate sand by the steady westward current, physical transport of particulate matter by freshwater discharge, and chemical dissolution of the least stable carbonate minerals in the sediment. A still untested corollary of this hypothesis is that sediments within the estuary are predicted to have a higher percentage of stable low magnesium calcite than the sediment load carried by the longshore current.

It is noteworthy that the piezometer used to collect the groundwater sample within the estuary was driven for about one meter into soft sediment. At that depth it encountered a layer of coarse, friable material. Water within the friable layer is partially confined by fine sediment and, in this case, rose in the piezometer tube to a level several centimeters above the water in the estuary. Such piezometers can be set in many parts of the estuary with similar results. It seems probable that the coastal aquitard has been eroded (or corroded) here (although the aquitard is present beneath Celestun, a town built on the coastal dune), and that corrosion of sediment grains may be widespread within the sediment column.

Although Ría Lagartos is not associated with the conspicuous structural features observed at Celestun and Bocas de Dzilam, it does have a large number of brackish water springs within the estuarine channel (Pope and Duller personal communication; Perry personal observation), including one that has several centimeters of head that has been encased in a large concrete drain pipe to supply water to fishermen. A moderate-sized salt extraction facility exists at Las Coloradas. Evaporation ponds have been placed along the sand dune, a placement that may have the undesired

consequence of limiting entry of seawater [and, hence, sodium (Na^+) and chloride (Cl^-) ions that form halite, NaCl] to Ría Lagartos.

Geochemistry of groundwater of the northern part of the east coast, especially in the Xcaret-Tulum area, has been studied in detail by Stoessell et al. (1989) and Stoessell (1995), and in the Xel Ha Zone by Back et al. (1979) and Back et al. (1986). It is similar in many respects to the geochemistry of water on the north coast of the peninsula, in that calcite-saturated groundwater combines with seawater to produce a mixed water that causes coastal erosion. The principal difference between the development of the two coasts appears to result from structural and stratigraphic differences. The east coast contains Pleistocene dunes that are raised, lithified, and fault-bounded (Weidie 1985). That contrasts with the gently sloping north coast described above. Farther south along the east coast (near Bacalar), there are freshwater lakes and cenotes very close to the coast whose waters have low chloride (Cl^-) content, indicating little contact with seawater [e.g., 104 parts per million (ppm) Cl^- for Lake Bacalar and 44 ppm for nearby Cenote Azul, compared to $> 19,000$ ppm for seawater]. Lake Bacalar is long, narrow, and low-lying, and its lack of contact with the sea is in apparent contrast to Estuario Celestun (on the west) or Xel-Ha (on the east). The difference may result from the chemistry of groundwater reaching this lake. Lake Bacalar water contains 1070 ppm SO_4^{2-} , and adjacent Cenote Azul contains 1240 ppm SO_4^{2-} .

Cenote Azul is a deep, well-mixed lake with a bottom measured at 64 m, and it apparently reflects closely the composition of groundwater arriving at this coast. Our analysis of Cenote Azul water shows it to be nearly saturated with respect to gypsum and strongly supersaturated with respect to both calcite and aragonite. (The saturation index for aragonite in this water is 0.58.) In contrast with Celestun or Xel-Ha, mixing of this water with seawater does not produce an aggressive water—a 50/50 mixture is still supersaturated with respect to both minerals. This absence of an aggressive water may be the major factor distinguishing Lake Bacalar from other coastal water bodies on the northern peninsula.

OTHER STUDIES

Radium

Carbonate minerals incorporate an appreciable concentration of uranium (U) into their structure. Consequently, intermediate radioactive decay products such as radium (Ra) are released when the host carbonate dissolves. Moore (1996a, b) has shown that several radium isotopes, which

can be detected at low concentration, can be used to estimate hitherto hidden fluxes of groundwater to the ocean.

Because groundwater is virtually the only form of discharge to the ocean from the northern Yucatán Peninsula, radium (^{226}Ra) isotopes were tested to quantify Yucatán groundwater discharge. Enhanced carbonate dissolution in the mixing zone was expected to produce a strong, easily measured signal. We made three traverses into the Gulf of Mexico, in directions approximately perpendicular to the coast, out to approximately 20 km (see Figure 7.1): one seaward from near Celestun, another from Progreso, and a third (collected by a former graduate student, J. Zhang) from Dzilam de Bravo (near Bocas de Dzilam). Preliminary results of ^{226}Ra measurements of these samples show that, at 20 km, ^{226}Ra values of 0.1 and 0.08 disintegrations per minute per liter (dpm/l) were comparable to values of 0.07 to 0.09 dpm/l for open water in the Gulf of Mexico (Moore personal communication). The most shoreward sample from the Dzilam de Bravo traverse has an exceptionally high value for a marine sample; the two reference samples taken on land are also exceptionally high. This is good news for future modeling of groundwater discharge, but perhaps not so good news for residents of the peninsula—the terrestrial background sample taken from the Celestun water works exceeds U.S. Environmental Protection Agency (EPA) guidelines for drinking water.

Hurricanes and groundwater

Measurement of oxygen (^{18}O) and hydrogen (^2H) isotopes in natural waters has become part of the standard set of geochemical tools used in hydrologic studies. Both isotopes are being used as natural tracers in order to refine our understanding of the water cycle on the Yucatán Peninsula. In particular, Lawrence and Gedzelman (1996) have observed that hurricanes and severe tropical storms deliver rain that is ^{18}O -depleted in comparison to normal tropical precipitation.

Because of the frequency with which hurricanes (and tropical storms that evolve into or degenerate from hurricanes) pass over the Yucatán Peninsula (Figure 7.6), we began in 1997 to collect background data from municipal wells, cenotes, lakes, the ocean, and rain to test whether severe tropical precipitation can serve as a tracer for the recharge of groundwater. Factors that make the peninsula a particularly good place to attempt groundwater tracer tests include storm frequency, lack of soil (and consequent rapid infiltration), lack of surface runoff, low hydraulic gradient, extensive saline intrusion, and high aquifer permeability. Evidence that the aquifer responds quickly to severe tropical storms comes from the report by Marin et al. (1990) that Hurricane Gilbert, which passed directly over northern Yucatán

in 1988, was followed immediately by a general rise of approximately one meter in the water table.

Opal and Roxanne passed over the Yucatán Peninsula in 1995, as did Dolly in 1996. In 1998, Hurricane Mitch devastated much of Nicaragua, Guatemala, and parts of the Mexican state of Chiapas. Then, with diminished intensity, it passed over Yucatán as a tropical storm, depositing 4 cm of precipitation at Mérida. Even though most of the storm's energy had dissipated before it arrived in Yucatán, groundwater and surface water was collection immediately afterward. Because the isotope sampling program began in the middle of an unusually frequent series of storm events, sufficient background data for rigorous analysis are lacking. Nevertheless, accumulated qualitative evidence shown that the stable isotope composition of Yucatán groundwater does respond to tropical storm events; demonstrating that the isotope composition of water in the freshwater lens changes rapidly. From the latter observation, residence time of water in the freshwater lens is relatively short.

Stable isotope tracer studies of groundwater are possible because, as a result of isotope fractionation related to evaporation and precipitation, there

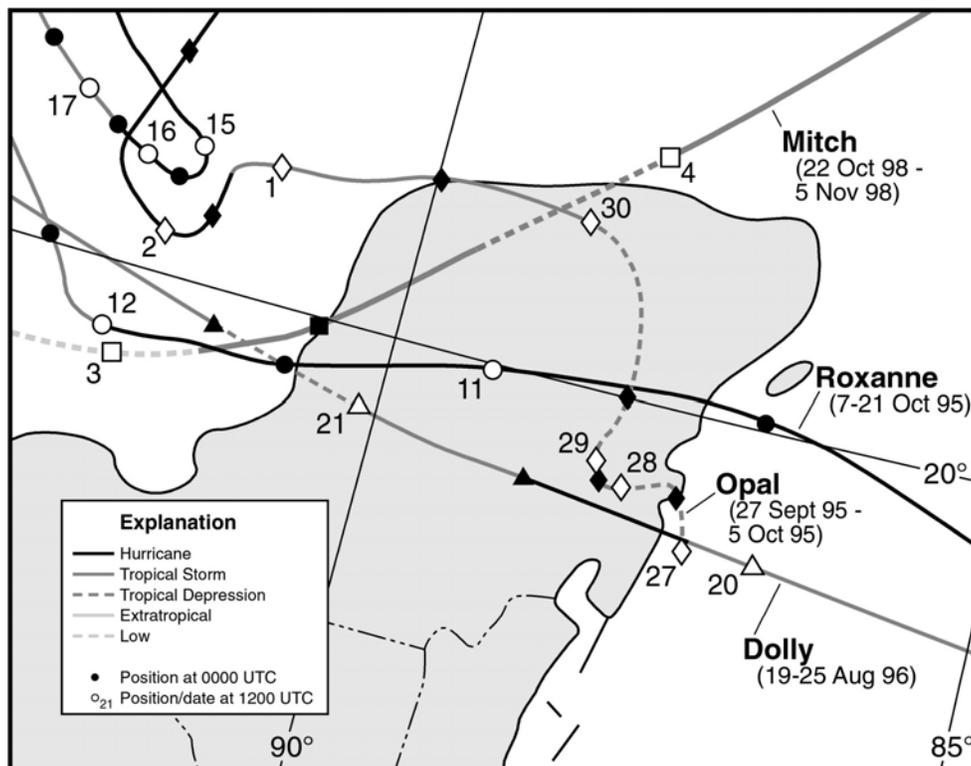


FIGURE 7.6. Tracks of recent hurricanes and tropical storms across the Yucatan Peninsula (from the National Atmospheric and Space Administration [NOAA]). Tropical storms/hurricanes are Dolly (Δ), Mitch (\square), Opal (\diamond), Roxanne (\circ). Filled symbols: 0000 Universal Time (UTC); open symbols: 1200 UTC.

is a remarkably regular relation between ^2H and ^{18}O in worldwide precipitation as shown:

$$\delta^2\text{H} = 8\delta^{18}\text{O} + 10$$

In this equation, $\delta^2\text{H}$ and $\delta^{18}\text{O}$ are parts per thousand (‰) ratios of the heavy isotopes to the more abundant isotopes, ^1H and ^{16}O respectively, compared to the same ratio in Vienna Standard Mean Ocean Water (VSMOW).

The above relationship, commonly referred to as the “Meteoric Water Line” (MWL), is remarkably general; as a result, rainwater is accurately “tagged” as to its origin. The most common process that can move water away from the MWL is evaporation, which, on a hydrogen-oxygen isotope plot (with $\delta^2\text{H}$ as ordinate and $\delta^{18}\text{O}$ as abscissa), shifts water down and to the right of the line.

Figure 7.7 shows the MWL together with the $\delta^2\text{H}$ - $\delta^{18}\text{O}$ isotope composition of Yucatán groundwater and rainwater. The figure includes an analysis of a sample of rain from Tropical Storm Mitch, which was collected for us in Mérida on 3 November 1998 by Ing. Ismael Sanchez. Its $\delta^{18}\text{O}$ value of -9.11‰ is well within the range of tropical storm values reported by Lawrence and Gedzelman (1996), and its $\delta^2\text{H}$ value is -60.5‰ . The composition of this water falls close to the MWL. It is more depleted in ^2H and ^{18}O than any other sample we have analyzed from Yucatán. Most of the groundwater samples are from municipal wells that typically pump water from depths on the order of 20 m within the freshwater lens.

Water samples taken in 1997 from Betania and Dziuche, in the south-central part of the study area, are more depleted than other samples in this sample suite (Figure 7.8a and 7.8b). These samples are from an area directly in the path of Hurricane Roxanne in 1995. This is also a transitional region where some seasonal streams are found. It may be that hydraulic conductivity of the aquifer is less here and that these stations were still recovering from the hurricane.

Of 11 localities for which data are available for both 1997 and 1998, nine increased in $\delta^2\text{H}$ for an average increase of 5‰ from one year to the next. The average change in $\delta^{18}\text{O}$ was less, amounting to only $+0.2\text{‰}$. In no case did the 1998 waters (sampled after the passage of Mitch) move on a $\delta^2\text{H}$ - $\delta^{18}\text{O}$ diagram in a direction indicating mixing with water from this tropical storm. In three of the localities sampled in both years, it was possible to sample shallow, completely covered cenotes within a few hundred meters of deeper municipal wells. In each of these localities, the isotopic composition of the shallow (cenote) water was significantly different from the corresponding well water. The general trend of the data suggests a system recovering from earlier (and locally more severe) tropical storms or hurricanes such as Opal, Roxanne, and Dolly.

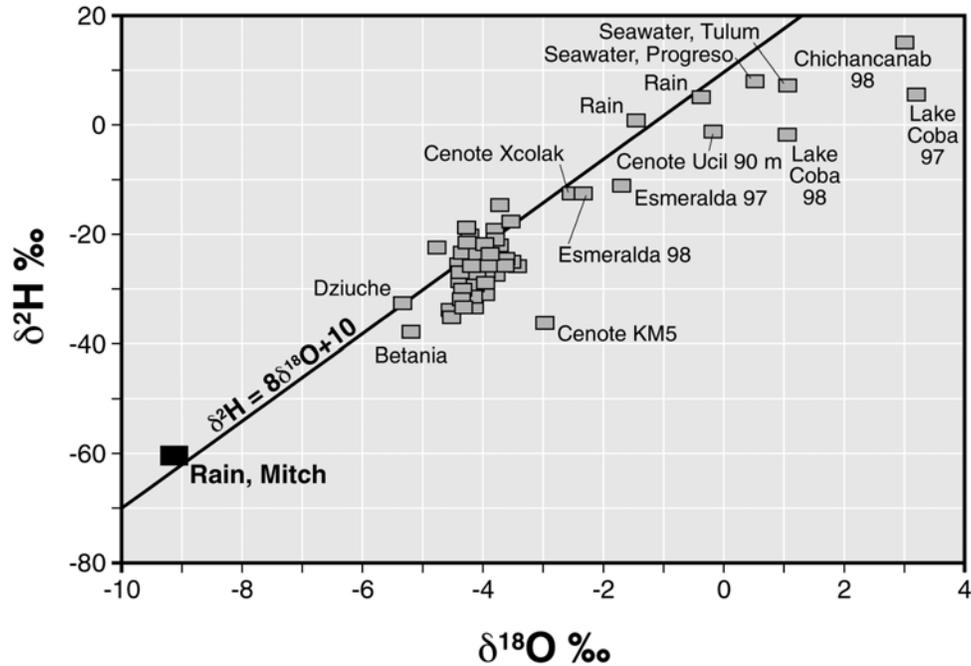
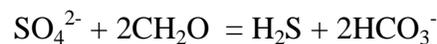


FIGURE 7.7. Hydrogen ($\delta^2\text{H}$) and oxygen ($\delta^{18}\text{O}$) isotope data from northern Yucatan plotted with reference to the "meteoric water line" (MWL).

Sulfur isotopes

Socki (1984) examined the sulfur isotope relationship in several Yucatán wells and cenotes. The most interesting of these is Cenote Xcolak (see Figure 7.1), which is 120 m deep. The interface between fresh and saline water is sharp at 50 m. Above that depth, water is thoroughly mixed, whereas below it is anoxic and contains increasing concentrations of hydrogen sulfide (H_2S) with depth. The cenote collects organic matter from a catchment area several times its size, and the organic matter reacts with sulfate-rich saline water below the interface according to the general reaction:



At the bottom of Cenote Xcolak, the isotopic composition of SO_4^{2-} shifts from a seawater $\delta^{34}\text{S}$ value of 21‰, found in deep Yucatán wells, to $\delta^{34}\text{S}$ 42.6‰. Sulfide values (total reduced sulfur precipitated by silver nitrate, AgNO_3) were lowest at intermediate depths, reaching a minimum of $\delta^{34}\text{S}$ – 33‰ at 80 m.

If oxidation-reduction reactions of this type were common in Yucatán groundwater, it would not be possible to use SO_4^{2-} or $\text{SO}_4^{2-}/\text{Cl}^-$ as groundwater tracers. In fact, ratios of $\text{SO}_4^{2-}/\text{Cl}^-$ significantly lower than the seawater ratio are relatively rare. Most variations from this ratio are toward

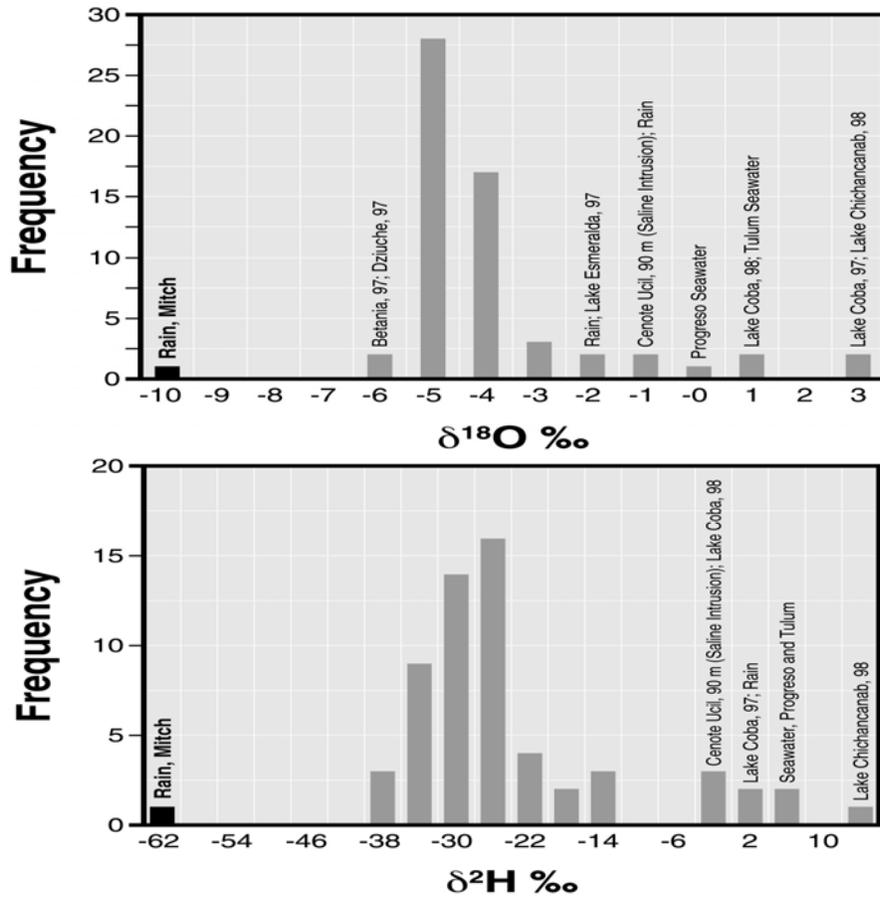


FIGURE 7.8a and 7.8b. Histograms of oxygen ($\delta^{18}\text{O}$) and hydrogen ($\delta^2\text{H}$) isotopic composition of Yucatán waters.

higher values, indicating that such reactions are relatively uncommon except where the aquifer is exposed to organic matter.

CONCLUSION

The unique combination of tropical climate, a partially emergent carbonate platform, and geologic history (giving rise to such features as specific faulting patterns and the selective exposure of evaporites) combine to make Yucatán a valuable environment in which to study the hydrogeology of carbonate rocks. There is almost no surface runoff on the northern Yucatán Peninsula. Because of the relative homogeneity of the near-surface rocks of Yucatán, their near-horizontal bedding, and the absence of extensive aquitards (other than the coastal aquitard), faults have a major influence in collecting and channeling groundwater.

Most groundwater of the peninsular aquifer closely approaches chemical equilibrium with calcite. Surface water of Lake Chichancanab is saturated

with respect to gypsum, but all analyzed groundwater from the freshwater lens is undersaturated with respect to this mineral. Nevertheless, some groundwater from the area around Lake Chichancanab does have a high SO_4^{2-} content, making sulfate a useful groundwater tracer. Other groundwater receives its dominant component of anions from the saline intrusion, as shown by chemical equivalent ratios of $100 \cdot \text{SO}_4^{2-} / \text{Cl}^-$, which are similar to the marine value of 10.3. The fact that values of this ratio approaching 10.3 are found over a large part of the peninsula confirms that the saline intrusion is truly extensive. Groundwater has had a major role in the sculpting of coastal features both by creating the coastal aquitard and also by providing freshwater that, when combined with seawater, forms an aggressive mixed water partly responsible for developing and maintaining coastal openings. This is true not only on the east coast, where it has long been recognized, but also on such north-coast openings as Celestun and Ría Lagartos.

Stable isotope determinations of oxygen (^{18}O) and hydrogen (^2H) show not only that severe precipitation from Tropical Storm Mitch was distinctly different from normal precipitation on the peninsula, but also that the Yucatán aquifer is a dynamic system. Each station that was sampled in both 1997 and 1998 showed a significant change in groundwater isotopic composition, with isotopically “heavier” values in 1998 than in 1997 suggesting that the aquifer was still recovering from being hit by storms such as Opal, Roxanne, and Dolly in 1995 and 1996. Other isotope tracers including radium and sulfur, discussed here, and strontium (not discussed) promise to enhance our understanding of aquifer behavior significantly.

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Chapter 8

Depression Soils in the Lowland Tropics of Northwestern Belize: Anthropogenic and Natural Origins

Timothy Beach
Nicholas Dunning
Sheryl Luzzadder-Beach
Vernon Scarborough

INTRODUCTION

For decades, Maya scholars have studied and speculated on depressions (or bajos) around ancient sites in the Maya lowlands. These depressions range from large structural basins to smaller karst dolines /1, 2/. Typically, these depressions contain seasonal wetlands with woody vegetation adapted to annual drought conditions. To archaeologists, these bajos have represented an obvious focus for ancient economic activities. After all, most scholars have maintained that these regions are agriculturally limited, yet were surrounded by vast populations that had to feed themselves by some means. Their propinquity to large ancient Maya sites (which, in many cases, spread

We conducted most of this research as part of the Programme for Belize Archaeological Project, directed by Fred Valdez, Jr., in cooperation with the Ministry of Tourism and the Environment and in conjunction with the Programme for Belize. We wish to acknowledge support by the National Science Foundation (granted to Vernon Scarborough and Nicholas Dunning), the Heinz Family Foundation, Georgetown University, George Mason University, and The University of Cincinnati. Timothy Beach and Nicholas Dunning also investigated in 1996 as part of Boston University's La Milpa Project, directed by Norman Hammond and Gair Tourtellot. Many people helped with this work, including Kerry Sagebiel (for ceramic identification), Jon Lohse, Jon Hageman, Julie Kunen, George Vrtis, Jeff Hom, Abby Sarmac, Meg Jones, Sheila Gulati, Josh Bacchus, Paul Hughbanks, and Skye Wagner.

out around bajos) and their surface variability of vegetation, soils, water features, and artifacts make them essential in any attempt to explain ancient subsistence. Moreover, interest in bajos grew even more intense when scholars started to recognize the remains of wetland agriculture in curious swamp polygons (Turner and Harrison 1983; Siemens and Puleston 1983; Pohl 1990). Jacob (1995b:71) summed up a generation of focus on bajos when he wrote: "Understanding the past and present dynamics of wetlands . . . holds a key to understanding the evolution of Maya civilization."

Cowgill and Hutchinson (1963) described many of the previous studies of bajos in their thorough study of an excavation in El Bajo de Santa Fé, Petén, Guatemala. They relate the "first intelligent account" by Fray Andrés de Avendaño of Loyola (Means 1917), who, in the wet season of 1695, crossed bajos with incessant difficulty. Despite these difficulties, scholars have been drawn to these seasonal wetlands. Cooke (1931) hypothesized that these depressions held shallow lakes in the Classic period, which subsequently became filled with eroded sediment (i.e., aggraded). Cooke argued that this loss of soil fertility and water resources led to the collapse of the Classic Maya civilization (see Bennett 1926); this hypothesis was adopted by Ricketson and Ricketson in 1937 and revived by Harrison in 1977. Other scholars argued that the bajo soils they had studied, however, formed from autochthonous parent material (see Cowgill and Hutchinson 1963 for El Bajo de Santa Fé; see Dahlin, Foss, and Chambers 1980 and Scudder, Foss, and Collins 1996 for bajos near El Mirador).

Jacob (1995b: 72) described preliminary research on the clayey, shrink-swell, bajo soils called Vertisols near the site of Nakbe, which is about 10 kilometers (km) from El Mirador (see Figure 8.1)³. He describes Vertisol topsoils (largely different from the current surface topsoil) that are buried by 50 to 150 centimeters (cm) of soil. These soils are similar to the soil studied by Cowgill and Hutchinson (1963), although they interpreted the horizon displacement as due to rotting roots. These highly distorted buried soils are darker, have distinct redoximorphic features (unlike the surface soils), and are possibly pre-Maya (based on one sherd in the overburden)⁴. Based on this evidence, and the evidence that the buried soils have a ^{12/13}C isotopic signature indicative (equivocally) of wetlands, Jacob (1995b) suggested that these bajos were more extensive wetlands in Maya times, but had filled from soil eroded from surrounding slopes (cf. Dunning et al., in press).

This article focuses on the aggradation, character, and formation of buried Vertisol paleosols in the bajos of northwestern Belize, within a region known as the Programme for Belize, in order to understand the environmental changes that buried and formed them /5/. After establishing the existence of two widespread paleosols in the depressions of this region, four questions were raised based on geoarchaeological work in this environment:

1. What is the nature of these sediments and soils?
2. What can these paleosols tell us about human-environmental relationships?
3. What caused the burial or aggradation of soils in this landscape?
4. What caused the once horizontal profiles of these soils to become deformed?

In the historical natural sciences, we must always begin with natural explanations because they have been so widespread over geologic time, however, human-caused change has grown to become a dominant force (Hooke 1994). The aggradation of the paleosols is clearly related to ancient soil erosion, but that deformation of the soil horizons was caused by a combination of anthropogenic and natural processes. Ancient agriculture did not rearrange the soil horizons by direct modification of the soils; rather, it was the heavy load of sediment from substantial upland erosion that allowed the soil deformation and buried Vertisol formation.

ENVIRONMENTS

The Three Rivers Region of the Maya lowlands lies in northwestern Belize, bordering Mexico and Guatemala, and is situated within the Cretaceous period carbonate rock plateau of the southern Yucatán Peninsula (King et al. 1992: 35; Dunning et al. 1998) (Figure 8.1). This region ranges in elevation from less than 20 meters (m) at Booth's River to above 200 m mean sea level (msl) along the La Lucha Escarpment.

Several normal faults slice through the region, aligned as a sequence of SSW-NNE trending horst ridges that rise about 100 m above the surrounding graben valleys^{6, 7}. With their east-facing escarpments, these faults give the region a stair-stepped appearance rising from Belize's Northern Coastal Plain, centered around the New River, into the Bravo Hills, around the Rio Bravo, and then toward the Petén to the west. The grabens, occupied by underfit streams, are low-gradient depressions (henceforth bajos) that contain a range of wetland ecosystems. We focus on soils in these alluvial lowlands and in karst sinks on the upland horsts.

As with much of the Maya lowlands, the Three Rivers Region consists predominantly of carbonate rocks (limestones and dolomites), with marl or saprolite layers and scattered concentrations of chert nodules. The uplands are covered with karst-solution features such as dolines and poljes (called rejollades where well drained, and aguadas where waterlogged) and rounded karst hills (mogotes). The region's natural vegetation is subtropical moist forest—a medium-high broadleaf, evergreen forest with a few dry-season deciduous trees. These diverse communities have an evergreen broadleaf, tall forest with an interior canopy of palm species such as corozo (Orbignya

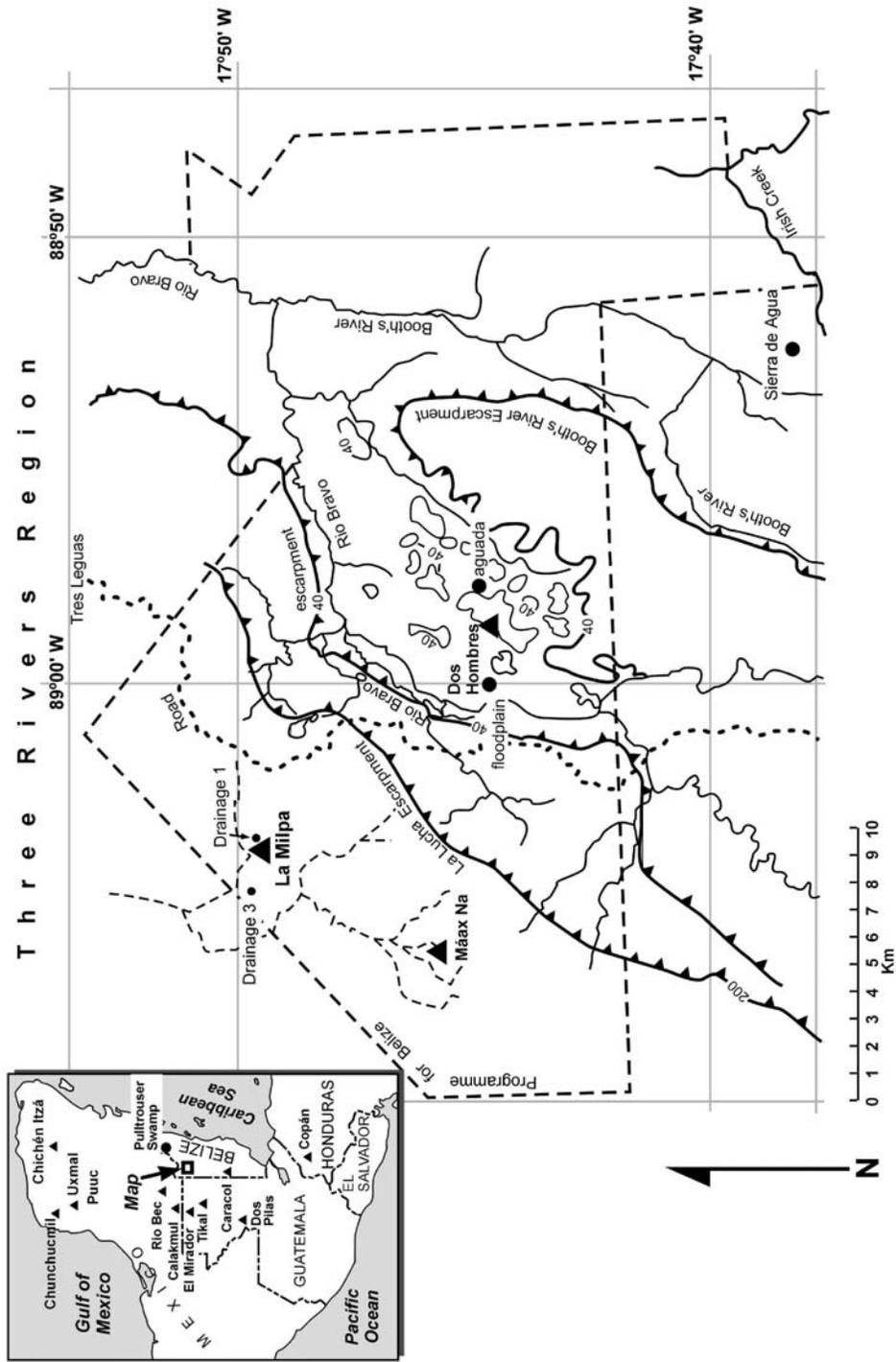


FIGURE 8.1. Map of the Three Rivers Region of northwestern Belize, with an inset showing the Maya lowlands. Black circles around La Milpa indicate the study sites.

cohume), and a patchy canopy of such tropical hardwoods as mahogany (*Swietenia macrophylla*) and cedar (*Cedrella odorata*) (Brokaw and Mallory 1993).

The climate is perennially hot and humid, with about 1,500 millimeters (mm) of rainfall annually; the Holdrige system places it in the Subtropical Moist Life Zone. Temperatures vary from a mean monthly maximum of 26.5 to 31.5°C. In United States Department of Agriculture (USDA) soil description terms, the soil temperature regime is hyperthermic (the warmest category), and the soil moisture regime is tropudic (or aquatic in many bajos), but the border of the tropudic regime is nearby (which means the soils in their control section are dry for nearly 90 consecutive days in most years; see Van Wambeke 1987). The wet season runs from June through December with bimodal peaks in June and September; the dry season occurs from January to May and has periodically severe moisture deficits exacerbated by the low available water capacity of the region's fine, clay soils. The end of the dry season in April and May shows dramatic signs of water deficits, with large soil cracks and widespread leaf wilting.

HOLOCENE HUMAN-ENVIRONMENT RELATIONS

In northern Belize, most human-environment relations occurred during the Late Holocene (i.e., during the last 5,000 years). Agriculture and deforestation began about 4500 14C yr. B.P., and widespread agricultural intensification occurred from 4000 to 3000 14C yr. B.P. (Pohl et al. 1996). The earliest artifacts found thus far in the Three Rivers Region are nonstructural materials dating to the Middle Preclassic (900–400 B.C.). This period probably had a small rural population that modified the environment by slash-and-burn practices. Indeed, Holley et al. (2000) found evidence for sedimentation in the Preclassic linked to upland erosion.

Large-scale urbanization in this regions started in the Late Preclassic (350 B.C. to A.D. 250) with the advent of monumental architecture at the large site centers. With this growing nucleus at the site center, however, population remained largely rural and diffuse throughout this period (Dunning et al. 1999). Growth was spotty in the Early Classic (A.D. 250–600) at the large sites of La Milpa and Dos Hombres in our study area, but the sites of Blue Creek and Rió Azul—approximately 25 km north and northwest of the study region—expanded significantly at this time (Adams 1995; Guderjan 1998). As with many agriculturally-based societies, the Classic Maya began to link their rulership symbols to ideas of agriculture and environment (Schele 1995). At this time, the major hydraulic manipulation of La Milpa and the lowlands also started (Scarborough 1993).

Any discussion of anthropogenic impacts on soils in this area must start with the last period of major disturbance—the Maya Late/Terminal Classic (A.D. 600–900). All evidence indicates that this period had the greatest environmental alteration, population, and construction, but it also had the greatest amount of soil conservation (Beach and Dunning 1995; Beach et al. n.d.). The bulk of settlement and architecture at La Milpa and many other regional sites date to after A.D. 700 (Hammond and Tourtellot 1999), and the sites seem to be abandoned with immediacy by A.D. 850 (Hammond et al. 1998). After the Maya Collapse, there seems to have been a shifting population, but populations must have been small because there are virtually no Postclassic artifacts. Whatever the case, we have found little environmental impact has been found in the Postclassic.

The growing evidence for a significant drought during the Maya Late Classic is also a potential impact on soil formation (Hodell, Curtis, and Brenner 1995; Hodell, Brenner, and Curtis 2000; Pope et al. 2000; Webster, Reeder, and Reynolds 2000). Major desiccation (especially if exacerbated by human-induced environmental alteration) could lead to any number of possible environmental changes—for example, increased fire, and thus increased soil erosion and sedimentation, or increased soil shrink-swell. Increased aridity may have other complex responses, however, if accompanied by other meteorological changes such as more intense, but less frequent, precipitation.

SOILS

The region's soils have been investigated in a variety of geomorphic positions over various catenas (toposequences) and landscapes since 1992, although there have been few soil studies in this region upon which to build (see also Coultas, Hsieh, and Post 1998; Reeder, Brady, and Webster 1998; Fedick 1995). Soils range from depression Histosols and Vertisols through upland Mollisols, Inceptisols, and Alfisols. Most of the unsaturated soils on uplands and some fans are Rendolls, in the Lithic and Vertic subgroups respectively.

According to government soil surveys (King et al. 1992, 221), the Yaxa soil suite covers most of this region⁸. These are well-drained to poorly drained clays that formed on Cretaceous to Early Tertiary period limestone. Yaxa and other regional soils, largely phyllosilicate clays, have formed mostly in place from impurities in the limestones, including chert nodules. Yaxa is composed of five subsuites, three of which occur in this region: Yalbac, Jolja, and Irish Creek⁹. Yalbac are generally fertile upland soils, although they are not well endowed with phosphorus (P) and potassium (K), and their major limitations are thinness and erodibility, especially to gully formation

(King et al. 1992, 224). One other limitation in these smectitic or vermiculitic soils is profile inversion and cracking, which is uncommon under forests but common in intensively-farmed areas (King et al. 1992, 223).

King et al. (1992, 223–225) describe a topographic- and drainage-based four-part subdivision of the Yalbac Suite: (1) the shallow soils (generally thinner than 60 cm) are probably Lithic Rendolls or Eutropepts in the USDA taxonomy (Rendzic Leptosols in the FAO/UNESCO taxonomy);¹⁰ (2) the modal soils (50–90 cm deep) are Vertic Rendolls and Eutropepts (or Vertic Cambisols), (3) the deep unmottled soils are Vertisols and Vertic Rendolls, and (4) the deep-mottled soils are probably Vertisols. The deeper soils that form in karst depressions also tend to have sapolite (sascab) parent materials (Darch 1981) as well as gypsum crystals in the lower horizons, although we found this only in bajos west of La Milpa. Beach (1998b) described a catena of soils similar to these in the Pasion Region of Guatemala's Petén with the same sequences occurring across the crest, shoulder, back, footslope, and depression.

The Irish Creek subsuite is a Tropopept (USDA taxonomy) of the wetland margins. The dominant feature of these deep soils is their redoximorphic gray and reddish mottles. These clay soils have some sand lenses, gypsum crystals, and iron (Fe) and manganese (Mn) concentrations, and were formed from the slopewash of upland calcareous clays in conditions of impeded drainage (King et al. 1992, 229). Ford and Fedick (1988) considered these soils along Irish Creek to be the site of ancient Maya wetland fields, but currently the poor drainage and modest fertility make them undesirable (King et al. 1992, 230).

The Vertisols and other soils analyzed here are located in karst depressions on escarpment horsts and floodplain grabens. Vertisols are said to be the easiest to identify soils because of their obvious diagnostic features: gilgai, or hogwallow topography; surface cracks; slickensides (i.e., active planes of shear), or smooth, shiny, often grooved, black surfaces; and wedged-shaped soil structures called sphenoids. These Vertic properties in soils are formed by shrink-swell processes related to high clay content (usually greater than 30 percent), large amounts of the fine clay fraction, and high fractions of 2:1 or 2:2 clays (especially smectites), although some are high in kaolinite (a 1:1 clay) (Coulombe, Wilding, and Dixon 1996; Eswaran et al. 1999). These factors lead to swelling with hydration and shrinking with dehydration; maximum Vertic properties occur with intense dry and wet seasonality. They occur in solutional karst sinks, throughout rejolladas and floodplains (drained most of the year), and on the margins of aguadas (saturated most of the year). The latter depressions commonly have Histosols in the most saturated areas, but Vertisols on the margins where sediment deposition and weathering have been sufficient to form soils 1 to 2 m in thickness.

METHODS

From 1992 to 1998, we studied depression and upland soils, in relation to geoarchaeology and paleoecology, in more than 30 trenches and pits around the Three Rivers Region (Dunning and Beach 2000; Dunning et al. 2000). All the sites occur around the major archaeological sites of La Milpa, and all have been largely undisturbed since the ancient Maya period. Soil pits of 1 m x 2 m up to 20 m were excavated by pick and shovel, or backhoe, usually down to bedrock. These were all level, very slowly draining sites that showed no evidence of erosion. In each pit and trench, we analyzed all exposed sides for soil morphology and formation processes and collected evidence about their chronology of formation. We carefully screened all the excavated material for artifacts that could provide chronological information about soil development, and we analyzed soil following standard methods for description and sampling (Soil Survey Staff 1996; 1998).

Morphology, color, texture, structure, HCl reaction, and other features were observed and described based on the Soil Survey Manual (Soil Survey Staff 1998). The University of Wisconsin-Milwaukee Physical Geography and Soils Lab analyzed pH; exchangeable cation concentration in calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^{+}), and potassium (K^{+}) cations by atomic absorption; particle size by the pipette method; base saturation; estimated cation exchange capacity (CEC) from exchangeable cations by the CEC method; organic carbon (O.C.) (Walkley-Black); and DTPA-extractable zinc (Zn) (Soil Survey Staff 1996) (Tables 8.1 and 8.2). They also analyzed phosphorus (P) through fractionation into three subsets (Table 8.3), and clay mineralogy through X-ray diffraction.

The Beta Analytic Laboratory also dated samples by standard and accelerated mass spectroscopy radiocarbon analyses and measured carbon isotopes (Table 8.4). Little charcoal was found throughout this region, and radiocarbon samples were mainly bulk soil carbon samples collected from the top of buried A horizons. Because such samples can give mainly the mean residency time of the carbon in the paleosols, these samples can only represent minimal dates (Birkland 1998, 138; Wang, Amundson, and Trumbore 1996; Smith and McFaul 1997). We attempted to sample to minimize the humate dates (^{14}C from soil organic matter; see Matthews 1985, 282) samples from the top 5 cm of buried A horizons. All soils were formed in the Holocene; moreover, most have some artifacts that provide another date (albeit broad) for comparison.

TABLE 8.1. Soil Textures: Pipette particle size analyses in percent (%). Numbers to the particles class (in μm [micrometers]). All samples fall within the clay texture class.

Site No. of Horizons	Sand > 50:	Co. Silt 50–20:	Med. Silt 20–5:	Fine Silt 5–2:	Co. Clay 2–1:	Fine Clay < 1 :
D05 A	10.1	13.8	10.9	7.8	3.1	54.4
D05 Ab2	11.2	11.1	2.3	0.8	0.8	73.8
D05 C1	4.9	11.2	0.8	0.8	1.6	80.8
D06 Ab1	7.9	14.4	6.2	4.7	0.8	66
BH9-2 AC	6.4	5.7	13.6	8.6	6.5	59.2
BH9-4 C	6.8	1.7	7.5	6.8	3.3	74.1
BH9-5a Ab	6.9	3.9	8.5	7.3	5.7	67.6
BH9-6Cb	6.8	3.4	9.4	8.2	6.7	65.4
RB2-10a-A	0.5	3.0	2.2	0.5	3.6	90.2
RB2-10a-Ab	6.4	10.4	8.4	3.9	6.9	64.0
RB59-2-1-A	4.8	5.5	5.1	4.7	4.0	75.9
RB59-2-1-AC	13.2	6.1	6.1	2.6	0.4	71.6
RB59-2-1-Ab	6.6	8.1	5.8	0	1.4	78.1
RB25V-A	4.8	2.6	6.5	5.2	1.0	79.9
RB25V- C	6.3	4.0	5.7	4.1	0	79.9
RB25V-Ab	8.9	3.4	5.7	3.3	1.1	77.6
RB2-9DAC	2.9	3.4	5.3	4.3	1.8	82.3
RB2-9DAb	6.0	4.6	7.6	4.6	3.8	73.4
RB25D9AC	12.1	5.7	9.4	5.6	0.6	66.6
RB25D9C	8.3	5.3	7.5	3.5	1.1	74.3
RB25D9Ab	3.9	0.5	12	10.5	9.8	63.3
RB25D9Cb	8.0	10.2	3.5	0.8	1.4	76.1

TABLE 8.2. Soil chemical characteristics

Sample Horizon	O.C. % WB	pH	SO ₄ ²⁻ mg/kg	Mg ²⁺ mg/kg	Ca ²⁺ mg/kg	Na ⁺ mg/kg	ex. K ⁺ mg/kg	Zn ²⁺ (DTPA) mg/kg	CEC meq/ 100g	BS %	N
TBVA2	1.82	6.8	-	2412	8198	72	86	-	113	-	-
TBVAB	0.64	6.7	-	2861	7216	86	62	-	117	-	-
<i>La Milpa Drainage 1: RB25</i>											
D05A	2.74	7.5	-	4410	8369	75	43	-	140	-	-
D05Ab2	0.78	7.6	-	6039	8900	93	62	-	184	-	-
D052C1	0.37	7.7	-	5819	7534	87	59	-	170	-	-
D06Ab1	0.78	7.7	-	3331	7338	161	86	-	125	-	-
<i>La Milpa Drainage 1: D09</i>											
D16 u 4 AC	1.25	8.0	-	2398	11361	99	79	0.000	146	97.7	0.09
D17 u 5 C	0.27	8.4	-	3125	9017	107	72	0.000	141	97.6	0.04
D18 u 6 Ab	0.96	8.3	91	5208	5829	394	79	0.000	140	99.1	0.06
D19 u 7 Cb	0.18	8.3	-	4942	3996	288	102	0.000	122	98.7	0.04
<i>La Milpa Aguada: RB25V</i>											
D7 11 A	1.97	6.1	178	1618	8118	87	67	0.001	100	97.3	0.17
D8 60 C	0.85	7.8	-	1464	10649	85	65	0.000	127	97.3	0.03
D9 100 Ab	0.86	7.9	90	1375	11470	89	75	0.000	133	97.4	0.08
<i>La Milpa Far West Bajo: Drainage 3</i>											
BH9 A2	6.6	5.8	-	940	6416	83	114	2	68	97.1	0.33

Sample Horizon	O.C. %	pH	SO ₄ ²⁻ mg/kg	Mg ²⁺ mg/kg	Ca ²⁺ mg/kg	Na ⁺ mg/kg	ex. K ⁺ mg/kg	Zn ²⁺ (DTPA) mg/kg	CEC meq/ 100g	BS %	N
BH9 C	1.79	4.5	-	1155	5952	314	27	0.2	75	98.8	0.02
BH9 Ab1	1.94	5.0	-	1450	6874	857	23	0.1	89	99.5	0.01
BH9 Ab2	8.3	7.6	-	-	-	-	-	-	-	-	-
BH9 Cb	0.96	7.11	-	1290	6342	988	49	0	83	99.5	0.01
<i>Dos Hombres Settlement Survey Floodplain: RB2op10a</i>											
D125-30 AC	1.25	6.9	190	2894	11094	175	49	0.000	151	98.4	0.09
D2 91-97 Ab	1.22	8.0	582	3798	9200	534	25	0.000	147	99.3	0.05
<i>Sierra de Agua: RB59op2-1</i>											
D3 10-13 A	3.29	6.2	-	2064	9204	117	70	0.001	110	97.9	0.33
D4 20-24 A2	-	-	495	-	-	-	-	-	-	-	-
D545-48 C	0.87	7.9	-	1599	10043	79	86	0.000	123	97.2	0.05
D6 79-82 Ab	1.10	6.1	253	1889	11828	86	125	0.000	143	97.5	0.04
<i>Dos Hombres Settlement Survey Aguada: RB59op2-1:</i>											
D11 U 2 AC	0.35	5.6	134	1421	7535	221	40	0.001	98	98.4	0.01
D12 116 C	-	-	258	-	-	-	-	-	-	-	-
D13 129 Ab	0.08	5.5	261	1594	7062	634	48	0.001	97	99.3	0.00
<i>Barba Terrace: Rb52op3a:</i>											
D22 50 Ab	4.55	7.7	-	3018	11358	90	74	0.000	135	98.0	0.44

TABLE 8.3. Phosphate fractionations

Site No. of Horizons	Frac 1a mg/kg	Frac 1b mg/kg	Frac 2 mg/kg	Frac 3 mg/kg	Sum Frac	Percent of Total P			Ratio* FI/FI
						F1	F2	F3	
TBVAb old	1	6	9	6	22	32.8	39.9	27.3	1.29
D05A	0	20	18	62	101	20.5	18.1	61.4	0.90
D05Ab2 old	0	8	3	4	14	54.6	21	24.4	0.38
D052C1	0	1.6	4.5	3.2	9.3	16.7	48.5	34.9	2.81
D06Ab1 old	0	11	4	3	18	62.2	23.3	14.5	0.36
RB25D9A	0	8.4	5.3	87.6	101.2	8.3	5.2	86.5	0.63
RB25D9Ab-0	0.5	2.2	10.9	3.6	17.1	15.7	63.4	20.9	4.04
RB25VA	0.6	21.9	11.2	5.3	38.9	57.7	28.7	13.5	0.50
RB25VAb	0	3.7	6.7	19.3	29.7	12.5	22.7	64.9	1.82
RB2-10aA2	0.1	5	3.8	5.1	14	36.2	27.4	36.3	0.76
RB2-10aAb	0.1	4	5	48.9	58	7.1	8.6	84.3	1.21
RB59-2-1-A	0	8.1	10	82.7	100.7	8	9.9	82.1	1.24
RB59-2-1-Ab	0.4	3.7	9.4	63.4	76.9	5.4	12.2	82.4	2.26
RB52-3a Ab	0	7.5	10.9	38.3	56.7	13.1	19.2	67.6	1.47
Mean					47	23.6	26.3	50.1	1.41
Mean A or AC					71.2				0.81
Mean Ab					36.6				1.60
Mean old Ab					29.6				

Mean value for sedimentary rocks = c.200 (Eidt 1984)

Note: Fraction 1a (NaOH/NaCl extraction) measures nonoccluded Al- and Fe-bound P; Fraction 1b [NaCl and citrate-bicarbonate (CB)] measures P sorbed by carbonates during the 1a extraction; Fraction 2 [citrate-dithionite-bicarbonate (CDB)] measures P occluded within Fe oxides and hydrous oxides; Fraction 3 (HCl extraction) measures Ca-bound P.

*Ratio (see Eidt 1984 and Lillios 1992)

TABLE 8.4. Radiocarbon dates in Text (AMS technique except where * appears)

Sample	Lab #	Site	Depth cm	Soil	¹⁴ C bk Conv B.P.	¹³ C/ ¹² C Ratio ^a	Cal ¹⁴ C 2 σ , 95% P
Beta-135557	D17	La Milpa D2	62	Ab terrace	1540+/- 80 B.P.	-23.5 ‰	365–655 A.D.
Beta-94465	D05	La Milpa D2	130	Ab Vert	3360 +/- 60 B.P.	-22.7 ‰	1745– 1450 B.C.
Beta-94770	DO6	La Milpa D2	130	Ab Vert	2990 +/- 70 B.P.	-20.2 ‰	1365– 1070 B.C.
Beta-112475	D09-3	La Milpa D2	25–70	Ab Vert	1810 +/- 40 B.P.	-28.5 ‰	120–340 A.D.
Beta-112476	D09-6	La Milpa D2	95– 170	Ab Vert	3440 +/- 50 B.P.	-29.2 ‰	1885– 1620 B.C.
*Beta-112471	B25pv1 5	La Milpa Aguada	100	Ab Vert	3080 +/- 100 B.P.	-25.0 ‰ ^b	3080 +/- 100 B.P.
Beta-135558	V45b-3	La Milpa Res A	105	Ab	2400 +/- 40 B.P.	-19.1‰	755–390 B.C.
Beta-135559	V41a-5	La Milpa Res B	125	Ab	3910 +/- 40 B.P.	-24.7 ‰	2465– 2330 B.C.
Beta-118305	Rb25bh 6-3	La Milpa D3	60–80	Ab Fluvial	1640 +/- 70 B.P.	-23.2 ‰	235–555 A.D.
Beta-118306	Rb25bh 6-5	La Milpa D3	120– 145	Ab Fluvial	2300 +/- 80 B.P.	-22.8 ‰	760–190 B.C.
Beta-112474	RB25v3 3a-6	La Milpa D3	60–80	Ab Fluvial	2880 +/- 50 B.P.	-31.0 ‰	1200– 910 B.C.
Beta-135563	BH1-4	La Milpa D3	80	Ab Fluvial	2270+/- 80 B.P.	-22.4 ‰	500–155 B.C.
Beta-135562	BH1-6	La Milpa D3	175	Ab bajo	7470+/- 40 B.P.	-24.1 ‰	6420– 6235 B.C.
Beta-121443	BH9-5b	La Milpa D3	50–90	Ab Vert	1840+/- 40 B.P.	-18.3 ‰	A.D. 15– 110
Beta-135564	BH12-9	La Milpa D3	180	Ab Vert	2140+/- 40 B.P.	-20.8 ‰	355–55 B.C.
Beta-135556	RB2- 8a36.8	Dos Hmbrs Plaza	400	Ab	2130 +/- 40 B.P.	-21.4 ‰	350– 50B.C.

TABLE 8.4 (continued)

Sample	Lab #	Site	Depth cm	Soil	¹⁴ C bk Conv B.P.	¹³ C/ ¹² C Ratio ^a	Cal ¹⁴ C 2 δ , 95% P
*Beta- 112469	RB2- 10A	Dos Hmbrs Fluvial	100	Ab	2000 +/- 100 B.P.	-25.0 ‰ ^b	B.C.205– A.D.240
Beta- 135555	RB2- 21a	Dos Hmbrs Aguada	91–97	AB Vert	1890 +/-140 B.P.	-19.8 ‰	195B.C.– 430A.D.
*Beta- 112470	RB59O p2-1	Sierra de Agua	80	AB fluvial	3020 +/- 100 B.P.	-25.0 ‰ ^b	1490– 940 B.C.

^aDifference in quantity of ¹³C and ¹²C is reported in units of ¹³C relative to the usual standard.

^bRatios estimated

SOIL FINDINGS: PHYSICAL AND CHEMICAL CHARACTERISTICS

Bajo soils on the upland ridges occur in several types of sinkholes or human-made depressions. The natural sinkholes are either seasonally inundated with water or freely draining, but both landscape positions are depositional and contain the deepest soils in this region. Bajo Vertisols occur within rejolladas or freely-drained dolines. In these locations, soils develop both by weathering of the parent material and deposition of eroded soil, producing a mean depth of around 150 cm. Soils studied in the lowest parts of aguadas, which are seasonally saturated dolines, are clayey Histosols with around 2 m of soil depth.

The typical soils of this region are chiefly clay in texture, ranging from 57.5 to 93.8 percent clay (see Table 8.1). Much of the region's limestone is high in calcite, and little residual mineral grains remains after dissolution, but the trace minerals from the limestone and aerial deposition with high carbonate concentrations form the dominantly silicate clay soils (Beach 1998a). Soil organic carbon ranges from high levels in the thin regional O horizons that cover undisturbed environments, to moderate levels (1.25 to 6.6 percent) in A horizons, and low levels in deeper horizons—except for buried, former surface soils (Ab horizons) that range widely (< 1 to 8.3 percent) (see Table 8.2).

Soil pH is generally neutral to moderately alkaline in upland soils (7.2–8.4) because of basic parent material, but can be basic or acidic in depression soils (4.5–8.3) depending upon the source of vegetation that goes into forming organic matter. Two seasonally inundated sites, BH9 and RB2-9D, had acidic conditions throughout their upper soil profiles.

Sulfate (SO_4^{2-}) is often high (up to 582 mg kg^{-1}) with common gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) crystals in the region's depression soils, as are magnesium (Mg^{2+}) (ranging from $940\text{--}6,039 \text{ mg kg}^{-1}$) and calcium (Ca^{2+}) (ranging from $3,996\text{--}11,828 \text{ mg kg}^{-1}$) in most regional soils due to the carbonate parent materials. Zinc (Zn^{2+}) is always low (very nearly 0 mg kg^{-1} in all but one case) in these parent materials and the regional soils, and sodium (Na^+) can be high (up to 988 mg kg^{-1}) depending on local impurities in the parent material. Most upland soils are generally fertile, however, with high cation exchange capacity ($68\text{--}184 \text{ meq/100 g}$), base saturation (nearly 100 percent), and the previously mentioned cations. In topsoils, nitrogen (N) is high ($0.33\text{--}0.44$ percent) and C:N ratios ($9.3\text{--}11.9$) conducive to plant uptake where organic matter is high. Farmers would have three major limitations here, though: (1) maintaining enough phosphorus and nitrogen to sustain crop yields after organic matter decomposes, (2) maintaining enough soil depth on these skeletal and erodible slopes for plant rooting and soil water storage through the dry season, and (3) managing high shrink-swell activity and poor drainage on the deforested, depression Vertisols (King et al. 1992, 223–224; cf Beach 1998a).

The 14 phosphate fractionation analyses show that phosphorus (P) is low throughout these soils (mean = 47 mg kg^{-1}), ranging from only 9.3 to $101 \text{ mg} \cdot \text{kg}^{-1}$ in the summary of all fractions. To begin with, the limestone parent material is low in P, as shown in the one sample from a near bedrock C horizon with the lowest summary of P fractions of 9.3 mg kg^{-1} (see Table 8.3). The mean is far lower than means of 538.9 and 233.5 mg kg^{-1} found in the northern Yucatán Peninsula (Beach 1998b). As in many calcium-rich soils, Fraction 3, which measures Ca-bound P, was the highest fraction—averaging about 50 percent of all measured P. The next large difference lies between A horizons and the Ab horizons or paleosols in this environment. The Ab horizons have been buried and removed from recycling of P and are thus depleted in P, having only half the quantity of the A horizons. The buried soils are especially depleted in the available Fraction 1, and thus have higher ratios of Fraction 2 to Fraction 1 (mean = $1.6:1$) compared with the A horizons (mean = $0.8:1$) (see Table 8.3). Fraction 2 measures P occluded within iron (Fe) and hydrous oxides, and several scholars have used it to suggest ancient P enrichment from fertilizers (Eidt 1984; Lillios 1992; Beach 1998b). The elevated Fraction 2 to Fraction 1 ratios may provide evidence for this because these show that, in Ab vs. A horizons, Fraction 2 remains at a higher ratio to fraction 1 in all but one of the paired results. Because no historical evidence

exists for fertilization that would have increased P Fraction 2, it is possible these heightened levels are linked to ancient intensive fertilization. We think most of these sites in the bajos were agricultural, and the P fractionations do not contradict this hypothesis.

X-ray diffraction of 10 soil samples by University of Wisconsin-Milwaukee Physical Geography and Soils Lab has provided evidence on clay mineralogy. The general findings from these analyses indicated four major peaks: (1) the air dry peak occurred in the low 2-theta region of 14.7 to 15.6 Å (angstroms), which expands somewhat with glycolation; (2) a broad but small peak in the 16–20 2-theta region; (3) a peak in the 12–13 2-theta region of 7.1–7.3 Å; and (4) a peak in the 24–25 2-theta region of 3.5–3.6 Å. These patterns to indicate randomly interstratified chlorite/smectite, with smaller amounts of smectite and vermiculite. A significant peak of calcite, and lesser ones of gypsum and quartz, occurred in some samples. The clay fraction is largely composed of 2:1 clays, but types that have much less expansion and contraction than does smectite. Nevertheless, the study area soils are fine clays with high specific surface area, which can still have substantial shrink-swell potential (Coulombe, Wilding, and Dixon 1996).

SOIL EXCAVATIONS AROUND LA MILPA

This study focuses on five main sites in northwestern Belize. These sites include a soil catena running from the backslope into the depression at La Milpa Drainage 1 and 2, a group of depression soils in La Milpa Drainage 3, alluvial soils in the Rio Bravo floodplain and in the Irish Creek floodplain near Sierra de Agua, and depression soils in an aguada near Dos Hombres.

We based the soil catena at La Milpa Drainage 2 on 15 soil pits to bedrock running from the backslopes, through footslopes and toeslopes, toward the center of the bajo (Figura 8.2). Crests and backslopes have thin Rendoll soils similar to those described in the Petén (cf Beach 1998a). Backslopes generally have 15 to 50 cm of O-A-AC horizons on shallow slopes of 5 to 10 degrees. The only deeper backslope soils we observed lie behind ancient Maya terrace walls. Backslope soils merge into footslope and alluvial fan soils on the edge of seasonally inundated depressions. Footslopes and fans have much deeper soils, gravel layers, and rudimentary slickensides.

Some of these soils have overthickened, cumulic A horizons (O-A1-A2-A3-C), but in La Milpa Drainage 2 the two fan soils have distinct buried paleosols (Figure 8.2: Op D5 and Op D8). The upper fan soil had the following sequence: O horizon from the surface to about 2 cm; A1 and A2 horizons that are black to very dark gray and reach down to 25 cm; AB horizon that is very dark gray, with 40–60 percent limestone gravel that reaches down to 45 cm; C1 and C2 horizons that are yellowish brown and

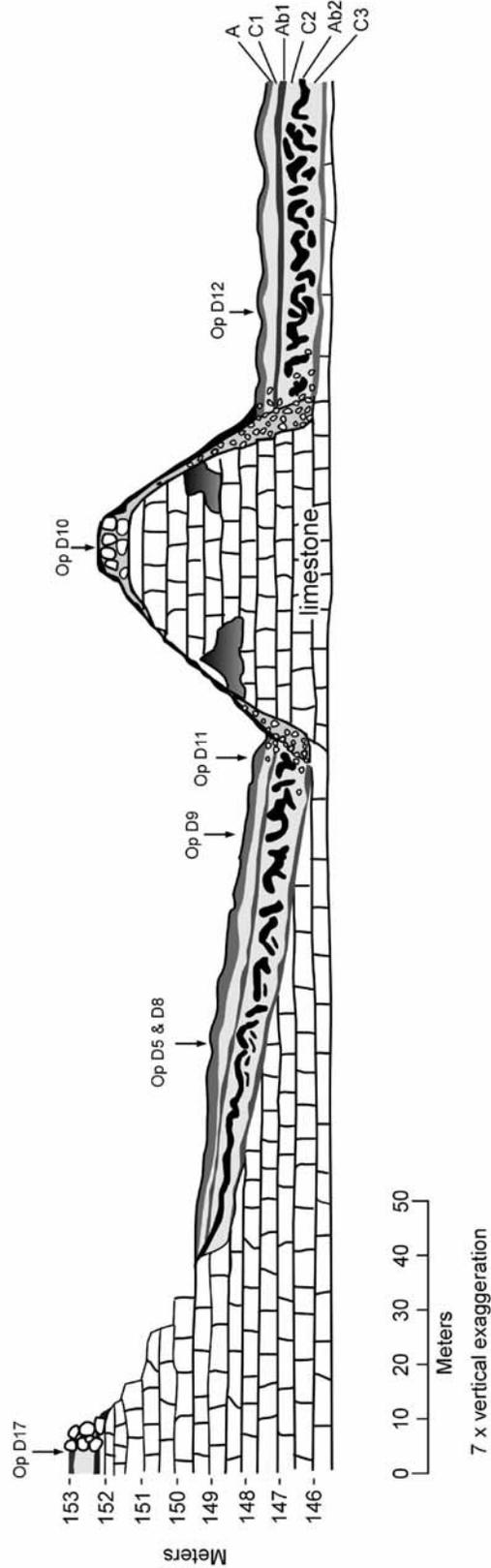


FIGURE.8. 2. Idealized cross section of La Milpa bajos. The arrows refer to site operations at La Milpa Drainage 1; the letters (A, C1, Ab1, C2, Ab2, C3) represent the sequence of soil horizons. (Note: Not all excavation units are shown.)

reach down to 77 cm; Ab horizons (Abss1 and Abss2) from 70 to 140 cm that are black and overlie additional C horizons (2C1 and 2C2) and weathered limestone down to about 150 cm (Figure 8.3).¹¹ This sequence has a low, almost flat gradient in the upper O through C1 horizons, but all the horizons below C2 are moderately deformed into a wavy pattern with incipient slickensides. Soil textures do not vary by different horizons except for the prominent gravel layers in the AC horizons.

The excavations that go farther into the bajo (D6, D8, D9, D11, D12) show a similar pattern of horizontal soil layers in the top 0–45 cm, but the underlying paleosols (Ab horizons) that also range down to 150 cm are deformed to the point of being broken apart. Each of the excavations reveal a similar arrangement of soil horizons. These paleosols, informally called “tiger Vertisols,” are deformed so much that segments have black A horizons and yellowish brown C horizons that run vertically and diagonally (see

**La Milpa Operation D-5:
Soil Profile of North Pit Wall**

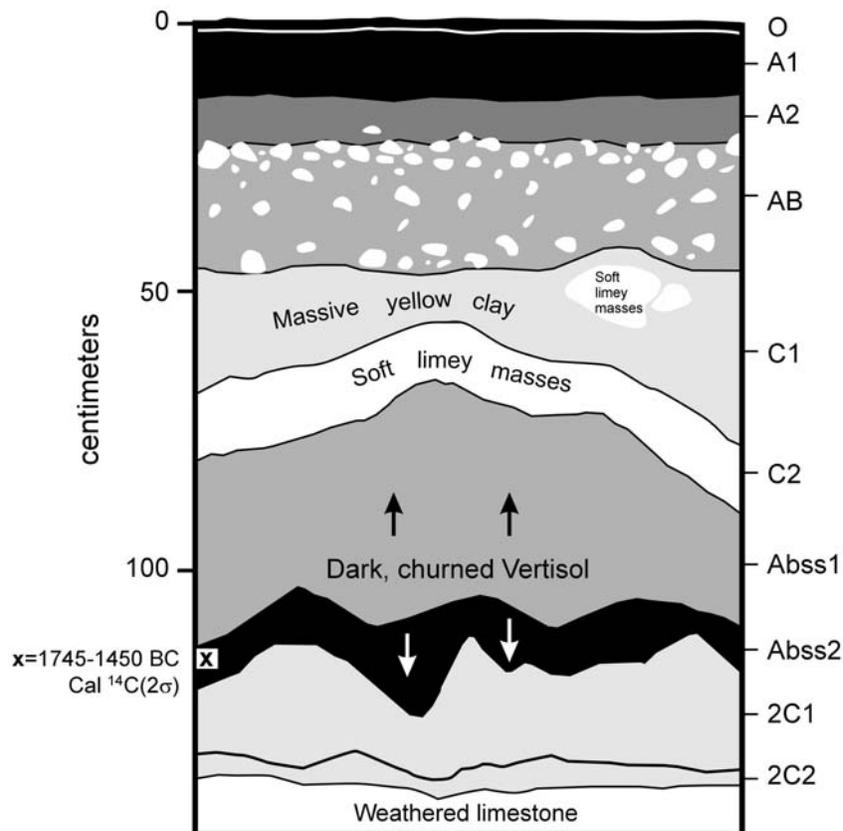


FIGURE 8.3. Soil profile of Operation D5 (Op D5) in the alluvial fan of the bajo of La Milpa Drainage 1. The soil profile is of the north pit wall.

Figure 8.4 for Op D6 [Corozal Bajo] and Figure 8.5 for Op D9 [La Milpa]). Despite the deformed lower soil horizons, the upper soil horizons remain horizontal over the 130-m distance in the five excavations (except the hillock separating D11 by 60 m from D12). Because the buried soils exhibit well-defined horizons (albeit massively deformed), they must have formed horizontally as A, B, and C horizons at some time and been deformed thereafter.

One of the excavations (D11) was placed at the edge of a bedrock outcrop, over what superficially appeared to be a channel, in order to investigate this transition from limestone outcrop to bajo. The excavation showed a 35 cm sequence of the same top three soil horizons (O-A-AC) overlying a 1 m deep gravel- and cobble-filled channel covered by boulder and larger cobble. Next to the channel, toward the bajo, the excavation showed a transition toward the same bajo sequence described above, with up to 1 m of horizontal fill over a distorted paleosol. The excavation suggests the following relative dating sequence: (1) a natural channel transitioning into a flat, upland soil; (2) mass wasting from the hillslope onto the channel and bajo; and (3) low-energy deposition over the channel and bajo.

Dating this sequence precisely is more difficult. We have only the relative dating suggested above, broadly datable artifactual material, and five radiocarbon dates from bulk carbon sources are available. Curiously, no charcoal for dating these excavations was found, and so relied on soil organic carbon was used. As the five radiocarbon samples can provide only mean residency time (MRT) dates on these two shallow paleosols and three deep paleosols, we consider these dates to be minimal ages.

The first paleosol (i.e., the excavation associated with Op D17) lies in the arroyo, approximately one hundred meters upstream from the bajo, and is buried 62 cm deep behind an ancient Maya cross-channel terrace (Scarborough et al. 1995). The paleosol yields a calibrated AMS date of A.D. 365 to 655 (95 percent probability), while ceramic evidence dates the soil surface to before the Late Classic (A.D. 600–900) (Beach et al n.d.). Operation D9 also yields an AMS date from 60 cm in an upper-buried soil that dates to A.D. 120–340 (95 percent probability), with ceramics dominantly Late Classic in age (Figure 8.5). These two radiocarbon dates give about the same age-buried soils from before the Late Preclassic and Classic (A.D. 250–900), with the top 60 a 62 cm of sediments depositing during or after the Classic. The archaeological evidence shows an abrupt collapse of the Maya at La Milpa by A.D. 850 and little human-induced environmental change thereafter (Hammond et al 1998).

The deeper-buried soils are all Vertisol paleosols buried from about 100 to 150 cm deep at D5, D6, and D9 and date to 1745 to 1450 B.C., 1365 to 1070 B.C., and 1885–1620 B.C. (calibrated AMS, 95 percent probability), respectively; therefore, these paleosols are from the Early Preclassic (1500–

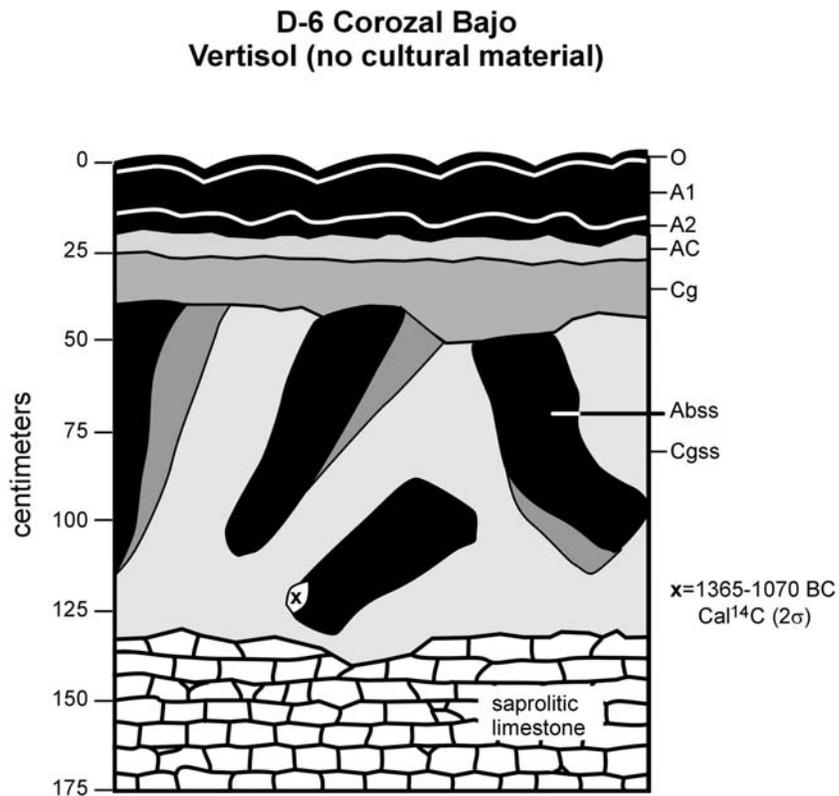


FIGURE 8.4. Soil profile of Operation D6 (Op D6) in Corozal Bajo near the mouth of La Milpa Drainage 2. The deeper-buried soils are all vertisol paleosols with no cultural artifacts found.

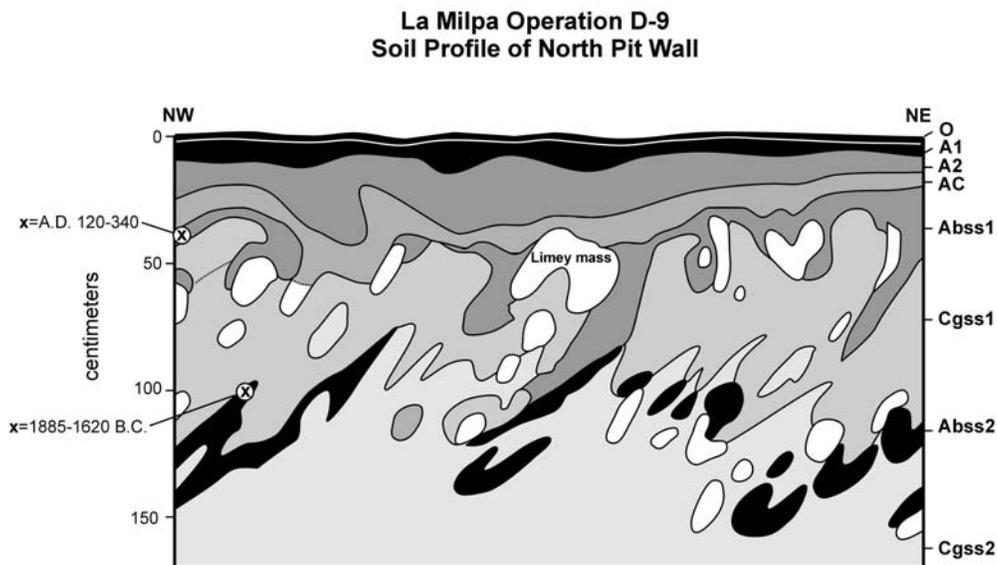


FIGURE 8.5. Soil profile of operation D9 (Op D9) in La Milpa Drainage 1. The soil profile is of the north pit wall.

900 B.C.), or earlier. We found no ceramic material in these deep layers; ceramics only reach down to about one meter. These paleosols appear to represent the pre-Maya mid- to late-Holocene soil surface because these MRT radiocarbon dates are consistently early, and the region's first archaeological evidence dates to the Middle Preclassic (900–400 B.C.) (Dunning et al. 1999).

A series of trenches from La Milpa Drainage 3 into the Far West Bajo were also excavated. These excavations sampled a sequence of geomorphic surfaces ranging from the floodplain of Drainage 3 to the fan delta of BH1 and BH6, as well as the open bajo at BH9 and BH12. The 6 m long excavation at V33a ran across the channel and floodplain of Drainage 3, revealing a complex fluvial sequence (Dunning et al., in press). The floodplain showed a Rendoll soil formed in the top 60–70 cm with A1, A2, AC, and C horizons overlying a Rendoll paleosol, and Ab, Bw, and C horizons over limestone. One calibrated AMS date of 1200–910 B.C. (95 percent probability) from the paleosol corresponds with the Early Preclassic dates of the deeper paleosols in Drainage 1. Channel and floodplain deposits above the paleosol show aggradation with evidence for at least one high-energy event and subsequent low-energy overbank deposition. The sediments above the paleosol had mostly unidentifiable or Late Classic ceramics.

Downstream, the channel disappears onto the bajo, and here 12 trenches were made through these sediments. This sequence of trenches shows a similar pattern to Figure 8.2 without the bedrock outlier of La Milpa Drainage 1. BH1 was particularly important not only because it ranged from the edge to 9 m into the bajo, but also because it yielded two paleosols. The A1, A2, and AC horizons formed in the top 60 cm of aggraded clay on top of an anthropogenically-disturbed paleosol that was created in 100 to 120 cm of aggraded clay, which, in turn, settled above a paleosol that is 130 to 150 cm deep. The topsoils are horizontal in the top 40 to 60 cm across the whole trench, but the upper paleosol ranges from horizontal at the bajo margin to a highly-deformed Vertisol with strongly developed slickensides from 4 to 9 m into the bajo. This upper paleosol has Abs_s, ACb_{ss} horizons, and zones of boulders, cobbles, and ceramics that may indicate human attempts to manipulate this soil, or occasional large magnitude floods. The lower paleosol, formed in the bottom 30 to 40 cm of the trench, has simple horizontal A1_{ss}, BW, and C horizons. Radiocarbon analyses from these two layers yielded dates of 500 to 150 B.C. in the upper paleosol and 6420 to 6235 B.C. in the lower paleosol (calibrated AMS, 95 percent probability). Again, because these dates represent MRT, the dates are minimal; hence, the first date come from the Late Preclassic or earlier, and the second represents the Early Holocene or before.

The trenches at BH6, BH9, and BH12 also yielded upper and lower paleosols. BH6 runs through a fan delta with evidence of higher-energy

sedimentation overlying the lower paleosol. The 5 m long trench at BH6 showed a largely horizontal topsoil sequence of A1, A2, A3, BW, and C horizons overlying a paleosol at 125 cm, with a similar sequence of Ab, ACb, and Cbss horizons. The upper A3 horizon was also a faint paleosol buried around 60 cm. Radiocarbon analyses from the two buried A horizons yielded minimal dates of A.D. 235–555 in the upper paleosol and 760 to 190 B.C. in the lower paleosol (calibrated AMS, 95 percent probability).

The 5 to 14 m long trenches at BH9 through BH12 show both horizontal and highly-deformed segments of the bajo, and all have both horizontal upper 30 to 40 cm layers and paleosols buried at approximately 1 m in depth. Radiocarbon analyses from two paleosols yielded dates of A.D. 15 to 110 in BH6 and 355 to 55 B.C. in BH12 (calibrated AMS, 95 percent probability). The BH9 paleosol is a thin Saprist (muck) layer that also contained a pollen assemblage indicative of a perennial wetland, whereas the BH12 paleosol is well-drained upland Rendoll (Dunning et al. 2000). The BH9 sample had visible leaf matter deposited over a short time period; thus, its radiocarbon date is more accurate.

Two lines of evidence from these trenches seem to point to rapid aggradation in parts of the environment—that, the BH9 trench has a buried organic soil at a depth of 120 cm, and BH10 has discernable laminations in the C horizon. Under the conditions of the current topsoil, organic carbon is high at this site (6.6%), but not as high as the buried muck (c. 20 percent); organic matter should decompose quickly if not rapidly buried and rendered anaerobic. Laminations also are very rare in this environment because bioturbation near the surface should expunge them if not buried quickly.

ALLUVIAL LOWLANDS: DOS HOMBRES AND SIERRA DE AGUA SURVEYS

A number of excavations were made to below 2 m deep, as well as to bedrock or saprolite (sascab) across the lowlands of Dos Hombres and Sierra de Agua (see Figure 8.1). Our survey ranged across the escarpment to the wet, active floodplain; to broken karst ridges; to upland bajos; to transitional uplands; and to an aguada. As with La Milpa Drainage 2 on the La Lucha escarpment, the cross-channel terraces on the Rio Bravo escarpment, were excavated, which also dated to the Late Classic (Beach et al. 2000). The soils ranged from thin, well-drained Rendolls to deep, waterlogged Inceptisols; to deep fluvial Mollisols; and to Vertisols.

Across all of these ecozones, soil pits were excavated—including four pits in the Rio Bravo floodplain at an elevation of approximately 20 meters. Two of the pits showed continuous clay alluvium from overbank flooding in the top 2 m, but two other pits had paleosols buried at 91 and 190 cm. Only

the shallower buried soil was tested. This site (RB10a—1,350 m west of Dos Hombres) in the Rio Bravo floodplain had a fluvial Inceptisol at the surface with a strongly-developed paleosol buried at about 90 cm deep (Figure 8.6). This is a typical soil sequence of O, A1, A2, AC, and C_{ss} horizons to a depth of 85 to 90 cm, which lie on top of the thick paleosol. The paleosol consists of a black (Munsell color: 2.5Y3/0), 25 to 30 cm thick Ab_{ss} horizon, with rudimentary slickensides that gradually transitions below to a highly mottled, redoximorphic, C_g horizon, which extends down to over 2 m in depth. A radiocarbon date (205 B.C.–A.D.240) from the top of the paleosol yields a Late Preclassic date, and we found unidentifiable ceramics throughout the topsoil to the very top of the paleosol were found.

Excavation and coring at the bajo site of Sierra de Agua provide yet another buried soil. Here, excavation to bedrock revealed a well-developed topsoil over the top 74 cm with O, A1, A2, AC, and C_{ss} horizons lying on top of a thin paleosol from 74 to 96 cm with Ab, AC_b, and C_b horizons formed on

RB2 op 10a: Rio Bravo Floodplain Cultural Artifacts Down to Ab_{ss}

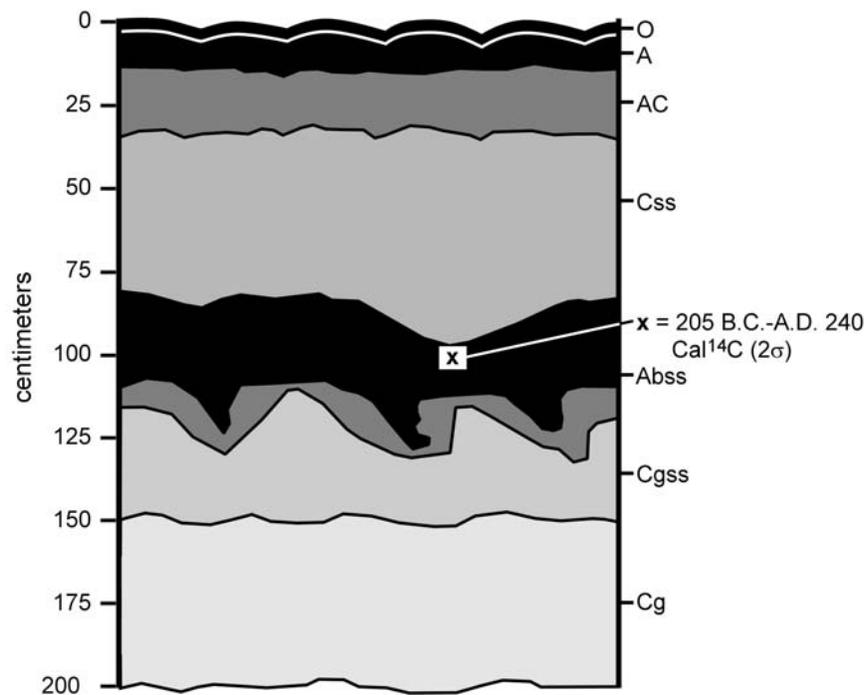


FIGURE 8.6. Soil profile from a Rio Bravo floodplain excavation (RB10a). This is essentially the same profile as a floodplain at Sierra de Agua. Cultural artifacts were found down to the Ab_{ss} horizon.

channel gravels and bedrock. Ceramics, mostly unidentifiable but with some Late Classic examples, occurred decreasingly downward throughout the topsoil, but the paleosol was free of artifacts. This soil profile was essentially the same as Figure 8.6, although the paleosol is much older here with a radiocarbon date of 1490–940 B.C. (calibrated AMS, 95 percent probability) (see Table 8.4). This paleosol again dates to the Early Preclassic like the lower paleosols at La Milpa, but this one had scant artifactual evidence.

Excavations across the large Rio Bravo graben-lowland showed typical Vertisol soils as in the upland bajos and footslopes with well-developed gilgai topography. The upland ridges and transitions had typical Rendoll soils, and the only paleosol studied throughout this zone was buried under architecture at Dos Hombres. This black Rendoll soil dates to 350–50 B.C. (calibrated AMS, 95 percent probability) and lies beneath Late Preclassic (350 B.C. to A.D. 250) artifacts. This soil again represents the surface the Maya first encountered at this later site and generally correlates with the Rio Bravo floodplain-buried soil.

Two excavations were also made in the far eastern escoba palm aguada on transect B of the Dos Hombres Settlement survey, about 1,500 m east of Dos Hombres. This area lies a short distance east of a densely populated, Late Classic Maya site on a shallow ridge with dry-slope terraces and a possible box terrace (Beach et al. 2000). In the aguada, two excavations showed highly-contorted Vertisol horizons beneath a horizontal topsoil of c. 35 cm (Figure 8.7). Again, the contorted horizons lie unconformably below the topsoil sequence of an O, A, and AC horizon. The buried and folded sequence includes an Abss, ACb, Cgss, and in situ decomposed limestone. One radiocarbon sample from organic sediment in the Ab horizon at c. 95 cm dated to 195 B.C. to A.D. 430 (95 percent probability, 2σ [sigma] level), which is the Late Preclassic to Early Classic. This date is comparable to the two other dates on buried paleosols across these lowlands and to the younger paleosols around La Milpa.

Another line of evidence on this site is the micromorphology of a soil monolith. The analysis found slickensides throughout, as was found in the field. It also described a sterile or acultural base (or Cg horizon) of iron-stained clayey marl, and an increase in organic matter, charcoal, numerous phytoliths, chert, and possibly freshwater sponge spicules in the Ab and ACb horizons. These organic parts of the core may or may not be associated with human activity. The book, therefore, is far from closed on agriculture in this site; because it always has been far above the perennial water table, wetland farming in this site could only have been seasonal. The lack of artifacts in these pits so close to dense habitation, however, does not suggest intensive agriculture. Although this is intriguing culturally, the most parsimonious explanation for soil morphology in this aguada is natural Vertisol and

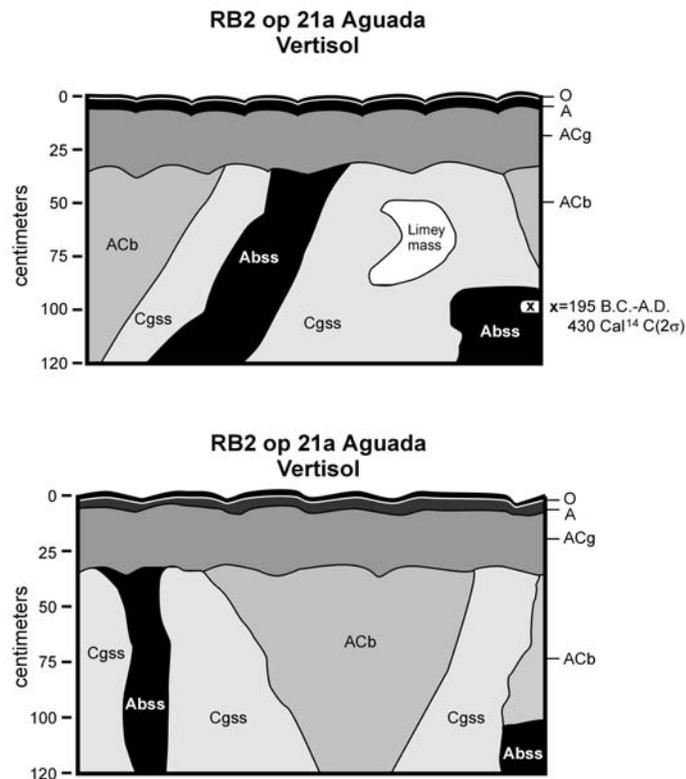


FIGURE 8.7. Two soil profiles (RB21 a) from an aguada located 1,500 m east of Dos Hombres.

geomorphic formation with human-induced aggradation in the Late Classic.

INTERPRETATION: RADIOCARBON DATES

Distinct paleosols (buried A horizon) exist in many different lowland bajo sites and situations around La Milpa. All of the ¹⁴C samples from the top 10 cm of the paleosols and organic sediments were obtained. The radiocarbon dates on buried A horizons run into two distinct groups: (1) approximately 50 to 75 cm deep paleosols that have calibrated AMS dates ranging from A.D. 15 to 655, and (2) approximately 95 to 150 cm deep paleosols that generally have calibrated AMS dates from earlier than 1000 B.C. These patterns do not fit such geomorphic situations as floodplains, where paleosols with younger dates are buried deeper, or the 150 cm deep paleosol at BH1 that dates to 6420 to 6235 B.C. All the other paleosols at this depth date to 1000 to 2000 B.C.; thus, this soil may represent localized early sediment burial, or much higher contamination from old carbon.

Most of the buried soils date to the Preclassic or Classic, but these dates represent the mean residence times for carbon in the soils; thus, they represent

minimal dates for these soils. The paleosols are not related to the current A horizons because morphology and chemistry are different. Ceramics of either unidentified or Late Classic dates occurred above and through each of the upper buried soils, but no ceramics occur as deep as the lower Ab horizons or in underlying Cg horizons.

Paleosols buried under architecture at the sites of La Milpa and Dos Hombres were also dated for comparison with bajo paleosols. In La Milpa's Plaza B, a Vertisol Abss horizon dates to 805–540 B.C.; in Dos Hombres plaza, an Ab horizon dates to 350 to 50 B.C. (both AMS calibrated, 95 percent probability). Both of these paleosols are buried beneath sites that started in the Middle to Late Preclassic (900 B.C. to A.D. 250) and lie beneath Early Classic (A.D. 250–600) structures. Paleosols under well-dated Late/ Terminal Classic period (A.D. 600–900) terraces date to A.D. 145 to 655. In each of these cases, the AMS radiocarbon dates of the paleosols range from 0 to 1,000 years earlier than the overlying structures. Another independent means of dating paleosols is datable artifacts. Many sherds were found in and through the later paleosols, but none as far down as the early paleosols.

The widespread nature of buried soils in regional lowland sites suggests a period of equilibrium pedogenesis associated with the development of mature topsoils that occurred through, or into the Preclassic. Sometime in the Preclassic or later, this site underwent a period of aggradation, with soils buried by about 60 to 130 cm. Two dates from one soil pit (see Table 8.4: D09) in La Milpa Drainage 1 provide additional information: (1) D09-6 is an Ab horizon buried up to 170 cm and dated at B.C. 1735 (intercept date), and (2) D09-3 is an A3 horizon buried up to 70 cm and dated at A.D. 235 (intercept date). Sometime in the intervening 2000 years, this site aggraded up to one meter; after about A.D. 235, in the Early Classic, the site aggraded again by up to 70 cm (with 40–60 percent pebble to cobble size chert and weathered limestone at this site just downstream from an alluvial fan). Several other sites also show aggradation of 50 to 100 cm sometime during or after the Early Classic.

ENVIRONMENTAL CHANGE AND BAJO AGGRADATION

What changes may have caused the large landscape alteration that inundated bajo soils across this landscape? Geomorphically speaking, either increased erosion from uplands and deposition onto lowlands, or increased deposition or aggradation could have buried soils across this landscape. Increased erosion certainly did occur because of devegetation caused by humans, and was probably accompanied by massive, widespread fire. On the other hand, increased deposition could be engendered by sea-level and thus

base-level rise in the region, which could cause stream profiles to rise or aggrade as an adjustment. This occurred north of the study region near sea level (Pope et al. 2000), but this is a highly unlikely scenario as this region is far removed and insulated by greater elevation from likely base-level influences.

The widespread nature of the older paleosols in regional lowland sites suggests a period of steady pedogenesis, with formation of well-developed topsoils through the Holocene to the Preclassic or later; sometime in the Preclassic (or later), some large systemic change caused sedimentation of soils by about 60 to 130 cm. The younger paleosol is not widespread and often occurs with the cumulic A horizon in many depression soils. It is associated with Classic period ceramics, and all evidence dates it to the Classic period—perhaps even to the less human-influenced Early or Middle Classic.

The soils, stratigraphy, and artifacts point to ancient Maya-induced soil erosion as the source of bajo aggradation based on three lines of evidence. First, aggradation in fluvial and karst systems induced by sea-level rise should have been a steadier process that would not have caused one disequilibrium of widespread aggradation in the Late Holocene when sea-level rise was slowing; otherwise, there should be several other older buried soils, rather than the one, very spatially-limited Early Holocene paleosol. Second, the coincidence of a buried soil with the Preclassic when pioneer cultivators first expanded onto hillslopes, and one with the Late Classic when land use was the most intense, is compelling. Third, the dominance of Late Classic or Terminal Classic artifacts in the top aggraded sediments, and those and earlier artifacts down to the old paleosol, shows humans were involved in these soils since the old paleosol.

Moreover, there are many examples in depressions in the southern Maya lowlands of paleosols buried by “Maya Clays” (Dunning, Beach, and Rue 1997). For example, in coastal northern Belize and the Belize River Valley, there are buried surfaces from the Early Preclassic, with Late Classic “Maya Clay” fill of about the same depth as this study region (cf. Jacob 1995b; Pohl et al. 1996; Holley et al. 2000). Evidence in northwestern Belize about these “Maya Clays” has only provided a broad date for the early buried soil surface and a *terminus post quem* date for the period of aggradation. Yet, the less common upper paleosol and pattern of artifacts suggest two episodes of aggradation in the Preclassic through Early Classic and the Late Classic, or later, sandwiching the latter paleosol, which perhaps developed in the Early Classic through Middle Classic. Especially telling here are agricultural terraces choked full of Late Classic ceramics that extend down into the younger paleosols buried under the terraces and on alluvial fans. This indicates a five-part sequence: (1) soil formation into the Preclassic, (2) soil erosion sometime before the Early Classic that buries soils up to 100 cm,

(3) less disturbed soil formation during the Middle Classic, (4) accelerated soil erosion again in the Late Classic, and (5) minimal change during the Postclassic. Even with widespread soil conservation in the Late Classic, soil erosion probably remained high because Late Classic ceramics choke regional deposits and terraces cannot stop all erosion (Beach and Dunning 1995).

HYPOTHESES ABOUT SOIL PROFILE DEFORMATION

Deforming normally horizontal soil layers into diagonally folded patterns by Vertisol processes requires a confining pressure created by a certain depth of overlying soil and the vertical upward force of the swelling pressure, which creates a shearing force (Eswaran et al. 1999). Shearing only occurs below about 60 cm, where the overburden of soil can counterbalance the upward swelling, and only at a critical soil moisture when the soils are plastic. The downward extent that slickensides can form each year is only to the depth of rain infiltration, because these soils must moisten and become plastic. Thus, leaching transports carbonate and gypsum below active slickensides, and calcic and gypsic horizons can form here. These Vertisol properties will vary across a landscape due to environmental gradients. For example, areas of undulating bedrock will place more potential for shearing in the basins because these will limit expansion. Moreover, seasonal wetlands will have less Vertisol-induced deformation near their low points, or other areas where they dry up the least, because such areas have the least contraction (Coulombe, Wilding, and Dixon 1996; Eswaran et al. 1999).

Another related process that can deform horizontal layers is the response of sediment to differential loading, and the formation of diapirs or piercement structures. In this process, clays can squeeze out from areas of greater to lesser overburden and ultimately spread out over the surface, while the overburden sags down into a lower horizon. This may form a sequence of diapirs, or domes of upward extruded clay, across a region. These formations are best known as salt domes that form in deltas of rapid deposition, but few studies have applied these ideas to soil studies (Paton 1974; Paton, Humphreys, and Mitchell 1995:98). The soil morphology uncovered in our trenches do not suggest this pattern of piercement from below—only aggradation from above, and shearing from below. Moreover, all paired radiocarbon dates from lower soils are older than upper soils, suggesting normal superposition.

The influence of tree roots, large earthquakes, and organism digging (bioturbation) can also greatly deform typical soil horizons (Schaetzl et al. 1990; Lutz and Griswold 1939; Saucier 1991). The mass of soil moved by root throws can be very high, and this can significantly alter the surface

topography and subsoil in this region (Beach 1998a). Similarly, earthquake-induced sandblows rupture and deform soil horizons; yet, no reports exist for any such events in this region. Moreover, ancient Maya (and animals) digging across this bajo to create wetland or other agricultural fields also could have greatly transformed soil stratigraphy, but a small minority of our excavations show a morphology associated with human and animal bioturbation. The most likely of these deformation agents is root throw, but this process is inadequate to explain the widespread and consistent occurrence of these buried paleosols. Also, the paired radiocarbon dates, as suggested above, do not indicate that younger soils lie below older soils in these examples, although the patterns in the Dos Hombres aguada (see Figure 8.7) and one excavation at La Milpa Drainage 2 (see Figure 8.5) probably suggest some tree root or bioturbation caused soil deformation.

The bajo Vertisols in this study all have a typical horizon sequence in the top three horizons (A-AC-Ab) to 70-cm deep, but have highly distorted melanges of horizons in the lower three or four horizons, which range downward to more than 180 cm. One explanation for this unusual arrangement of horizons suggests disturbance to the lower horizon before the upper unit was deposited. Any explanation, however, must explain several factors: first, the development of normal soil horizons; second, the disturbance of the lower soil horizons; and third, the deposition of the upper unit. Ceramic evidence and radiocarbon dates indicate the following sequence: (1) erosion from upland soils deposited the top 35 to 70 cm of three or four cumulic and occasional buried A horizons, and (2) earlier erosion deposited 40 to 110 cm on the lower widespread paleosol.

The following hypothesis is suggested to explain this soil formation. Up until the Early Preclassic, the bajo soils were 35 to 60 cm thick and formed in limestone saprolite with lesser amounts of allochthonous material. When Maya farmers first became a factor of soil formation in the Early Preclassic, they began to farm these bajos and the slopes around them, which accelerated erosion and the deposition of “Maya Clay.” We think the lower sediment of 40 to 110 cm started the deformation process in the Preclassic or Early Classic by the shearing described above—that is, sediment loading on clays that provided counterbalance mass, which then led to shearing against upward swelling. Deformation may also have been exacerbated by greater extremes in soil moisture with the first anthropogenic burning and deforestation and concomitant root decomposition and krotovina formation. The last 35 to 70 cm of horizontal deposition occurred during and after the Classic Period, which forming weakly-developed topsoils above the lower, deformed sequence. This later episode of erosion and deposition corresponds to urbanization at La Milpa, and may be tied with the building of masses of check dams and diversion channels throughout La Milpa Drainage 2 (see Figure 8.2). The expansion and contraction had little affect on the upper,

aggradational unit because rapid reforestation following this site's collapse would have maintained more stable and moister soil conditions.

A changing hydrology in antiquity may have complicated soil formation here. The three best known environmental changes were deforestation, altered water recharge regimes, and the "Maya Drought." It is well known that deforestation would lead to increased runoff and higher water tables in most regions, including the tropics (see Lal 1990:433). Jacob (1995b), for example, writing about Cobweb Swamp, Belize, north of this study area, reasons that because forests transpire huge amounts of moisture, deforestation associated with the first Maya by 3900 14C yr. B.P. may have influenced the rising of water levels in the swamp after 3400 14C yr. B.P. Also, Tindall and Kunkel (1999, 234) state that roots deplete "water at a rate far in excess of that by soil evaporation alone."

Deforestation started here in the Preclassic and continued until the Terminal Classic with periods of forest regrowth, such as occurred during the Middle Classic. The first response to deforestation should, therefore, have been moister soil conditions and less of the clay contraction needed to drive Vertisol formation. But this is a much more complex challenge because we are unsure about how two important variables may have affected soil moisture—that is, ancient Maya deforestation and drainage (see Beach et al. n.d.; Scarborough et al. 1995). Additionally, the rapid accumulation of clay sediments in many depressions may have sealed them from perched aquifers. Such aggradation by clays could have interfered with recharge and discharge, thus altering the soil moisture and wetland ecology of these bajos (Dunning et al. 2002).

Further complicating the enigma is the "Maya Drought" (Hodell, Brenner, and Curtis 2000; Gill 2000). We have no evidence in the study area proper for the Classic Period Maya drought discussed previously, but Pope et al. (2000), working north of the study area in northern Belize, and Webster, Reeder, and Reynolds (2000), working south of the study area in the Vaca Plain in central Belize, both suggest separate lines of evidence for this drought. A period of aridity would clearly induce greater clay contraction, and possibly greater Vertisol development. The drought alone, however, could not explain all of the deformation, because deformation required a greater depth that was supplied by ancient soil erosion and deposition.

Whatever the complicated and poorly-known factors, the soil horizon sequences, ceramics, and radiocarbon dates in these lowland soils indicate the following sequence: (1) equilibrium soil development before and possibly into the Preclassic, (2) disequilibrium conditions in the form of 45 to 110 cm aggradation from the Preclassic to the Early Classic, (3) the start of buried soil deformation with differential sediment loading, (4) a brief episode of equilibrium soil formation in the Early to Middle Classic, (5) a period of

erosion and aggradation from the Early Classic through Late Classic, and (6) a Postclassic period of little change.

CONCLUSION

Depression soils in northwestern Belize are diverse, and many are deformed by ancient aggradation. They include a few thin Rendolls formed in the upper 30 cm of bedrock and saprolite, deep fluvial Inceptisols and Rendolls in active floodplains and fans, and deep Vertisols in karst sinks. These soils are dominantly clay in texture, and the clay minerals are randomly interstratified chlorite/smectite, with smaller amounts of smectite and still smaller amounts of vermiculite. Even though the soils exist in seasonally inundated depressions, they generally have low amounts of organic carbon, and are high in CEC, base saturation, and Ca^{2+} and Mg^{2+} cations. Soil pH ranges from very strongly to moderately acid in moist soils, to slightly to moderately alkaline in most other soils.

The edges of these bajos are surrounded by ancient Maya footslope terraces and diversion networks, and the bajos themselves have a significant number of mounds as well as artifacts scattered through all but the lower paleosol. Thus, the ancient Maya clearly used these bajos in antiquity, even though our phosphate fractionation tests show equivocal evidence for ancient fertilization.

Most of the study's trenches show one or two buried paleosols, especially along the peripheries of depressions, and in floodplains and alluvial fans. One of the paleosols appears to be an anomalous holdover from the Early Holocene, perhaps buried by some rare natural event. The most widespread paleosol lies buried from beneath 70 to 180 cm of sediment, and probably represent the pre-Maya soil surface of the Preclassic or earlier. Above this lies up to 180 cm of aggraded sediment, which we trace to two episodes of erosion. The first episode is an artifact-poor period that we associate with the Preclassic and Early Classic, and ends in an infrequent paleosol or simply artifact-rich strata buried at 50 to 65 cm. We think the first episode of erosion coincides with the Preclassic Maya pioneer farmers moving from the bajos onto the hillslopes, and then using fire to clear forests.

The second paleosol may have formed in the Early to Late Classic, and it is infused with Late Classic to Terminal Classic ceramics from this layer up to the surface. Thus, the second episode of erosion is almost certainly associated with the highest populations and agricultural intensification of the Late Classic, especially after A.D. 700. Both of these paleosols together parallel the "Maya Clays" of many lake cores in the Petén and depressions in Belize that originate about 3,000 years ago and last through the Late Classic through Terminal Classic to the Tenth Century A.D.

The karst depression soils are much more deformed and contorted than the floodplain and fan soils. All such paleo-Vertisols occur below 35 to 70 cm of relatively horizontal top A and C horizons that show incrementally less distortion to the surface, as if they were filled in over a hummocky gilgai surface. The ancient paleosol has diagonal and contrasting Ab, Bwb, and Cb horizons that must have formed originally as horizontal layers. They probably began to deform diagonally in the Preclassic with the first episode of deforestation, erosion, and sedimentation. The actual processes for deformation are complicated, but the explanation that explains most of their morphological clues is differential sediment loading that induced shearing by expansive clays against the sediment overburden.

The hydrologic changes induced by deforestation and the possible Maya Drought may have influenced this soil deformation. Reforestation occurred in the Postclassic, and hydrologic regimes became steadier possibly with the return of moister conditions after the Late Classic dry period. Thus, erosion and sedimentation returned to background levels, and Vertisol expansion and contraction certainly continued thereafter, but compelled considerably less under the dense forest of the last millennium.

NOTES

1. Karst refers to weathered limestone landscapes that often have sinkholes and caves.
2. Dolines are dissolved or collapsed sinkholes that are often formed in limestone bedrock.
3. Vertisols are one soil order in the USDA Soil Taxonomy. Vertisols are generally clayey and go through seasonal sink and swell cycles.
4. Redoximorphic features are soil colors and features different from the soil matrix; they are caused by reduction and oxidation of iron (Fe) and often manganese (Mn).
5. Paleosols are soils formed in a different environment of the past, and sometimes they may be buried by sediments and surface soils.
6. Horsts are up-faulted blocks on normal faults.
7. Grabens are down-faulted blocks on normal faults.
8. Suite refers to a group of related soils.
9. Subsuites are the soils within a suite.
10. The USDA taxonomy is an American soil classification system, while the FAO is an international taxonomy adopted by the United Nations (U.N.).
11. AB refers to an intergrade between A and B soil horizons; Ab is a buried A horizon; and Abss refers to a buried A horizon with slickensides.

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Chapter 9

Interaction of Microorganisms with Maya Archaeological Materials

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INTRODUCTION

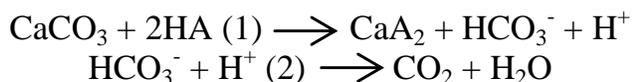
The Maya archaeological sites in southern Mexico are among the most important cultural artifacts in the Western Hemisphere. These ancient structures provide us with important insights into the history and culture of Mexico. The exposed remains of Maya cities, such as Uxmal and Chichén Itzá in the Yucatán Peninsula, are at risk from microbial degradation. The combination of high temperature and humidity has stimulated very active microbial activity with consequent deterioration. In addition, the increase in tourism in recent years has accelerated degradation of these structures.

Most of the materials used for construction of the Maya structures are limestone. Limestone is often highly porous and mechanically weak (Kumar and Ginell 1995). The major causes of deterioration of these Maya structures after archaeological excavation are the inherent characteristics of the building stone, cyclic changes in temperature and humidity, and active microbial growth (Kumar and Ginell 1995). Nonbiological processes may contribute to

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the deterioration of materials by ultraviolet (UV) light, chemical oxidation, and physical weathering. Weathering of the stone depends on several factors, including the nature of the surface, material composition, and other physical processes. Limestone is also susceptible to microbial degradation under the high humidity and temperature conditions of southern Mexico.

Acids produced by microbial metabolism adsorb onto and interact with the limestone. The general mechanism for weathering of limestone by acids is as follows:



Reaction 1 shows that acids (2HA) react with calcium carbonate (CaCO_3), chelating the cation (Ca^{2+}) and forming bicarbonate (HCO_3^-); the mechanism is completed (reaction 2) when the bicarbonate is neutralized, forming carbon dioxide (CO_2) and water (H_2O). In neutral pH conditions, the carbonate is relatively insoluble. The presence of acid, however, accelerates the degradation of the carbonate by consuming the products of the reaction. The calcium/cation salt (CaA_2) is soluble and results in exfoliation and cracking of the limestone surfaces by a process of wetting, evaporation, and re-crystallization.

Microorganisms have been implicated in the decomposition of a wide range of building and industrial materials, including stone (Gu, Ford, and Mitchell 2000a), metals (Ford and Mitchell 1990b; Gu, Ford, and Mitchell 2000b), and artificial polymers (Gu et al. 2000c). Colonization by lichens occurs on most limestone, causing serious deterioration (Gracia-Rose and Saiz-Jimenez 1991). Growth of fungi into the interstices of the limestone has also been associated with stone damage (Hirsch, Eckhardt, and Palmer 1995; Wollenzein et al. 1995). The fungi appear to resist both dehydration and UV irradiation. In addition to lichens and fungi, bacteria grow well on stone (Garcia et al. 1995; Urzi et al. 1991). Endolithic microorganisms such as cyanobacteria have also been implicated in stone degradation; these microorganisms may be a larger problem than originally suspected because they can persist at high temperatures, in dry, UV-irradiated, inhospitable environments (Salvadori 1999). Microorganisms that cause deterioration of limestone materials act by forming biofilms on the stone surfaces. These biofilms create acids and other metabolic products that are involved in the solubilization of the stone substrate.

MICROBIAL BIOFILM FORMATION

Active degradation processes are initiated when a microbial community adheres to a material and forms a biofilm (Figure 9.1). Microbial biofilms are collections of individual and aggregated bacterial cells on surfaces that are maintained by electrostatic forces (Marshall 1976; Neu 1996) and/or adhering exopolymers (Costerton, Geesey, and Cheng 1978). The resultant metabolic products of the biofilm are responsible for the degradation of the underlying material.

Planktonic bacteria are capable of colonizing nonbiological material surfaces (Gu et al. 1998a; Little et al. 1986). All surfaces exposed to moist environments form biofilms (Costerton et al. 1995; Geesey and White 1990; Marshall 1980). The initial contact with a surface is made possible by flagella, Brownian cell motion, hydrophobic forces, or deposition. Cell-to-cell signaling molecules, which control the density of bacterial cells in the growth medium, trigger the synthesis of exopolymers when a specific density is reached (Davies et al. 1998). The production of exopolymers is thought to induce bacterial attachment (Bonet, Simon-Pujol, and Congregado 1993; Freeman and Lock 1995; Vandevivere and Kirchman 1993; Whitfield 1988).

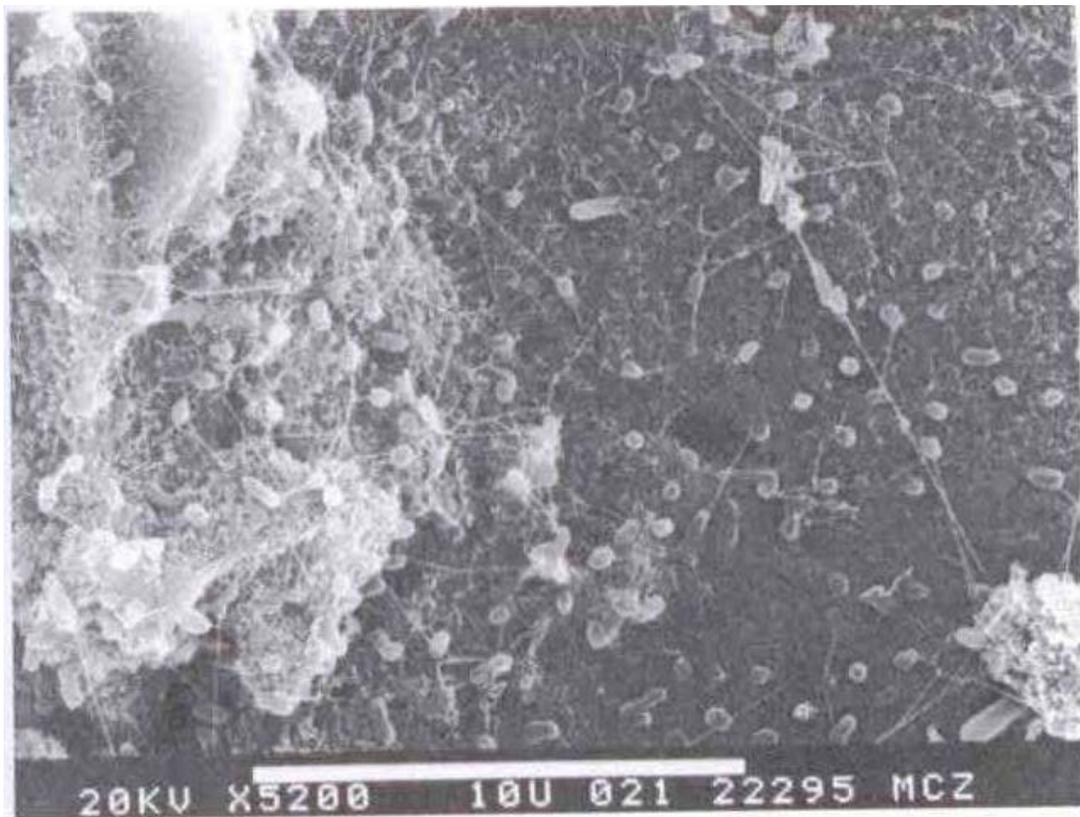


FIGURE 9.1. Scanning electron micrograph of a biofilm growing on a limestone surface (magnification 5,200 x).

This attachment may be reversible, but cells that persist on the surface as a result of electrostatic forces synthesize exopolymeric material that encapsulates the bacterial population, thereby forming an irreversible community (Marshall, Stout, and Mitchell 1971).

Formation of microbial biofilms in natural and artificial environments follows a predictable sequence of events: initial adhesion of a conditioning film of organic molecules on the surface, bacterial colony formation, and growth to a mature biofilm. Biofilm growth, senescence, and sloughing off are continuous processes (Caldwell et al. 1997; Fletcher 1996; Maki et al. 1990, 1989). The adsorbed layer of organic molecules may help overcome short-range repulsion forces between the bacterium and the substratum, or consist of molecules that serve as cues for the planktonic bacteria (Kelly-Wintenberg and Montie 1994).

The structure of the surface also affects microbial adhesion. Hydrophobicity of a surface favors biofilm formation, while hydrophilicity discourages settlement (Busscher, Sjollem, and v. d. Mai 1990; Neu 1996; Schmidt 1997; Sneider et al. 1994); these generalizations are not fully understood. Multicellular organization may also have some role in biofilm structure and ecological function (Wolfaardt et al. 1994). Conversely, biofilm matrices also affect the physical and chemical conditions of the substratum. Several models have been proposed to explain the selectivity of different materials on bacterial adhesion (Fletcher 1996; Wiencek and Fletcher 1995). The fundamental mechanisms of bacterial adhesion, and behavioral response of bacteria to surface selectivity, are still poorly understood.

Cell-to-cell signaling has been proposed as a key factor mediating biofilm formation (Davies et al. 1998). *N*-Acyl homoserine lactone molecules stimulate exopolymer production in response to planktonic cellular density. This production of exopolymer is involved in biofilm formation. After initial bacterial attachment, reproductive growth and colony formation occur. When the biofilm reaches a maximum thickness (20–100 μm), the film may slough off due to hydrodynamic shear forces, or the production of exozymes. The remaining cells on the surface divide and continually form new biofilm matter. During cellular division, the daughter cell may not be attached to the biofilm and may be released into the planktonic phase. The planktonic cells are then free to settle on available surfaces, thereby providing the initial colonization for new biofilm development.

Chemical factors such as solution ionic strength, type and concentration of available cation(s), presence of surfactant, and substratum characteristics also influence biofilm formation. Generally, higher ionic strength, higher ion concentrations, and higher cation valences favor the formation of biofilms by decreasing the electric diffuse double layer, which is a barrier against bacterial movement towards a surface. When a bacterium approaches a surface, it must

overcome a critical energy level before it can firmly attach. The higher ion concentrations and cation valences can compress the diffuse double layer, allowing the planktonic cells closer to the substratum surface and thus facilitating adhesion (Marshall 1976). Because of the myriad of factors affecting biofilm formation, it is important to understand that experimental results from the laboratory can be extrapolated to natural environments only to a limited extent only.

MICROBIOLOGY OF MAYA ARCHAEOLOGICAL STRUCTURES

Biofilms are common on many surfaces, especially those under high humidity conditions (Gu et al. 1998b; Little et al. 1990). The interactions among the Maya archaeological structures, microbial biofilms, and the environment are extremely complex. In order to investigate these interactions, microbial populations in biofilms were sampled from stone structures in Uxmal and Chichén Itzá, and then characterized. The microorganisms were inoculated onto limestone cubes in the laboratory, incubated under different environmental conditions, and analyzed as to how these conditions affected the resultant community. Extreme natural fluctuations in microbial activity and numbers in soil and rock substrata occur due to the wide range of physiochemical parameters (Doelman et al. 1994).

A comparison of sampling techniques was performed to investigate the relationship of the culturable population size to collection methods. Samples of microbial biofilms were collected using two different techniques: (1) pieces of stone and associated microflora were collected, and (2) a swab wetted with saline and dilute nontoxic surfactant was rubbed against the stone surface in order to collect the surface microflora. Both the stone and swab were stored in saline and dilute surfactant solutions to release the microorganisms. Qualitative and quantitative analysis of the microflora was performed using methods modified from Gu et al. (1997). Figure 9.2 shows the result of the two different sampling methods, as well as the relative efficacy of collecting different predominate groups of microorganisms. The swabbing technique was considered more effective because it resulted in the collection of larger numbers of all groups of microorganisms. These larger collections may be the result of release of a greater number of microorganisms from the biofilms due to the physical rubbing of the swab against the stone.

An analysis of the microbial populations at two different Maya sites was then used to investigate microbial diversity. Structures at the sites of Uxmal and Chichén Itzá had relatively similar populations of culturable microorganisms (Figure 9.3). At both sites, heterotrophic bacteria—general

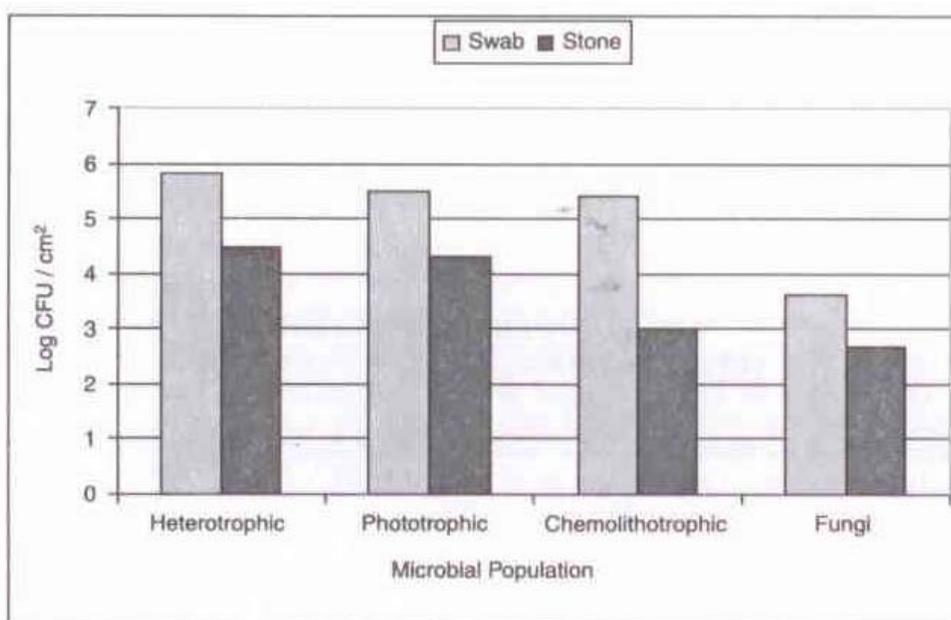


FIGURE 9.2. Comparison of two sampling methods. Microbial samples collected by swabs yielded a larger and more diverse microbial community than those collected directly from stones. (Note: CFU is “colony-forming unit” —cells that proliferated under the specific growth condition provided.)

consumers using organic carbon as a nutrition source (e.g. *Proteus* sp.)—were the most dominant type of microorganism. Phototrophic and chemolithotrophic populations were also well represented at both sites. Chemolithotrophic bacteria utilize inorganic molecules, such as sulfur, as their terminal electron receptor; air pollution is a potential source of this sulfur. At both sites, fungi such as *Aureobasidium* sp. and *Fusarium* sp. were also present.

An analysis of the phototrophic organisms at Uxmal revealed that most of this population is made up of cyanobacteria (Figure 9.4). The remainder of the Uxmal population was found to be comprised of primarily green algae. Cyanobacteria were prevalent in the interior of rooms where the light levels were low. The algae probably represented sampled surfaces where there was higher light intensity.

To examine the effect of environment on biofilm composition, the Uxmal microbial community was inoculated onto sterile limestone samples and incubated in different environments for four weeks in a laboratory study. Inoculated limestone samples were stored at high humidity, with low concentrations of introduced organic matter, in darkness or high light environments. In high light, phototrophic and chemolithotrophic bacterial populations were stimulated, while heterotrophic bacterial and fungal populations were suppressed (Figure 9.5). In high light, only the phototrophic and chemolithotrophic populations had sufficient energy sources for their growth. In contrast, the samples in the dark displayed a very different

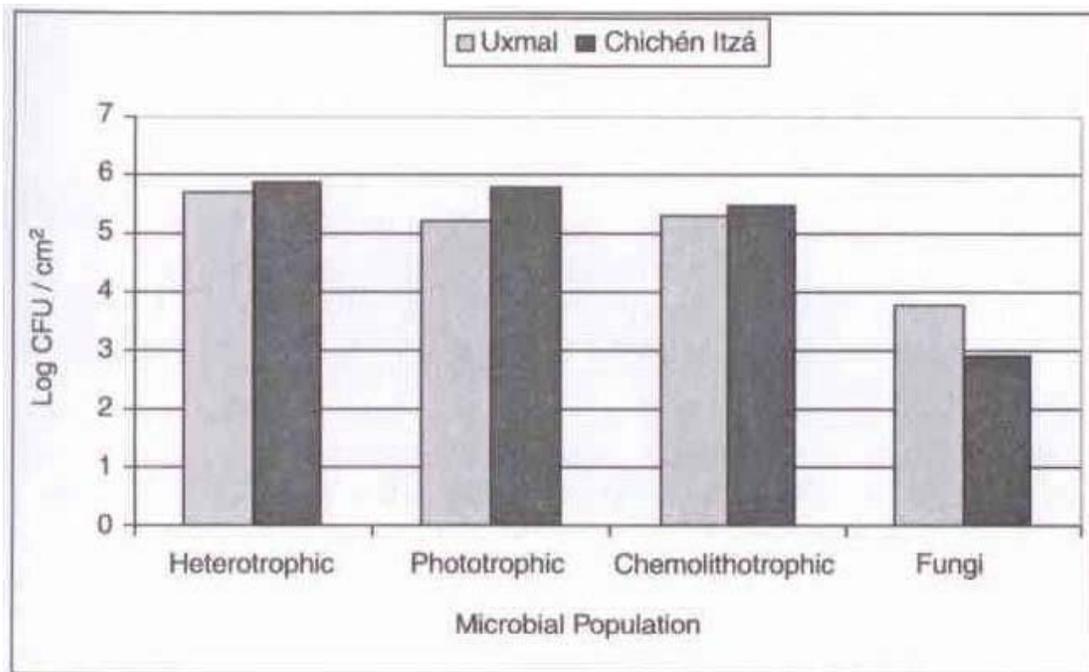


FIGURE 9.3. A comparison of the microbial communities in biofilms on stone structures in Uxmal and Chichén Itzá. (Note: CFU is “colony-forming unit.”)

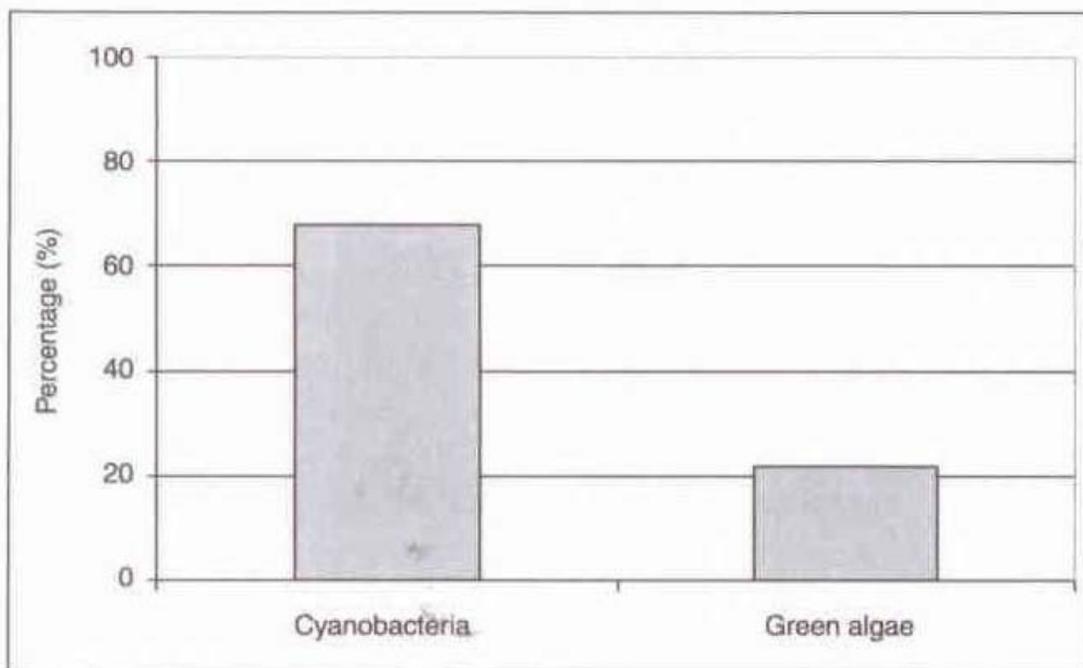


FIGURE 9.4. An analysis of the phototrophic organisms at Uxmal. The population was dominated by cyanobacteria.

population composition (Figure 9.5). The chemolithotrophic bacteria and the fungi grew well, while the heterotrophic and phototrophic bacterial populations were suppressed because there was not an ample carbon source or light source, respectively.

Our laboratory data for fungal and heterotrophic bacterial biofilm growth failed to mirror the field data. It is probable that the ample organic carbon sources available in the field favored heterotrophic bacteria. Attempts are being made to develop laboratory conditions that will stimulate a complex microbial community on limestone that parallels the biofilm community observed in the field.

MATERIAL DEGRADATION PROCESS AND ANALYSIS

Activity of microorganisms on surfaces may result in deterioration of underlying materials, including the substratum and associated artificial polymers (Ford and Mitchell 1990a; Gu, Ford, and Mitchell 2000a; Gu et al. 2000c; Hamilton 1985; Little et al. 1990). Microorganisms may utilize organic materials in the presence or absence of oxygen as sources of carbon and energy. Different groups of microorganisms use widely divergent strategies to achieve the goal of decomposition. Most bacteria require close proximity to a substratum because the bacteria need to immediately capture the released

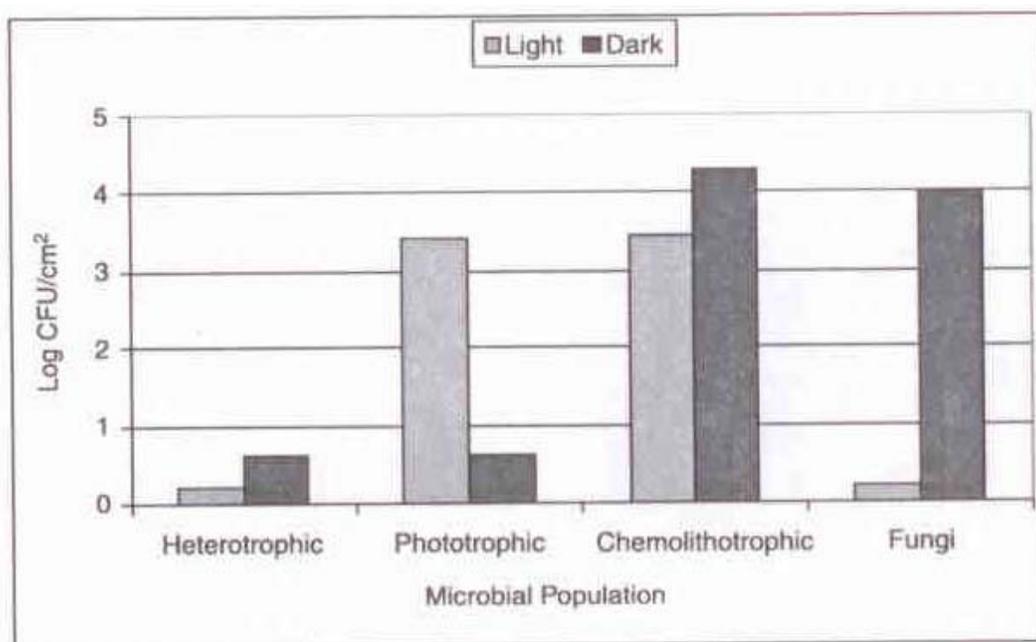


FIGURE 9.5. An analysis of the microbial community at Uxmal. The community was inoculated onto sterile limestone samples and incubated in different environments under controlled laboratory conditions. (Note: CFU is “colony-forming unit.”)

compounds for their metabolism. Close proximity allows degradation products to be easily assimilated into cells for further utilization (Gu et al. 2000). This efficient process allows bacteria to maximize their energy conservation.

Conservation scientists have not developed precise methods to measure degradation of carbonate stones. Common techniques include depth measurements using calipers, reference surfaces, and macro stereophotogrammetry (Winkler 1986). Optical methods, such as scanning electron microscopy (SEM), provide an image of surface degradation but fail to detect loss below the observed surface. Nuclear magnetic resonance (NMR) effectively measures pore size distribution (Alesiani et al. 2000). Unfortunately, SEM and NMR require destruction of the sample. Although ion measurements of water runoff and acid extraction establish the degree of weathering, they provide neither an understanding of the depth of degradation, nor of the effects of crust formation. Acoustic wave velocity provides information about discontinuities in the stone and has the advantage of being nondestructive. Papida, Murphy, and May (2000) monitored physical and chemical deterioration of limestone using this technique and found that changes in ultrasonic velocity were related to porosity, dry density, and surface hardness of the stone.

The novel application of micro-computed tomography (micro-CT) can provide a useful tool as a means of nondestructively analyzing the processes involved in the deterioration of limestone materials. Figure 9.6 shows an image of a limestone surface captured by integrating cross-sectional scans of the sample. The micro-CT yielded quantitative information about material changes on the exterior and in the interior of the stone. The use of tomography provided precise information about changes in the volume of material both on the stone surface and at exact locations inside the stone.

EFFECTS OF AIR POLLUTION

Urban air pollution is rich in both nitrogen dioxide and sulfur dioxide. These pollutants are mainly derived from fossil fuel combustion, and are transported via wind (dry deposition) or water (wet deposition) to stone surfaces (Saiz-Jimenez 1993). Dry deposition of nitrogen and sulfur dioxides on stone occurs when gas particles transfer directly onto a surface. Dry deposition is primarily dependent on physical characteristics of the stone such as surface structure and alkalinity (Grossi, Murray, and Butlin 1995), and on environmental factors such as surface temperature, relative humidity, and wetness (Spiker et al. 1995). Henriksen (1995) found that limestones are especially susceptible to dry deposition of sulfur dioxide. Wet deposition of pollutants refers to the transport of gases by aqueous means (e.g., rain, snow

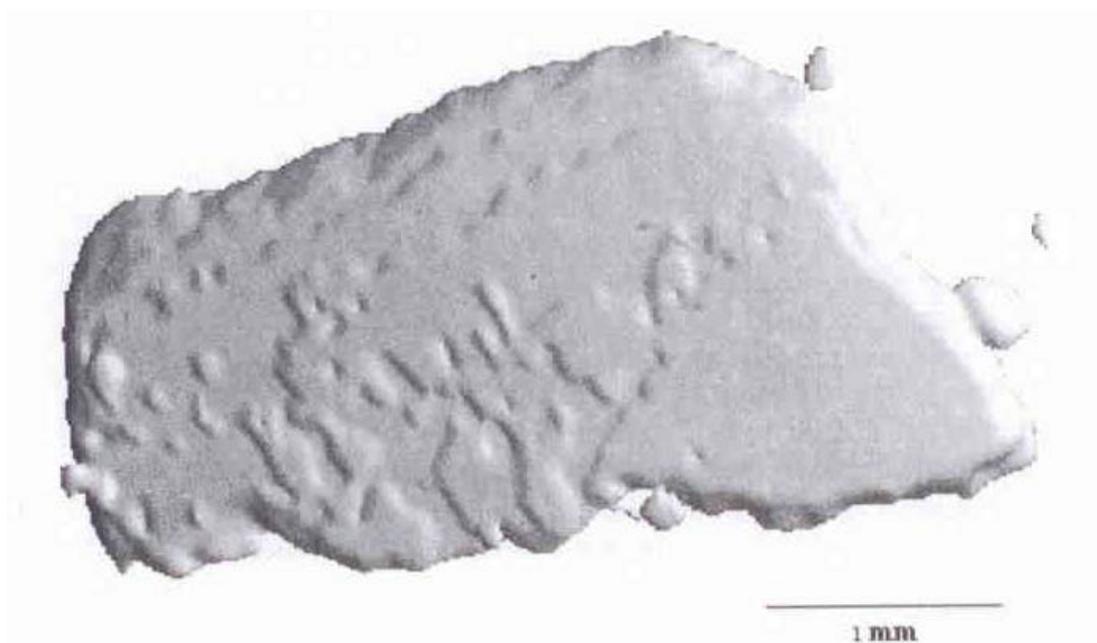


FIGURE 9.6. An image of a limestone surface captured by integrating micro-CT cross-sectional scans of the sample.

or fog). In the case of calcareous stones, the physical and chemical composition of acid rain accelerates the solubility rate of calcium, thereby rendering the stone weak and friable. Kucera et al. (1995) proposed that the dry deposition of these pollutants may be more harmful than wet deposition. In both types of deposition, the pollutants are oxidized—forming nitric and sulfuric acids (Yerrapragada et al. 1996) that react with the stone as described in reactions (1) and (2) above.

Microorganisms are also able to produce acids as metabolic products. Almost all microorganisms secrete organic acids. These acids are frequently responsible for stone solubilization and are capable of complexing cations. Production of extracellular polysaccharides in biofilms can concentrate these acids in close proximity to the stone substratum (Sand and Bock 1991). The acid interaction with the stone causes formation of salts. Dehumidification results in an increase of solid salts that accumulate at the stone surface. These salts can exert physical pressure on the surface, which results in exfoliation of the material (Arnold 1985).

The reaction of stone carbonate with sulfuric acid from chemical or biological sources causes the formation of gypsum. Gypsum crystals combine with dust, aerosols, and other atmospheric particles to form black or brown sulfated crusts. The composition of these crusts varies and is dependent on the particular airborne pollutants in individual areas (Saiz-Jimenez 1993). The chemistry involved in the formation of these crusts is still not fully understood. Gypsum may temporarily passivate the limestone, but the crusts

ultimately exfoliate and cause extensive deterioration (Gauri and Holdren 1981). Gypsum can also be formed through microbial interaction with atmospheric pollutants and limestone.

Chemolithotrophic organisms are capable of oxidizing reduced sulfur and nitrogen from air pollution to form sulfuric and nitric acids, respectively; the resultant acids solubilize the stone (Gu, Ford, and Mitchell 2000a). These acids degrade the stone as described in reactions (1) and (2). We have found that sulfur-oxidizing bacteria of the genus *Thiobacillus* colonized weathered surfaces of marble in a polluted area (Mitchell and Gu 2000). These bacteria, through production of sulfuric acid, cause degradation of acid-sensitive materials including limestones and concrete (Gu, Ford, and Mitchell 2000a; Gugliandolo and Maugeri 1990; Sand 1994). Nitrifying chemolithotrophic bacteria are able to derive energy by oxidizing nitrogen-containing inorganic substrates (Mansch and Bock 1996), which ultimately results in the formation of nitric acid. Mansch and Bock (1996) investigated biogenic nitric acid attack on stone and compared it to the effects of a smoggy atmosphere. Their studies indicated that microbiologically-formed nitric acid corrosion was eight times more harmful than the corrosion caused by smog.

Air pollution is involved in the deterioration of Maya archaeological materials. While air pollution levels in rural Mexico (e.g., Chichén Itzá and Uxmal) are low compared to urban centers (e.g., Mexico City), there is site-specific pollution from diesel tour buses and other localized sources. This pollution can elicit the same effects as wide-spread pollution. Steps need to be taken to minimize the deterioration of these important sites.

PREVENTATIVE MEASURES

Microorganisms can persist in dry environments. Active metabolism, however, requires appropriate levels of relative humidity and temperature. A combination of low humidity and low temperature is the simplest way to control microbial growth, but this treatment may not control fungi (Gu, et al. 1998b) and is impractical in the climate of southern Mexico. Biofilm bacteria respond differently to biocides than planktonic bacteria. Biofilms protect microorganisms from biocides because mass transfer is diffusion limited within the biofilm (Cargill and Pyle 1992; Liu et al. 1998; McFeters et al. 1995; Stewart 1996). Regular cleaning may be the most effective treatment for preventing biofilm formation and subsequent biodeterioration of materials; however, this approach is not practical for large structures.

Microbial biocides are commonly used to control unfavorable biofilm formation. Figure 9.7 shows the fungus *Penicillium pinophilum* being

controlled by different concentrations of a commercial biocide, Proxel GXL (19.3% 1,2-besisothiazolin-3-one; Zeneca Inc., Wilmington, Del.) soaked into a paper disk on solid growth medium. Biocides are widely used in commercial and industrial products. Because microorganisms are capable of quickly acquiring chemical resistance, no one chemical can be relied on for long-term use; frequently, several chemicals need to be combined and/or concentrations need to be increased in order to achieve effective eradication of microbial populations. An environmentally acceptable and practical treatment needs to be developed.

Consolidants have been used for some time to conserve archaeological stone from biological and chemical weathering. Consolidation is used as a means of generating structural strength in a disintegrating material. It is an artificial means of repairing the damage caused by natural processes (Council 1992). A consolidant is applied by spraying, brushing, or injecting it into stone, which binds particles of the stone together to create an impregnated surface layer. Two of the most common types of consolidants used for archaeological stone are ethoxysilanes and acrylic resins. Ethoxysilanes are partly inorganic and partly organic, chemically creating bonds between the molecules through the processes of hydrolysis, condensation, and polymerization (Council 1992). However, ethoxysilanes only enhance the bonds of relatively sound silicate materials because they cannot bridge gaps or hollows between stone particles. Acrylic resins act as consolidants by penetrating inside the pores and coating loose particles. A chemical reaction normally does not take place between the polymer and the material; rather, strengthening is obtained by setting of the resin during solvent evaporation.

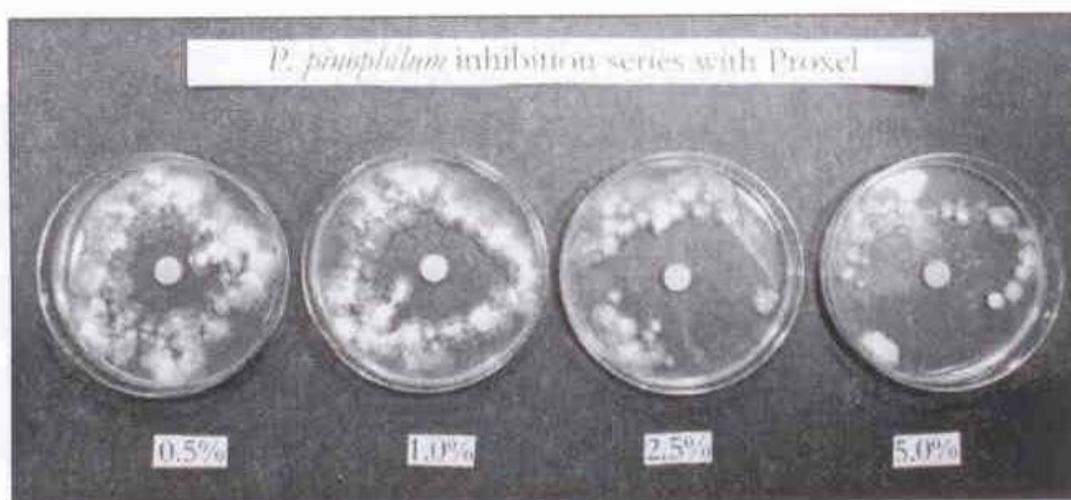


FIGURE 9.7. A test showing control of a fungus, *Penicillium pinophilum*, by different concentrations of a commercially available fungicide, Proxel GXL.

The efficacy of consolidants on outdoor stone is controversial because they can upset the natural saturation and evaporation of moisture from within the stone, often resulting in exfoliation and cracking of stone surfaces (Boyes 1997). Also, application of consolidants is not easily reversible, which is a serious drawback when dealing with ancient monuments. Some consolidants may also discolor as they degrade due to aging, photochemical processes, and oxidation (Biscontin, Frascati, and Marchesini 1976; Gonzalez 2000). Consolidants can also be susceptible to biodegradation (Koestler et al. 1994; Young, Murray, and Cordiner 1999). A wide range of consolidants has been tested for effectiveness to protect Maya limestone in Belize (Kumar and Ginell 1995), and most of the polymers tested proved to be susceptible to microbial degradation under local environmental conditions of the Yucatán.

Although problems associated with the use of consolidants for the protection of archaeological stone are numerous, they still are one of the only means of preventing the disintegration of stone grains due to exposure and weathering. The addition of a biocide to a consolidant would help to prevent microbial degradation, thus helping to insure the longevity of the treatment. There are also commercially available and environmentally acceptable biocides that could be used as additives in consolidants. Future research in this area is necessary.

CONCLUSION

The structures of the Maya archaeological sites at Uxmal and Chichén Itzá in the Yucatán Peninsula are at risk from microbial degradation. The high temperature and humidity of the region serve to stimulate metabolic activity of microbial biofilms. The degradation process will be accelerated in the coming years by tourism and atmospheric pollution. Microbial biofilms can be controlled by biocides, and Maya structures can be stabilized by the use of polymeric consolidants. However, both conventional biocides and consolidants are susceptible to degradation by the biofilm microflora in the environmental conditions normally found at Uxmal and Chichén Itzá. New approaches to conservation of these important cultural sites will require the use of environmentally acceptable treatments that are capable of resisting the microflora stimulated by the high temperatures and relative humidity of the Yucatán region.

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Chapter 10

Impacts of Hurricanes on the Forests of Quintana Roo, Yucatán Peninsula, Mexico

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Edgar Cabrera Cano
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INTRODUCTION

Hurricanes are common throughout the Caribbean (Alaka 1976; Vega and Binkley 1993), and they often cause extensive disturbance to forests (Walker et al. 1991; Yih et al. 1991; Smith et al. 1994; Zimmerman et al. 1994; Bellingham, Tanner, and Healley 1995; Bellingham et al. 1996; Foster, Fluet, and Bosse 1999; Stoddart 1963). Within the Caribbean, the Maya zone (southeastern Mexico, Belize, and portions of Guatemala) is an area that has been impacted by many hurricanes (López 1983; Konrad 1996). In fact, the most severe hurricane ever recorded in the Caribbean (Hurricane Gilbert) occurred in the Maya zone (Whigham et al. 1991).

Several recent studies have focused on the impacts of hurricanes in the Caribbean as well as the short-term and long-term recovery of forests

Our research has benefited from the efforts of many colleagues and volunteers who assisted with our measurements. We are especially indebted to our deceased colleague Jim Lynch, whose interests and support led to the establishment of our long-term study plots at Rancho San Felipe. We are also indebted to our deceased friend Patricia Zugasty Towle and to Felipe Sanchez Roman for allowing us to establish the plots on their property. Funding for our research came from the World Wildlife Fund (U.S.) and the Smithsonian Institution's International Environmental Sciences, Environmental Studies, and Research Opportunities programs. Jay O'Neill reviewed and improved earlier drafts of the manuscript.

following hurricane damage. A special issue of *Biotropica* (Walker et al. 1991) was devoted to impacts of hurricanes in the Caribbean, and several papers in a second special issue (Walker et al. 1996) dealt with recovery of forests from hurricane damage (e.g., Scatena et al. 1996; Vandermeer et al. 1996). Other investigators have also focused on the recovery of Caribbean and Central American forests from hurricane damage (Dallmeier, Comiskey, and Scatena 1998; Granzow de la Cerda et al. 1997; Reilly 1998; Rogers and Reilly 1998; Weaver 1998a; Whigham and Lynch 1998; Vandermeer, Granzow de la Cerda, and Boucher 1997; Vandermeer, Brenner, and Granzow de la Cerda 1998).

A general consensus seems to be that the species composition of hurricane-damaged forests changes little (Bellingham, Tanner, and Healley 1995; Walker, Zimmerman et al. 1996b; Harrington et al. 1997; Frangi and Lugo 1998; Reilly 1998; Whigham and Lynch 1998), even though severely damaged areas are often invaded by herbs, vines, *Carica papaya*, and *Cecropia* sp. (Dallmeier, Comiskey, and Scatena 1998). Vandermeer et al. (1996) suggested that hurricanes maintain species diversity by decreasing competition in a density-independent manner. Ecological processes (e.g., rates of tree growth and annual litter production) also appear to return to pre-disturbance levels within relatively few years following hurricane damage (see Scatena et al. 1996; Vandermeer, Granzow de la Cerda, and Boucher 1997; Reilly 1998; Whigham and Lynch 1998).

In this chapter, short-term and long-term studies of forests damaged by Hurricane Gilbert (1988) and Hurricane Roxanne (1995) will be summarized. Both hurricanes impacted forests on the Caribbean coast of the northern Yucatán Peninsula, an area that is part of the Maya zone. One objective is to demonstrate that the primary long-term impact of Hurricane Gilbert was a decrease in the basal area of live trees, which will take decades to reach pre-hurricane levels because of slow rates of tree growth. Additionally, data from a long-term study of marked trees in permanent plots are used to demonstrate that the recovery of ecological processes was relatively fast. Long-term mortality appeared to be independent of the degree of hurricane damage, and changes in species composition were minimal. We discuss similarities and possible differences between hurricane damage to forests in Quintana Roo, Mexico, compared to other forests in the Caribbean region and in Central America will be discussed. Finally, we suggest that the direct impacts of hurricanes are potentially less important than the effects of subsequent fires—a phenomenon that may be especially important in dry tropical forests.

HURRICANES ON THE YUCÁTAN PENINSULA

The Yucatán Peninsula is impacted primarily by hurricanes that originate in the Atlantic Ocean, the Caribbean, and the southern Gulf of Mexico. Hurricanes that have their origin in the Pacific Ocean impact portions of southeastern Mexico, but rarely cause significant damage in the Yucatán Peninsula (hereafter called “the peninsula”). Between 1871 and 1999, 52 hurricanes struck the peninsula; most impacted the northern portion of the peninsula and the Caribbean coast (Konrad 1996; Pereira and Vester 2000). Most hurricanes that had their origin in the Caribbean have traversed the peninsula and continued into the Gulf of Mexico.

Figure 10.1 we show the trajectories of the two hurricanes that impacted forested areas studied: Hurricane Gilbert in September 1988, and Hurricane Roxanne in October 1995. Table 10.1 we compare the characteristics of Gilbert and Roxanne with the 18 hurricanes that hit the peninsula since 1886 within a 100-kilometer (km) radius of Puerto Morelos (Jordan-Dahlgren and Rodríguez-Martínez in press), a coastal village near our primary study site. All category H3-H5 hurricanes have hit the peninsula after 1950.

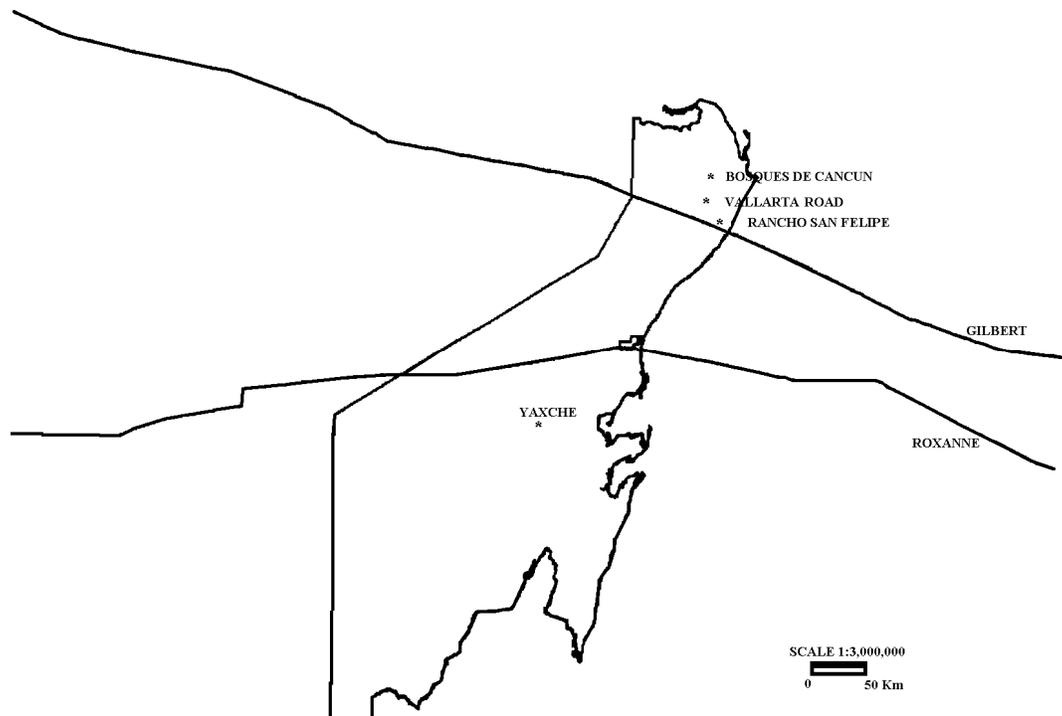


FIGURE 10.1. Outline map of Quintana Roo, Mexico, showing the tracks of Hurricane Gilbert (1988) and Hurricane Roxanne (1995). The location of the study sites described in the paper are also shown (modified from Vester & Olmsted 2000).

TABLE 1. Summary data for Hurricane Gilbert, Hurricane Roxanne, and 18 other hurricanes that impacted the northern part of the Yucatán Peninsula since 1886

Variable	Gilbert	Roxanne	Others
Category	H5	H3	(6) H1, (10) H2, (2) H3
Maximum wind speed (km hr ⁻¹)	300–340	186	156
Lowest eye pressure (mb)	892	958	970
Diameter of eye (km)	20	27	No data

Source: From Jordan-Dahlgren and Rodriguez-Martinez in press.

Gilbert was the only hurricane to reach category 5, and it impacted the northern part of the peninsula. Hurricane Gilbert had, by far, the highest recorded wind speeds and the lowest barometric pressure in the eye of the hurricane (Table 10.1). Wind speeds associated with Hurricane Roxanne were also higher than average, and the barometric pressure in the eye of the hurricane was slightly lower than the average values for the other 18 hurricanes.

METHODS

Study sites damaged by Hurricane Gilbert

The impacts of Hurricane Gilbert have been monitored at Rancho San Felipe, located on the Caribbean coast approximately 10 km south of Puerto Morelos (Quintana Roo). This study site is located about 2 km from the coast; based on annual precipitation, the forest would be classified as medium-statured semievergreen (Miranda 1958), or dry or very dry in the Holdridge system (Whigham et al. 1990). Twelve plots, each 40 m by 40 m, were established in 1984, and all stems ≥ 10 cm dbh (i.e., diameter at breast height) at a height of 1.5 meters (m) were marked and identified. All marked trees have been measured annually since 1984 during the months of January and February. We used the yearly census data to determine annual mortality. Mortality reported for any one year (e.g., 1989) represents trees dying during the preceding 12 months (e.g., between the 1988 and 1989 census). In-growth in 1993 and 2000 was determined by marking and identifying all new stems ≥ 10 cm dbh. In addition to tree growth and mortality, annual litter production

was measured between 1984 and 1991 (Whigham et al. 1991; Whigham and Lynch 1998).

The immediate impacts of Hurricane Gilbert (September 1988) were evaluated within two weeks by scoring the amount of damage incurred by each marked tree in the 12 plots. We assigned each tree to one of six damage classes: (1) crown completely removed but the trunk not snapped; (2) only larger branches remaining; (3) most large branches remaining; (4) only twigs and small branches remaining; (5) trunk snapped; and (6) tree uprooted. At the time of the first census, we could not locate a few tagged trees; eventually, all trees were found and damage was categorized during subsequent sampling periods. In February 1989, the amount of coarse woody debris in the plots was measured for comparison between pre-hurricane and post-hurricane conditions (Harmon et al. 1994).

Beginning in March 1989, extensive fires (135,000 hectares [ha.] in northern Quintana Roo) occurred throughout much of the area impacted by Hurricane Gilbert. Some fires were contained locally, and all remaining fires were extinguished by rain in August 1989. At Rancho San Felipe, the site was protected the site except for small areas of two plots that were burned when fire jumped the fire lane. In 1990, we sampled all live trees ≥ 10 cm dbh in four plots, each 40 m x 40 m, in a burned area within 500 m of our study plots.

In January 1990, six additional plots (each with a total area of 1,600 m²) were established in other areas impacted by Hurricane Gilbert. One set of three plots was about 8 km west of Rancho San Felipe along the Vallarta Road. Two of these plots were in a burned area, and the third was a control plot in an adjacent unburned area. The other three plots were established at a site known as Bosques de Cancun, about 25 km inland from the Cancun Airport and 40 km northwest from Rancho San Felipe. Two plots at Bosques de Cancun were established in an area where some trees survived the fire, and the third plot was in an unburned area. In each plot, all living and dead trees ≥ 10 cm dbh were identified, and dbh and height were measured.

Study site damaged by Hurricane Roxanne

In October 1995, the semievergreen forest near Felipe Carrillo Puerto was hit by strong winds just outside the eye of Hurricane Roxanne. Felipe Carrillo Puerto is located in Quintana Roo, about 200 km south of Puerto Morelos. Five years after the hurricane, an area—locally known as Yaxche—that was about 40 km from the coast (see Figure 10.1). The forest at Yaxche was younger than the forest at Rancho San Felipe, based on the abundance or absence of some species as well as the lower basal area of trees ≥ 10 cm dbh (approximately 20 m² ha.⁻¹). *Bursera simaruba*, a common species of early

successional sites was very abundant at Yaxche, while a species typical of older forests (*Brosimum alicastrum*) was absent. In addition, there was only one stem ≥ 10 cm dbh of *Manilkara zapota*, a species that is also common in older forests. Four species (*B. simaruba*, *Coccoloba spicata*, *Gymnanthes lucida*, *Thouinia paucidentata*) were among the ten most abundant species at the Rancho San Felipe and Yaxche sites, and a Sorenson Index of Similarity (45 percent) indicates that the two forests had many similar characteristics. The Sorenson Index would have been greater had more plots been samples at Yaxche. In March 2000, five years after Hurricane Roxanne occurred, 25 plots, each 10 m by 10 m, were sampled and identified and the diameter of all trees that had a dbh ≥ 10 cm. were measured. The amount of damage that had been done to each tree was recorded using the categories applied at Rancho San Felipe.

RESULTS

Hurricane Gilbert

Hurricane impact

The immediate impacts of Hurricane Gilbert at Rancho San Felipe on birds (Lynch 1991) and plants have been previously documented (Whigham et al. 1991; Harmon et al. 1994) and are summarized here. First, it is important to note that the Rancho San Felipe site is located within 2 km of the coast and was impacted by the full force of the most intense storm ever recorded in the region (see Table 10.1). The impacts of Gilbert on the forest at Rancho San Felipe should thus be considered to be at the upper end of the range of disturbances associated with hurricanes (Whigham, Dickinson, and Brokaw 1999).

The forest canopy was completely defoliated, and all marked trees were damaged. The majority of trees sustained structural damage, and approximately 30 percent of the trees were uprooted, had snapped trunks, or had most of the major branches removed (Whigham et al. 1991). Seventeen months after the hurricane, 155 (10.7 percent) of the marked trees had died, including 15 (9.3 percent) that were killed by fire that burned parts of two plots. Trees not killed by fire (90.7 percent) occurred in all damage categories, but most (54.6 percent) were in only the three damage categories listed previously (Whigham et al. 1991). Mortality also occurred in all sizes of trees (data not shown). Mortality resulted in a decrease of the basal area of trees in the 12 plots from 26.9 ± 0.9 (1 standard error, SE) $\text{m}^2 \text{ha}^{-1}$ in 1988 to 24.1 ± 0.7 $\text{m}^2 \text{ha}^{-1}$ in 1989 and 22.4 ± 0.8 $\text{m}^2 \text{ha}^{-1}$ in 1990 (Figure 10.2).

Two species were eliminated from the population of marked trees by the hurricane, and both had only one marked individual in the plots. The trunk of the single 23.5 cm dbh *Senna racemosa* snapped in the hurricane, and a 12 cm dbh *Amyris elemiflora* was uprooted.

Defoliation of the forest canopy resulted in the transfer of more than 800 g m⁻² of litterfall, mostly green leaves, to the forest floor—an amount approximately twice the annual litterfall measured in the four prehurricane years (Whigham et al. 1991). Because most of the litterfall consisted of green leaves, the concentrations of nutrients in litterfall and the total amounts of nutrients transferred to the forest floor were higher than any of the previous pre-hurricane years (Whigham et al. 1991). The biomass of coarse wood transferred to the ground was also massive (> 4000 g m⁻²) and represented almost a doubling of the coarse woody debris that was present prior to the hurricane (Harmon et al. 1994).

Initial recovery

Some aspects of recovery have been reported (Whigham and Lynch 1998), and other data are presented in this paper. Compared to other tropical

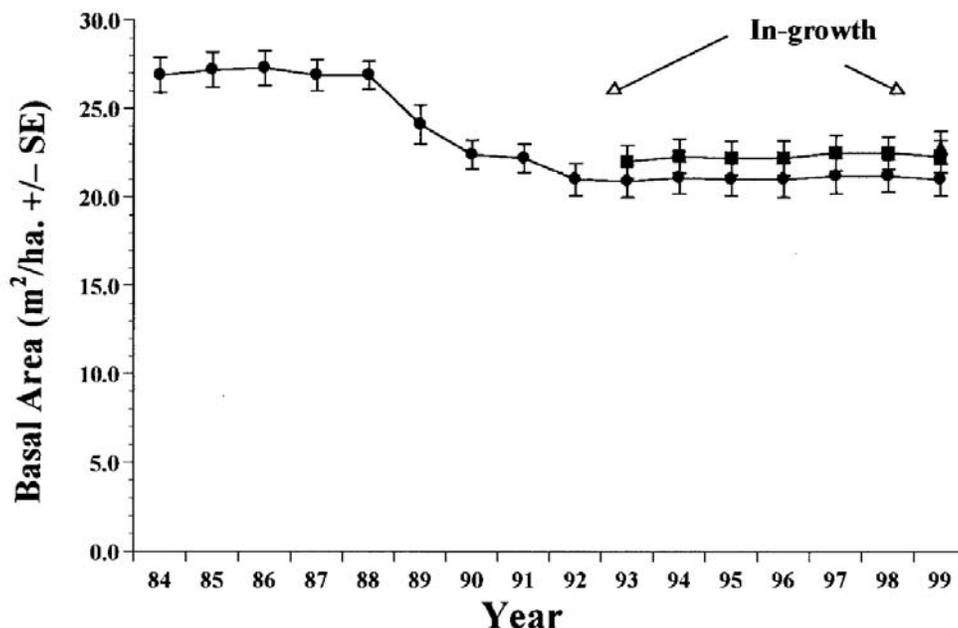


FIGURE 10.2. Total basal area (m²ha.⁻¹) for 12 plots at Rancho San Felipe. Values are means ± 1 standard error (SE). Data are separated into the original group of trees that were marked in 1984 and in-growth measured in 1993 and 2000.

forests, mortality rates of canopy trees in Yucatán forests are very low (Whigham et al. 1990; Dickinson, Whigham, and Hermann 2000). Thirty-nine (2.6 percent) of the marked trees died in the four years prior to Hurricane Gilbert, and mortality appeared to be inversely related to the total annual precipitation (Whigham et al. 1990). Mortality associated with Hurricane Gilbert was greater, especially within the first five years of the disturbance, and the mortality pattern was consistent among the damage classes (Figure 10.3). Mortality was low in 1989 for all damage classes except trees that were uprooted. Mortality of uprooted trees decreased after 1989 and reached prehurricane rates by 1993. Mortality rates were also higher in the “crowns removed” and “trunk snapped” damage categories and—similar to other damage categories—varied from year to year, with the highest rates measured in 1990 and 1993.

Mortality resulted in the loss of seven more species of marked trees between 1989 and 1992. All but one species (*Daphnopsis americana*) had a single marked stem. Two species were eliminated in 1989 (*Coccoloba swartzii*, *Bunchosia swartziana*), one species in 1991 (*Platymiscium yucatanensis*),

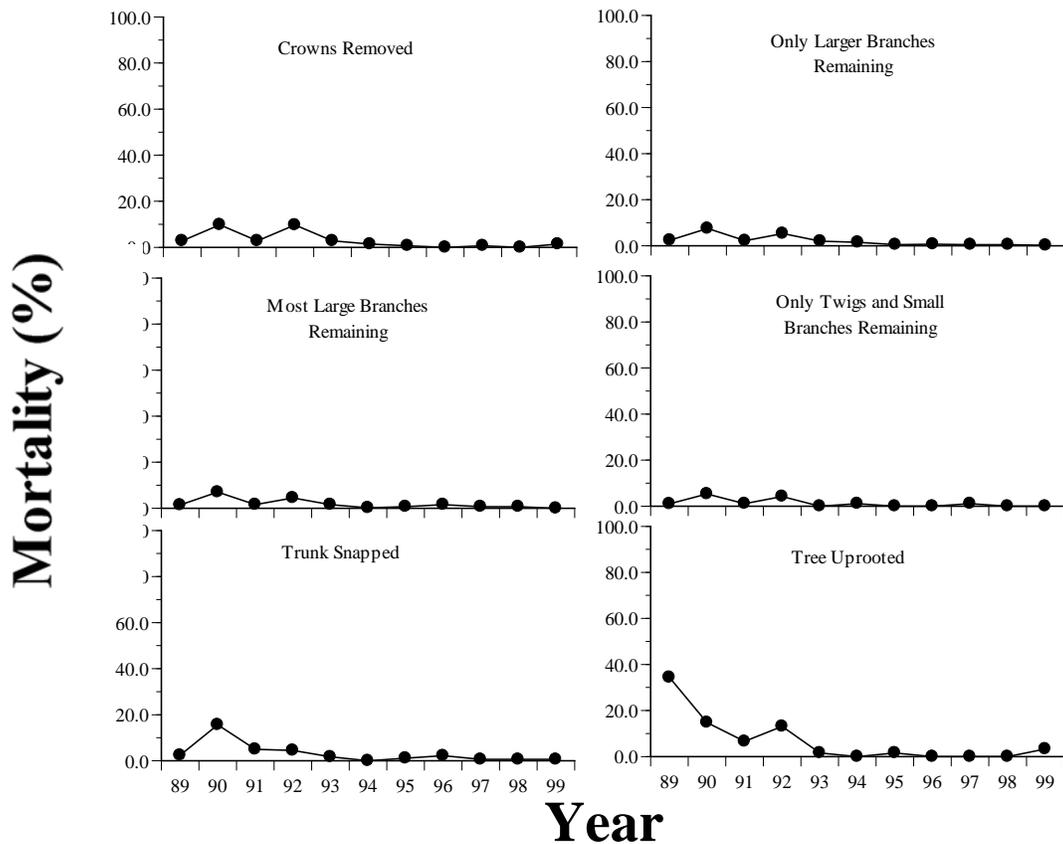


FIGURE 10.3. Mortality of trees in six damage categories described in the Methods section. Mortality for each damage category was calculated as follows: Number of trees that died each year = Number of trees in the damage category in 1998 x 100.

and three species in 1992 (*Protium copal*, *Coccoloba* sp., *Casearia nitida*). One individual of *D. americana* died in 1989, and the second in 1991. Stems of the seven species ranged in size from 10 to 24.4 cm, and they were in damage classes 2, 3, 5, and 6. An unexpected result was the elimination from the permanent plots of 98 percent of all tree-sized individuals of *Brosimum alicastrum*, a widespread and common species (Whigham and Lynch 1998).

Based on prehurricane data, a significant negative relationship was found between annual litterfall and annual precipitation, demonstrating that more leaves were shed during years with lower precipitation (Whigham et al. 1990). Following the hurricane, annual litterfall was less than pre-hurricane levels, but we continued to find a significant negative relationship between litterfall and annual precipitation (Whigham and Lynch 1998). This result suggests that there was little impact of the hurricane on annual litterfall, even though there must have been less total leaf biomass in the forest canopy during the first few posthurricane years. Total phosphorus in the leaf litter reached prehurricane levels within two years of the hurricane because the concentration of phosphorus in leaf litter was higher compared to pre-hurricane years (Whigham and Lynch 1998).

Relative basal area growth one year after the hurricane (1989) was greater than the rates that had been measured in all but two of the five pre-hurricane years (Figure 10.4). Relative growth rates were slightly lower in 1990 and 1991 and increased in 1992 and 1993. The characteristic low rates of tree growth at Rancho San Felipe (Whigham et al. 1990) resulted in no noticeable increase in the basal area of live trees during the first five years following the hurricane, even when in-growth was included in 1993 and 2000 (see Figure 10.2.)

Ten years and beyond

After 1993, our study at Rancho San Felipe was limited to measurements of the marked trees. Tree mortality returned to pre-hurricane levels by 1994, and they have not changed measurably since then (see Figure 10.3). Because of low tree growth rates, the total basal area of live trees also has changed little since 1994 (see Figure 10.2).

Three additional species were eliminated after 1993 as tree-sized individuals. Similar to previous years, species that were eliminated (*Bauhinia divericata*, *Hampea trilobata*, *Lonchocarpus rugosus*) had very few marked individuals ($n = 2-3$) and represented a range of sizes (10.4–21.9 cm) and damage classes (1–6). One of the marked trees belonging to *B. divericata* died in 1990, and the last remaining tree from this species died in 1993. Three individuals of *H. trilobata* died between 1988 and 1993, while three individuals of *L. rugosus* died between 1994 and 1996.

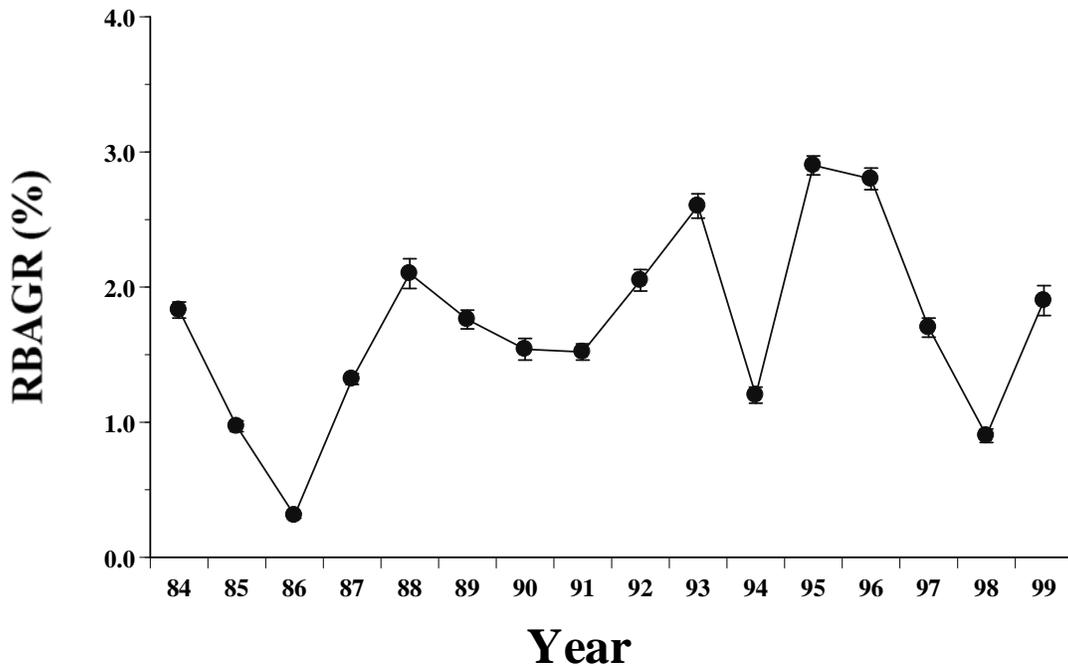


FIGURE 10.4. Relative basal area growth (RBAGR) for all trees in the 12 plots at Rancho San Felipe. Values are means \pm 1 standard error (SE). $RBAGR / (BA_{t+1} - BA_t) = BA_t \times 100$

Seven new species were identified and marked as part of the in-growth measurements in 1993, and another genus (*Agonandra* sp.) was added in 2000. Species added in 1993 were *Ardisia escallonioides*, *Cecropia peltata*, *Jatropha gaumeri*, *Malpighia glabra*, *Neomillspaughia emarginata*, *Pithecellobium dulce*, and *Pouteria campechiana*. All new species were present as single individuals except for *C. peltata*, which was almost completely restricted to portions of two plots that had burned. *Cecropia* and a few other short-lived species that did not reach tree size (e.g., *Carica papaya*, *Cnidocolus aconitifolius*) also invaded non-burned plots, but the number of individuals was small and they all were short-lived.

Fire impacts

The fires that followed Hurricane Gilbert were extensive and resulted in widespread damage to the forests. The damage ranged from the death of all trees in some areas to no fire-related death in areas where fires had been suppressed. At Rancho San Felipe, attempts were made to keep fire from entering the plots by cutting fire lanes around the site and by actively suppressing the fire with water. Fire jumped the fire lane at two locations, resulting in the death of 15 trees in two of the study plots. There were between 15 and 57.5 trees ha^{-1} (average = 42) in the four plots that we sampled in a burned area within 500 m of the Rancho San Felipe plots. By comparison, the

density of trees ha^{-1} in the 12 plots at Rancho San Felipe was 768 ± 23 (SE). The basal area of live trees in the four burned plots was $2.6 \pm 0.9 \text{ m}^2 \text{ ha}^{-1}$, approximately 10% of the values measured in the 12 unburned plots (see Figure 10.2).

Most of the burned plots had a dense growth of bracken fern (*Pteridium aquilinum*) as well as a few short-lived shrub species that are common in abandoned milpas and other disturbed habitats (e.g., *Solanum erianthum*, *Pluchea odorata*). A few seedlings of short-lived successional trees (e.g., *Cecropia peltata*, *Carica papaya*) were also present. Most of the fire damage sustained by the trees was restricted to the base of the stems and the roots. Most of the soil in the plots had completely burned.

In January 1990, we measured two forested areas further inland from Rancho San Felipe (Olmsted et al. 1991). At the Vallarta Road site, the unburned control plot had a basal area of $27.3 \text{ m}^2 \text{ ha}^{-1}$, a value similar to the basal area of the Rancho San Felipe plots (see previous discussion and Figure 10.2). In contrast, the basal area of live trees in two burned plots was much less, 2.4 and $6.7 \text{ m}^2 \text{ ha}^{-1}$. The total basal area of dead standing trees in the burned plots was $24.0 \text{ m}^2 \text{ ha}^{-1}$. The impact of the fire was less severe at the Bosques de Cancun site (Olmsted et al. 1991). Total basal area of live and dead trees in the unburned plot was 24.8 and $2.9 \text{ m}^2 \text{ ha}^{-1}$, respectively. In the two burned plots, the basal area of live trees was 11.2 and $8.3 \text{ m}^2 \text{ ha}^{-1}$; the basal area of dead trees was 14.2 and $10.7 \text{ m}^2 \text{ ha}^{-1}$.

Hurricane Roxanne

Hurricane impact

Hurricane Roxanne had lower maximum wind speed and higher barometric pressure than Hurricane Gilbert (Table 10.1). The impacts of Roxanne would, therefore, be expected to be less damaging than those associated with Gilbert. The Yaxche site impacted by Roxanne was sampled five years after the hurricane (Vester and Olmsted 2000). There were 294 live and dead trees in the 25 plots, and hurricane-related damage could still be recognized on 132 (44.9 percent) trees.

Most of the trees that could not be placed into damage categories (162; 55.1 percent) were in the lowest damage category used at Rancho San Felipe (i.e., “only twigs and small branches remaining”). By comparison, trees in the lowest damage category at Rancho San Felipe only accounted for 7.3 percent of the damaged trees (Whigham et al. 1991). For the 132 damaged trees at Yaxche that could be categorized, three damage categories (“tree uprooted [n = 19; 14 percent],” “trunk snapped” [n = 21; 16 percent], “crown removed” [n = 33; 25%]) accounted for 55 percent of the trees. The same damage categories at Rancho San Felipe accounted for 27.6 percent of the damaged trees (Whigham et al. 1991). Two intermediate damage categories (“only larger branches remaining,” “most large branches remaining”) accounted for

45 percent of the trees at Yaxche compared to approximately 70 percent at Rancho San Felipe (Whigham et al. 1991).

At Yaxche, 18.2 percent of the trees in the “crown removed” category, 52 percent of the trees in the “trunk snapped” category, and 58 percent of the trees in the “tree uprooted” category were dead after five years. A smaller percentage of trees (9.7 percent) were in two intermediate damage categories (“only larger branches remaining,” “most large branches remaining”). In comparison with Rancho San Felipe, a higher percentage of trees at Yaxche were in the lowest damage category, but a higher percentage of trees died in the highest damage categories.

DISCUSSION

Permanent plots at Rancho San Felipe have been monitored for four prehurricane and 11 posthurricane years and three other areas have been sampled in northern Quintana Roo that were damaged by hurricanes. Sánchez Sánchez and Islebe (1999) also sampled an area near Rancho San Felipe that was damaged by Hurricane Gilbert. The immediate impacts of Hurricane Gilbert were clearly detectable, but the long-term impacts have been minimal.

There have been few short-term or long-term studies of hurricane impacts on the peninsula, but comparisons can be made among the few studies that have been conducted. It also seems appropriate to compare results from studies on the peninsula with those conducted elsewhere in the Maya zone, along with studies in a range of forest types that have been conducted elsewhere in the region (e.g., Caribbean islands, Florida, and Nicaragua). An obvious similarity between forests on the peninsula and elsewhere is that there are many similar short-term impacts. There has been an increase in litter, coarse woody debris, and increased tree mortality everywhere that hurricane impacts have been measured (e.g., Whigham et al. 1991; Harmon et al. 1994; Scatena et al. 1996; Rogers and Reilly 1998; Weaver 1998b).

Similar to other forests, hurricane damage to forests in northern Quintana Roo (Olmsted et al. 1991; Snook 1993; Sánchez and Islebe 1999; Vester and Olmsted 2000) and elsewhere in the Maya zone (Stoddart 1963) is spatially variable. The forest at Rancho San Felipe suffered severe damage. However, given the intensity of Hurricane Gilbert, it would be expected that the damage would have been even greater. Even as far inland as Yaxche (see Figure 10.1), Roxanne, a less intense hurricane than Gilbert, caused sufficient damage to be noted five years after its occurrence. In fact, the percentage of trees in the highest damage classes (i.e., crown removed, trunk snapped, and tree uprooted) was higher in Yaxche than at Rancho San Felipe. The percentage of trees that died during the first five years after the hurricane in the three

highest damage classes was also higher at Yaxche. Elsewhere in the Caribbean, portions of forests in Jamaica (Bellingham 1991), Nicaragua (Vandermeer et al. 1996), and St. John Island (Weaver 1998a) were more severely damaged by hurricanes that were less intense than Hurricane Gilbert. Several factors could possibly contribute to lower levels of hurricane damage to forests on the northern Yucatán Peninsula. First, hurricanes are very common on the peninsula (Konrad 1996). Forests that experience repeated hurricane disturbance might be expected to have lower average canopy heights; the lower the canopy, the less severe the impacts of a hurricane. Second, the peninsula is a very flat landscape, and forests would not experience the extreme levels of damage associated with topographically complex areas (e.g., Caribbean islands and mountainous areas further south in Central America). Forests appear to be most heavily damaged when they are located on elevated ridge crests, topographically exposed areas, and in valleys where hurricane winds are funneled (Bellingham 1991; Reilly 1998).

Other factors may also be partially responsible for lower-than-expected levels of hurricane damage following Hurricane Gilbert. Soils in the northern part of the peninsula are typically very shallow. Soil depth in the permanent plots at Rancho San Felipe averaged less than 20 cm (Whigham and Cabrera 1991), and most soil occurred in depressions between exposed limestone rocks. Therefore, trees have very shallow root systems that are interwoven and anchored to the fissured limestone. The percentage of trees that were uprooted at the Rancho San Felipe site (4.5 percent) was low compared to the percentage of trees with snapped trunks (12.4 percent). Dallmeier, Comiskey, and Scatena (1998), as well as Everham and Brokaw (1996), also found that uprooting in other forests was less likely to occur when there was root grafting and anchorage to rocks in areas with shallow soils. Low rates of tree uprooting have also been reported for hurricane and fire impacted forests in southern Quintana Roo (Dickinson, Hermann, and Whigham in press).

Within the Maya zone—the Caribbean and Nicaragua—hurricanes appear to have little long-term impact on species composition, unless the forests are burned following the hurricane. Short-term and intermediate-term changes in species composition can, however, be significant in topographically complex landscapes where some portions of the forest are heavily impacted (Lugo et al. 1983; Vandermeer et al. 1996; Dallmeier, Comiskey, and Scatena 1998; Reilly 1998; Rogers and Reilly 1998). At Rancho San Felipe, for example, mortality resulted in the loss of a few species of marked trees, but individuals of other species have reached tree size since the hurricane, resulting in no significant change in species composition. All eliminated species had few individuals, which is a pattern similar to the one found by Reilly (1998) on St. John Island following Hurricane Hugo.

Few, if any, future changes are anticipated in species composition at the Rancho San Felipe site because mortality rates have returned to prehurricane levels (see Figure 10.3). In addition, there was almost no recruitment of new species as seedlings (Whigham personal observation). One interesting impact of Hurricane Gilbert was the complete death of all tree-sized individuals of *Brosimum alicastrum* (Whigham and Lynch 1998). This response was completely unanticipated because trees survived the impact of the hurricane at the Vallarta Road and Bosques de Cancun sites, and *B. alicastrum* is one of the most widespread species in the region (White and Darwin 1995). Perhaps trees at Rancho San Felipe were physiologically impacted by the hurricane (perhaps by desiccation), which, when compared to other hurricanes, had less associated precipitation. The trees died slowly (Whigham and Lynch 1998), and they all regularly produced unsuccessful sprouts between the time of Hurricane Gilbert and their death. The death of the trees that were originally tagged will not, however, eliminate the species from the plots as seedlings and saplings were common, and one individual reached tree-size by the time of the 2000 in-growth census.

With the possible exception of mangroves and palms, a common feature of many hurricane-damaged forests is the ability of surviving trees to produce sprouts on stems and roots (Bellingham 1991; Walker 1991; Scatena et al. 1996). All of the surviving trees in our plots produced stem sprouts, but few species produced root sprouts. Root sprouting may be more common in forests with higher rainfall and a shorter dry season. Reilly (1998), for example, made no mention of root sprouts following Hurricane Hugo in the St. John Island, an area with annual precipitation that is similar to this study's site. Root sprouts were found, in contrast, in wetter hurricane-damaged forests in Nicaragua (Vandermeer, Granzow, and Boucher 1997) and Puerto Rico (Walker 1991). Root sprouts were also common in taller forests in southern Quintana Roo that are impacted by logging activities (Dickinson, Whigham, and Hermann 2000). The amount of sprouting may also be positively related to the amount of damage. *Gymnanthes lucida*, for example, did not sprout at Rancho San Felipe, but sprouts were abundant in the Vallarta Road plots that had been damaged by both Hurricane Gilbert and subsequent fires (Olmsted personal observation).

Following Hurricane Gilbert, herbaceous vines (e.g., *Cionocissus excisus*, *Momordica charantia*) and the short-lived tree *Carica papaya* germinated in the study plots. Overall, however, the plots were invaded by few early successional species—a pattern that differed from many other hurricane-damaged forests that have been studied in the region (Walker 1991; Vandermeer, Granzow, and Boucher 1997; Dallmeier, Comiskey, and Scatena 1998). The presence of a dense layer of leaf litter and branches probably inhibited seed germination (Guzmán-Grajales and Walker 1991), but we found that almost no long-lived tree species emerged from soils that were

collected from the plots and watered regularly in a common garden (data not shown).

Why there were so few tree species in the buried seed bank at Rancho San Felipe; to our knowledge, there have not been any studies of soil seed banks in forests that are similar to those that we have studied (Garwood 1989). Based on Garwood's review, however, several factors might have contributed to low levels of viable tree seeds in the soil. First, Garwood suggested that seed production is low in forests with low production. This factor does not seem to be important at Rancho San Felipe, even though tree growth rates are very low compared to other tropical forests (Whigham et al. 1990). We have noted seed production of many of the tree species at Rancho San Felipe, and seedlings were often abundant for such common species as *Manilkara zapota*, *Myrcianthes fragrans* (Whigham and Cabrera 1991), *Drypetes lateriflora*, and *Brosimum alicastrum*. Many of the species, however, may not produce seeds that remain viable in the soil for long periods of time. Soils also seem to contain more tree species in forests where treefall gaps are commonly produced and where the average gap size is large (Garwood 1989). Both factors are not important at Rancho San Felipe. The rates of treefall creation in Quintana Roo forests appear to be among the lowest reported for tropical forests, and the average gap size is small (Dickinson, Whigham, and Hermann 2000). The dynamics of soil seed banks in forests on the peninsula clearly needs further study as the forests studied by Rico-Gray and Garcia-Franco (1992) in Yucatán state, which mostly had seeds of early successional species, were different from the forest that occur in much of Quintana Roo.

Rancho San Felipe, as well as other nearby sites not impacted by fire, shared a common type of structural change with all other hurricane-damaged forests in the region. The basal area of live trees decreased from approximately 26 to 21 m² ha.⁻¹ at Rancho San Felipe; similar values (27.3 and 24.8 m² ha.⁻¹) were measured at the two other sites that were impacted by Hurricane Gilbert, but had not burned. Unlike most other forests that have been examined, however, the increase in basal area at our site has been minimal. Based on the annual census data and inclusion of in-growth measurements (see Figure 10.2), we have found almost no increase in basal area, and we anticipate that it will take several decades for the forest to return to pre-hurricane levels. The rate of recovery of forest basal area appears to be much lower than the recovery rate that has been reported for other forests where tree growth rates are higher (Dallmeier, Comiskey, and Scatena 1998; Weaver 1998b).

Hurricane Gilbert had no detectable short-term or long-term influence on tree growth. Relative growth rates were higher in the first few post-hurricane years for all trees combined and for some species. Increased growth, however,

was a reflection of higher amounts of rainfall during the same period, rather than a hurricane response (Whigham and Lynch 1998). In contrast, changes in growth rates—either positive or negative—have been found in other hurricane-impacted forests in the region. Reilly (1998) found lower post-hurricane growth rates in St. John Island forests following Hurricane Hugo. Vandermeer, Granzow, and Boucher (1997), as well as Vandermeer, Brenner, and Granzow (1998), found higher growth rates following Hurricane Joan in Nicaragua, especially in forests that had been heavily damaged. Scatena, Moya, Estrada, and Chinaea (1996) also found evidence for high growth rates of trees and understory plants following Hurricane Hugo in Puerto Rico.

The lack of a clear growth response at the Rancho San Felipe is due to two related factors. First, a positive relationship between precipitation and growth (Whigham et al. 1990). We believe that this pattern is characteristic of dry tropical forests that occur in areas with an extensive and variable dry season. Second, the soils at Rancho San Felipe are very shallow, typically less than 20 cm (Whigham and Cabrera 1991). The combination of shallow soils, which dry very quickly after rain events, and a distinct dry season result in a strong climatic control of tree growth.

Higher annual precipitation in the first few post-hurricane years also resulted in less annual leaf litterfall compared to prehurricane years (Whigham and Lynch 1998). The close relationship between annual leaf litterfall and precipitation in pre-hurricane and post-hurricane years suggests, however, that hurricanes had little impact on annual litter production in post-hurricane years. There was an increase, however, in the concentration of phosphorus in leaf litter after a hurricane (Whigham and Lynch 1998). This result can be interpreted as an increase in rates of nutrient cycling, most likely due to the release of phosphorus from decomposing organic debris generated by hurricanes (Scatena et al. 1996). Scatena, Moya, Estrada, and Chinaea (1996) found that leaf litterfall was lower in the first post-hurricane year and returned to pre-hurricane levels by the third year.

The results described to this point are appropriate for forests that do not burn following a hurricane. In general, fire has not been reported to be an important post-hurricane factor in wetter forests (e.g., Vandermeer, Brenner, and Granzow de la Cerda 1998; Weaver 1998b; Foster, Fluet, and Bosse 1999) or drier forests on Caribbean islands (Weaver 1998a). Fire is, however, clearly an important factor in Quintana Roo. Snook (1993, 1998) reviewed the literature on fires and found that fires are caused by natural and anthropogenic activities. The largest recorded fires in the region followed hurricanes in 1942, 1974, and 1988 (Snook 1993). When burned and unburned forest areas in the northern part of the peninsula are compared, data clearly shows that fires have a much greater influence on forest structure and species composition. Fire-damaged areas that were sampled and fire-damaged forests in the southern

portion of the peninsula (Snook 1993) had lower basal area of live trees. It also appears that few species are able to survive intense fires, especially in areas where the soils also burn because they are very shallow and have a high content of organic matter.

Postfire vegetation proceeds through successional pathways that differ from those associated with hurricane damage, especially in areas that have been severely burned. Many more trees survive hurricanes than fires; as was found at Rancho San Felipe, there are few changes in species composition in hurricane-damaged forests. The models developed by Vandermeer et al. (1996) appear to apply to hurricane-damaged forests in the Maya zone that do not burn. Successional pathways following fire depend on the intensity of the fire. In areas that are severely burned, shade-intolerant species (e.g., *Bursera simaruba*, *Vitex gaumeri*, *Metopium brownei*) are common (Snook 1993; Olmsted et al. 1991); they are also abundant in areas that were cleared for agriculture, and then abandoned. In areas where fires were less intense, succession is dominated by tree species that can sprout following nonlethal fires (e.g., *Dendropanax arboreus*, *Guettarda combsii*) and understory species that generate better under "light shade." Olmsted et al. (1991) found *B. simaruba*, *D. arboreus*, *G. combsii*, *Gymnanthes lucida*, *V. gaumeri*, and *M. brownei* sprouting from burned saplings in intensely burnt forest in northern Quintana Roo, some of them sprouting roots.

Modern-day forest vegetation in the Yucatán Peninsula appears to be influenced primarily by historic patterns of land clearing (Gómez-Pompa, Flores, and Sosa 1987; White and Darwin 1995; Mizrahi, Ramos-Prado, and Jiménez-Osornio 1997) and by the combined impacts of hurricanes and fire (Snook 1998; Olmsted and Loope 1983). Studies in the northern part of the peninsula demonstrate that there are few long-term direct impacts of hurricanes, except for a decrease in basal area of the forest that will persist for decades. Forests in the northern portion of the peninsula are clearly adapted to a climatic regime that includes frequent disturbance. The forests are quite resistant to hurricane damage, but are also quite resilient when disturbances (e.g., fire) result in major changes in structure. Furthermore, medium-scale to large-scale disturbances caused by hurricanes and fires may play an important role determining the abundance of important species such as Mahogany (*Swietenia macrophylla*) in southern Quintana Roo (Snook 1993; Dickinson and Whigham 1999) and *Manilkara zapota* throughout the peninsula (Olmsted et al. 1991).

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PART III:
BIODIVERSITY

Chapter 11

The Role of Periphyton in the Regulation and Supply of Nutrients in a Wetland at El Edén, Quintana Roo

Eberto Novelo
Rosaluz Tavera

INTRODUCTION

Wetlands are unique ecosystems that are neither wholly terrestrial nor aquatic, but are characterized by the fact that they are inundated long enough to promote significant alterations in the soil properties due to chemical, physical, and biological changes (Vymazal 1995; Kadlec and Knight 1996). Wetlands are one of the most biologically active ecosystems; as a consequence, wetlands are ecosystems with very high net primary productivity. The algae in wetlands regulate the nutrient flow rate from sediment interstitial water, either through the algal assimilation of sediment nutrient, which prevents their release to the water column, or by forming an oxidized microzone produced by epipellic algal photosynthesis at the sediment-water interface (Carlton and Wetzel 1988).

Algal ensembles differ based on their capacity to remain in fluctuating conditions; the result is an association of species often growing in different life-forms. One such association—periphyton—corresponds to those algae growing firmly or loosely attached to emergent or submerged vegetation, or any other substrate (Sladecková 1962; Marvan et al. 1978; Hillebrand 1983;

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Roos 1983). This concept can include life-forms such as epipelton, plocon, and epiphyton, given that all are attached to some substrate; periphyton, then, represent a broad spectrum of communities distinguished by the way they grow as well as by their species assemblages.

Based on studies of wetlands (e.g., tundra, temperate, and subtropical) in North America, Europe, and Australia, Goldsborough and Robinson (1996) proposed a model explaining how the interaction between physical and chemical factors determines the type of periphyton and their spatial and temporary variation in wetland areas. Their model proposes four relatively stable stages: (1) lake, (2) open, (3) protected, and (4) dry. In each stage, the following life-forms predominate: phytoplankton, epiphyton, metaphyton, and epipelton, respectively. Wetland ontogeny does not assume cyclic passage of a wetland through all four stages; instead, the dominant algal assemblage is determined by several factors, including natural grazing pressure and water column stability (Goldsborough and Robinson 1996). Although several aspects of tropical wetlands have been intensively studied (Gopal, Junk, and Davis 2000), further studies on algal life-forms and communities are necessary.

The inundated savanna of the El Edén Ecological Reserve is one of the most interesting tropical zones for studying algae. In addition to differences in soil and vegetation types, duration of the period of inundation, radiation intensity, and wind exposure, the site is exceptional in its extensive algal growths, which cover the entire substrate. In this area, algal growths are different in texture, color, shape, and species composition. To explain relationships between the environment and differences in species composition, four representative sites within the El Edén wetland were chosen. Measurements of nutrients in the water, soil, and periphyton (*sensu lato*) revealed the common role of algae in controlling nutrient flux. Every hydrologic cycle, algae take nutrients from the water column and soil, thus impoverishing the water and preventing the establishment of a phytoplankton community; then, during the dry period, the periphyton supply nutrients, which enriches the soil. Given that the phytoplankton community is not firmly established during periods of flooding, the algal community model proposed for wetlands (Goldsborough and Robinson 1996) should be reanalyzed for El Edén.

STUDY AREA AND SAMPLING METHODS

The 1,492 hectare (ha.) El Edén Ecological Reserve is located in the Yalahau region of the northeast Yucatán peninsula, in the state of Quintana Roo, Mexico. El Edén is situated at 5–10 meters (m) above sea level, between lat. 21°11'30"N and lat. 21°14'N and long. 87°10'30"W and long. 87°12'30"W.

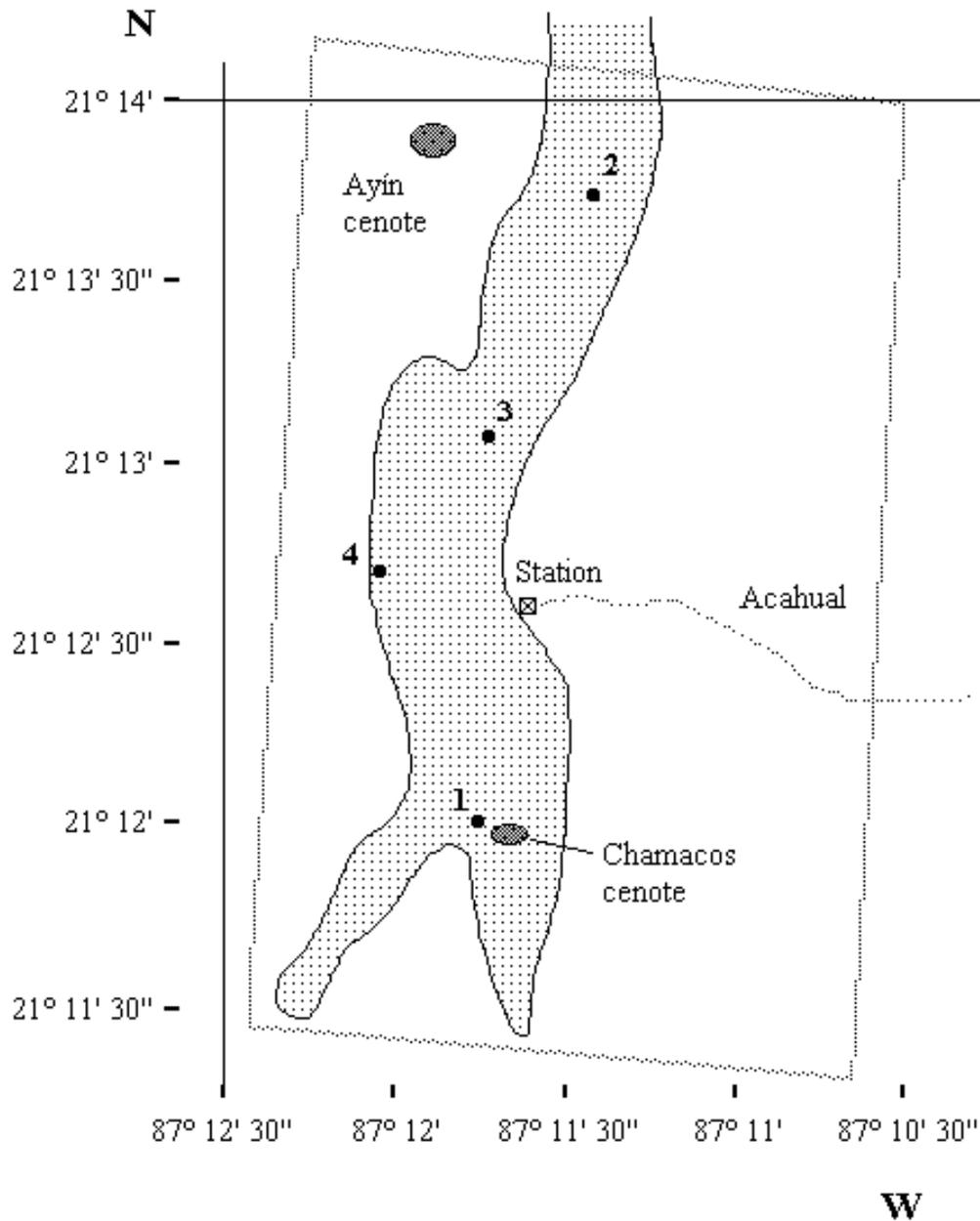


FIGURE 11.1. Sampling sites 1 through 4 within El Edén Ecological Reserve. The shaded area represents savanna that is flooded for three to four months each year.

All conspicuous and distinct algal growths (periphyton assemblages) were collected during July and October of 1999 and in April, August, and November of 2000. Collections were made at four established sites ($4 \times 8 \text{ m}^2$) within the flood zone of El Edén (Figure 11.1):

1. Savanna (lat. 21°12'06.3"N; long. 87°11'44.6"W), with a vascular vegetation canopy less than 30% with *Solanum donianum* Walp. as dominant; soil depth 10–15 cm.
2. Savanna (lat. 21°13'42.2"N; long. 87°11'26.3"W), with a vascular vegetation canopy less than 40% with *Cladium jamaicensis* Crantz. as dominant; soil depth 10–30 cm.
3. Tintal (lat. 21°13'01.1"N; long. 87°11'44.8"W), with a vascular vegetation canopy less than 5% with *Haematoxylon campechianum* L. as dominant; soil depth 3–5 cm.
4. Ecotone tintal–subdeciduous tropical forest (lat. 21°12'44.1"N; long. 87°12'01.6"W), with a vascular vegetation canopy less than 10% with a mixture of *H. campechianum*, *Erythroxylon confusum* L., *Manilkara sapota* (L.) P. Rogen, and *Crescentia cujete* L.; soil depth 5–15 cm.

Other samples outside the studied sites were collected when the macroscopic appearance of periphyton was quite different from those found in the permanent sites. Phytoplankton was collected from the water during the flooded period, and in permanent water bodies (cenotes and ponds) during both the dry and flooded periods.

Samples of algae from each assemblage were taken directly in plastic bottles for herbarium documentation. Periphyton samples were made on a constant area (~25 cm²) for herbarium documentation; subsamples of 1 cm² were separated for quantification of chlorophyll *a* for biomass estimation. A periphyton sample of ~100 cm² was collected at the same time for nutrient quantification. During the flooded period, phytoplankton and water samples were taken for herbarium specimens with a 10 µm pore net; also, two water samples were taken for analysis of nutrients and chlorophyll *a* (200 ml from one liter of water). All determinations were made in the laboratory immediately after collection.

Formaldehyde (3 percent)-preserved algal samples have been deposited in the Herbarium of the Faculty of Sciences at the Universidad Nacional Autónoma de México in the Edén–FCME collection. Species description will be prepared for a later publication; a list of genera is included here (Table 11.1).

Soil samples were taken using a PVC coring device (5 cm diameter, 35 cm length). Nutrient determinations of algae and soils were made on dried samples; algal growths (periphyton) were treated as plant tissue for nutrient analysis. Quantification of chlorophyll *a* was based on the 1 cm² samples of periphyton collected, and is expressed in volume units following the extraction method. For more accurate results, detritus was previously removed; algal mucilage does not interfere with the extraction method used.

TABLE 11.1. Algae of El Edén Ecological Reserve, Quintana Roo, Mexico

Cyanoprokaryota	Chlorophyta	Heterokontophyta Bacillariophyceae	Xanthophyceae	Chrysophyceae	Euglenophyta	Dinophyta	Glaucophyta
Anabaena sp.	Ankistrodesmus spp. (3)	Achnanthes spp. (3)	Ophiochyium sp.	Dinobryon sp.	Euglena spp. (2)	Peridinium spp. (2)	Glaucocystis sp.
Aphanocapsa spp. (5)	Aphanochaete sp.	Amphipleura sp.	Vaucheria sp.	Mallomonas sp.	Peranema sp.		
Aphanothece spp. (5)	Botryococcus sp.	Amphora spp. (2)			Phacus spp. (2)		
Bacillaria sp.	Bulbochaete sp.	Asterionella sp.			Trachelomonas spp. (3)		
Calothrix sp.	Carteria sp.	Caloneis sp. (2)					
Campylonemopsis sp.	Chiara sp.	Campylodiscus sp.					
Chlorogloea sp.	Chlamydocapsa sp.	Cocconeis spp. (2)					
Chroococcus spp. (6)	Chlamydomonas sp.	Cyclotella sp. (2)					
Coelmoron sp.	Cladophora sp.	Cymbella spp. (6)					
Cyanokybus sp.	Closterium spp. (2)	Denticula sp.					
Entophysalis spp. (2)	Coelastrum spp. (2)	Diploneis spp. (3)					
Eucapsis spp. (2)	Coelastrum spp. (2)	Epithemia sp.					
Gloeocapsa spp. (5)	Coelosphaerium sp.	Eunotia spp. (4)					
Gloeocapsopsis sp.	Coenocystis sp.	Fragilaria spp. (4)					
Gloeothoece spp. (8)	Cosmarium spp. (4)	Gomphonema spp. (3)					
Gloeotrichia sp.	Crudigeniella sp.	Gyrosigma spp. (3)					
Gomphosphaeria sp.	Desmidiium sp.	Hantzschia sp.					
Heteroleiblenia sp.	Dictyosphaerium sp.	Mastogloia sp.					
Hydrocoleus sp.	Dimorphococcus sp.	Melosira sp.					
Jaaginema sp.	Euastrum spp. (2)	Navicula spp. (6)					
Kormvophoron sp.	Gloeocystis spp. (2)	Neidium sp.					
Leibleria sp.	Gloeotaenium sp.	Nitzschia spp. (6)					
Leptolyngbya sp.	Kirchneriella sp.	Pinnularia spp. (4)					
Limnithrix sp.	Microtrinium sp.	Rhicosphenia sp.					
Lyngbya spp. (2)	Microsterias sp.	Rhopalodia sp.					
Merismopedia spp. (2)	Monoraphidium spp. (3)	Stauroneis sp.					
Microcoleus sp.	Mougeotia sp.	Synedra sp.					
	Nephrochlamys sp.						
	Nephrocytium spp. (2)						

TABLE 11.1 (continued)

Cyanoprokaryota	Chlorophyta	Heterokontophyta Bacillariophyceae	Xanthophyceae	Chrysophyceae	Euglenophyta	Dinophyta	Glaucophyta
Microcystis spp. (2)	Nitella sp.						
Nostoc spp. (2)	Oedogonium spp. (3)						
Onkonema sp.	Oocystis sp.						
Oscillatoria spp. (2)	Pediastrum spp. (2)						
Phormidium spp. (5)	Planctosphaeria sp.						
Planctolyngbya sp.	Pleodorina sp.						
Pseudanabaena spp. (2)	Pleurotaenium sp.						
Rhabdoglea sp.	Raphidocelis spp. (2)						
Rivularia sp.	Rhizoclonium sp.						
Schizothrix sp.	Scenedesmus spp. (9)						
Scytonema spp. (4)	Selenastrum sp.						
Stigonema sp.	Sphaeroszoma sp.						
Synechococcus sp.	Spinocosmarium sp.						
Tychonema sp.	Spirogyra spp. (2)						
	Staurastrum sp.						
	Stigeoclonium sp.						
	Tetraedron sp.						
	Ulothrix sp.						
	Willea sp.						
	Zygnema sp.						

LABORATORY METHODS AND MATERIALS

- Phytoplankton and periphyton growths: Chlorophyll *a* was determined by modified fluorimetric method 445.0 without acidification, using a Turner AU10 fluorometer (USEPA 1997).
- After aqueous extraction, all periphyton growths were examined for dissolved inorganic nitrogen (NO_3^- by cadmium reduction and NH_3 with salicylate), and phosphorus, including particulate phosphate determined as orthophosphate (molybdate digestion with ascorbic acid as a reducing agent and molybdovanadate). All determinations were made with a DR/2010 spectrophotometer and based on accepted USEPA methods according to Hach (1997)
- Water samples: Analyzed for nutrients using the methods mentioned above.

Soil samples: Dissolved inorganic nitrogen was determined by the above methods after extraction by shaking 3 g of air-dried soil in 30 ml of 0.01 M CaSO_4 for 15 minutes, and then filtration with a Whatman No. 2 filter. Soluble reactive phosphorus determination followed the same methods, after extraction by shaking 1 g of air-dried soil in 20 ml of 0.5 M NaHCO_3 , pH 8.5, for 30 minutes, and then filtration with a Whatman No. 2 filter.

RESULTS

Species composition of periphyton

In the flooded period, the open wetland environment contains both periphyton and rhizobenthos communities, but phytoplankton communities are very scarce. In the dry period, the dominant communities are all periphyton (“plocon” *sensu* Goldsborough and Robinson 1996).

Periphyton structure consists of a dense web of entangled cyanophycean filaments as well as empty sheaths accumulated from several seasons of growth. In some cases, sheaths of at least two years of age are visible. Among the wefts are mucilaginous algal colonies to which detritus adheres. Periphyton in the flooded period looks like a brownish sponge, but does not disaggregate when touched.

An epiphytic algal assemblage of a few filamentous species grows upon the vascular vegetation. Most of these leaves and stems fall down at the end of the flooded period, and the epiphytic algae join the wefts of periphyton on the substrate. As the wetland dries, this “dry” periphyton acquires a crusty appearance, eventually forming the gray crusts so evident in the dry period.

To date, 230 species of algae have been recognized in El Edén. These species belong to the following Divisions: Cyanoprokaryota, Chlorophyta, Heterokontophyta, Euglenophyta, Dinophyta, and Glaucophyta. Their distribution in the permanent water bodies and study sites is shown in Tables 11.2 and 11.3. In spite of this apparent diversity, a high proportion of algal component comes from species of Cyanoprokaryota.

Structure, types, and distribution of periphyton in El Edén

The species composition shows a very rich flora with aquatic, subaerial, and edaphic components. A clear distinction exists when comparing typically aquatic algae in the permanent bodies of water (e.g., ponds and cenotes) with those algae from sites in which a flora with a high capacity for desiccation resistance predominates. Only 30 species are present in periphyton in the dry period, and they survive such conditions successfully; by comparison, there are more than 70 species present in the permanent bodies of water, and only some of these are found in the study sites during flooded periods. In the subdeciduous tropical forest and “acahual” (secondary successional forest),

TABLE 11.2. Compared species richness of algae between permanent water bodies and sites 1 through 4. Species of other environments within El Eden are not included.

	Sites	Ponds	Cenotes	Total species
Cyanoprokaryota	35	31	19	56
Chlorophyta	32	55	19	68
Heterokontophyta	18	21	64	66
Euglenophyta	2	1	3	5
Dinophyta	1	1	1	2
Glaucophyta		1		1

TABLE 11.3. Species richness in each group (division) of algae in sites 1 through 4.

	Site 1	Site 2	Site 3	Site 4	Total species
Cyanoprokaryota	27	11	18	5	35
Chlorophyta	31	7	3		32
Heterokontophyta	10	6	2	4	18
Dinophyta			1		1
Euglenophyta	2				2

the only massive growths of algae found are of *Nostoc* spp., even though these areas are partially flooded once a year.

The types of periphyton are distinguished by their species composition. The main recognized types are as follows:

1. Type *a*: Compact wefts, mainly subaerial.
2. Type *b*: Loose epiphytic wefts, mainly aquatic.
3. Type *c*: Compact edaphic wefts forming crusts.
4. Type *d*: Subaerial flakes, mainly edaphic and covered by type *c* crusts.
5. Other forms with limited distribution.

The first two types cover the most area in El Edén and dominate the landscape. When wet, these growths can reach a thickness of up to 10 cm.

The periphyton types are quite variable in time and space (Figure 11.2); there are, however, some recurrent species:

1. Type *a*: Compact wefts, mainly subaerial (Figure 11.3). The upper part of the periphyton is formed by at least three species of *Scytonema* and one species of *Camptylonemopsis*. The lower part is formed by a complex weft of Oscillatoriales, composed mainly of several species of *Phormidium*. Colonial species of Cyanoprokaryota such as *Chroococcus*, *Gloeocapsa*, *Gloeothoece*, *Aphanothece*, or *Aphanocapsa* are intermingled. The main weft is formed by the former filamentous, heterocytic nitrogen-fixing species. The presence of *Chara*, a chlorophyte, is noteworthy, as it behaves as an annual herb with massive and rapid growth during the flooded period, but whose thalli disintegrate in the dry period. These growths were evident during the flooded period in sites 1 and 2.
2. Type *b*: Loose epiphytic wefts, mainly aquatic (Figure 11.4). These are composed of filamentous species of Cyanoprokaryota and Chlorophyta. The abundance of colonial species is less than in the previous type. Species of *Phormidium*, *Leptolyngbya*, *Oedogonium*, *Bulbochaete*, and *Ulothrix* are the most frequent. The former two genera form the wefts, which are responsible for the majority of the periphyton's structural composition. These wefts are found in sites 1 and 2 during the dry period.
3. Type *c*: Compact edaphic wefts forming crusts (Figure 11.5). Wefts are similar in appearance to type *a* periphyton, but species composition does not include as many colonial species; filaments are found exclusively from species of *Stigonema*, which is another Cyanoprokaryota. Type *c* periphyton were present in all sites during the dry period.

4. Type *d*: Subaerial flakes, mainly edaphic, and covered by type *c* crusts (Figure 11.5). These growths are formed by one or two species only, and are found in zones that remain wet during a prolonged period, but never fully inundated. These flakes reach a thickness of 2 cm between the soil and the compact edaphic wefts. *Gloeocapsa*, *Gloeothece*, *Aphanocapsa*, and *Aphanothece* species are present in these flakes, but the main component is a *Cyanokybus* species, which is a monotypic genus known in Cuba and Venezuela from marine environments. These flakes are present in sites 3 and 4 during the end of flooded and dry periods.
5. Other forms with limited distribution (Figure 11.6): Other visible periphyton growths in El Edén are found only sporadically, or in restricted areas. The most conspicuous are growths of *Nostoc* spp., which can sparsely cover several square meters in the more poorly illuminated zones with rich humus soil. Another algal growth consists of loose mats of green filaments (*Mougeotia*, *Spirogyra*, etc.) with many companion species. None of these growths are present in the study sites, but were found only along the edges of subdeciduous tropical forest and “acahual” communities, or in some places with very open canopies inside these communities.

Periphyton and phytoplankton biomass

When evaluated in terms of chlorophyll *a*, periphyton showed a differential growth rate in each period (Figure 11.7); this may be interpreted as a biomass increase from dry to flooded periods.

The four studied periphyton types had similar growth rates. Although in the first two types (subaerial and aquatic wefts in sites 1 and 2), the chlorophyll *a* values showed a trend of being conserved or slightly decreasing

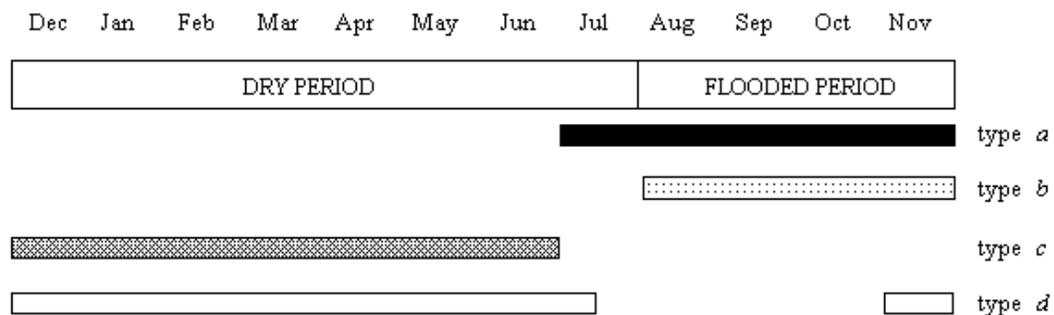


FIGURE 11.2. Temporal distribution of periphyton types in El Edén Ecological Reserve.



FIGURE 11.3. Compact wefts of periphyton (type a) during the flooded period. Note the continuous weft on the substrate.



FIGURE 11.4. Loose epiphytic wefts of periphyton (type b), on *Cladium jamaicensis* leaves, during the flooded period

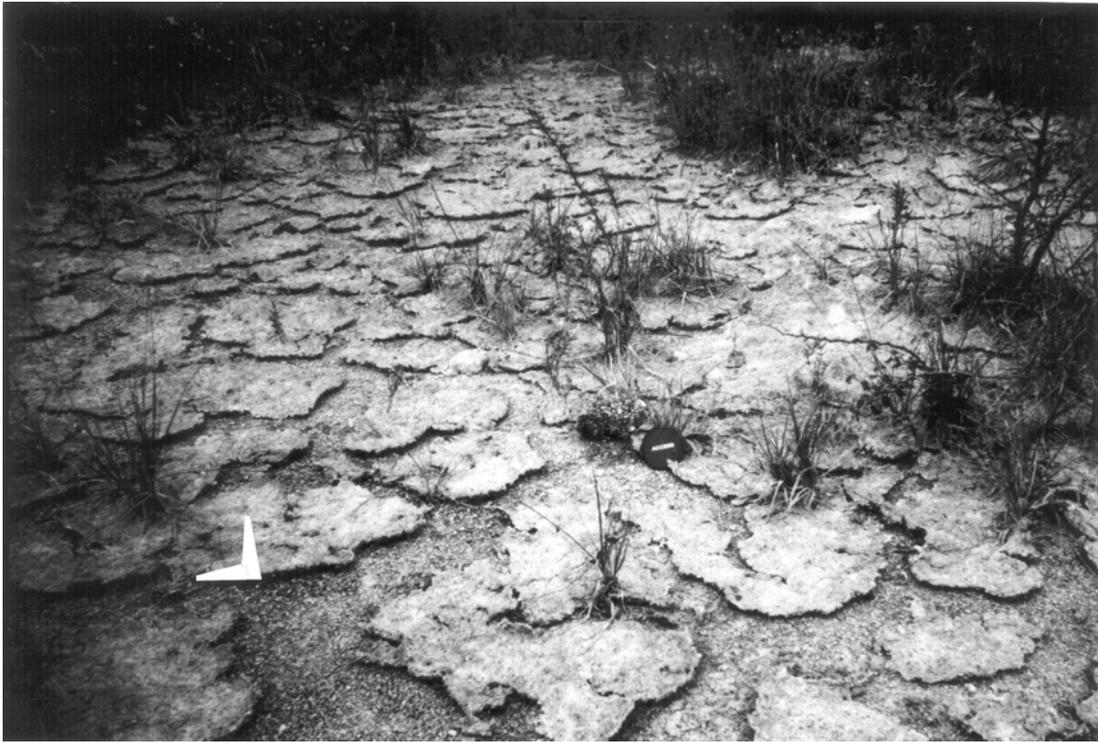


FIGURE 11.5. Compact edaphic wefts (type *c*) and subaerial flakes (type *d*; see arrow) during the dry period.



FIGURE 11.6. Loose mats of filamentous algae—floating unattached to any substrate.

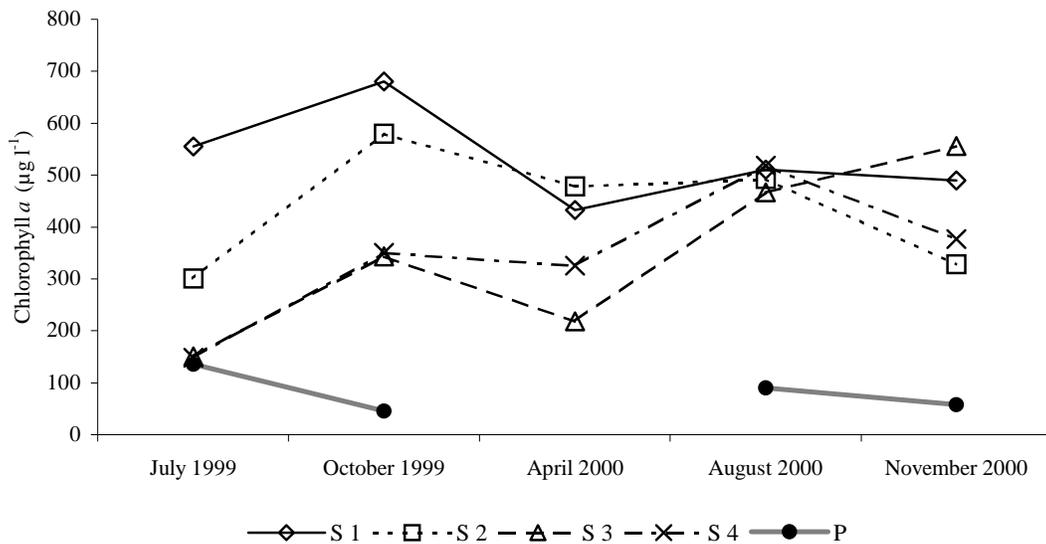


FIGURE 11.7. Periphyton and phytoplankton biomass: S1–S4 = periphyton; P = phytoplankton (average values from sites 1 and 2 when flooded).

through the hydrologic cycle, biomass of the two other types (compact edaphic weft and subaerial flake types in sites 3 and 4) increased in the flooded period and was maintained for a longer time.

The biomass of phytoplankton in water was high in sites 1 and 2 at the beginning of the rainy season (Figure 11.7). By the end of the flooded period, phytoplankton biomass decreased. The average values from sites 1 and 2 in 1999 were 135 at the beginning and 45.5 $\mu\text{g l}^{-1}$ at the end. In 2000, the average values from these sites were 90.5 at the beginning and 57.5 $\mu\text{g l}^{-1}$ at the end. In sites 3 and 4, which were prone to rapid and intermittent flooding, phytoplankton biomass was much lower in the flooded period, but the area did not remain inundated for sufficient time to evaluate fluctuations.

Nutrients in soil, water, and periphyton

In the flooded period, inorganic nitrogen compounds in the soil were higher than in periphyton and water (Table 11.4, Figure 11.8). In sites 1, 2, and 3, for example, nitrate (NO_3^-) was 2 to 17 times higher in the soil than in water, and in site 4 about 40 times higher. Nitrate in soil was 8 to 16 times higher than in periphyton. Nitrate in periphyton was higher than in water in sites 1 and 4 (1.8 to 2.5 times); in sites 2 and 3, nitrate was 2 to 4 times less. Ammonia (NH_3) was always higher in periphyton than in soil or water, except in site 2.

With the exception of site 3, phosphorus (expressed in terms of orthophosphates, PO_4^{3-}) was also higher in the soil than in periphyton.

TABLE 11.4. Values obtained for dissolved inorganic nitrogen compounds and phosphorus expressed as orthophosphate for each site in a hydrologic cycle.

	Sites	Dry period			Flooded period		
		NO ₃ ⁻ (mg l ⁻¹)	NH ₃ (mg l ⁻¹)	PO ₄ ³⁻ (mg l ⁻¹)	NO ₃ ⁻ (mg l ⁻¹)	NH ₃ (mg l ⁻¹)	PO ₄ ³⁻ (mg l ⁻¹)
Soil	1	6.3	6.9	464.0	15.8	3.7	272.0
	2	3.4	12.9	344.0	3.1	20.8	312.0
	3	7.8	2.0	64.0	6.3	1.5	8.8
	4	7.0	2.6	200.0	16.0	3.1	120.0
Water	1				0.9	0.4	0.3
	2				1.4	0.4	0.05
	3				0.9	0.2	0.1
	4				0.4	0.0	0.02
Periphyton	1	0.9	0.2	65.2	1.7	4.0	46.3
	2	3.9	0.5	77.0	0.38	3.5	48.5
	3	0.26	0.3	78.0	0.38	3.9	45.9
	4	0.4	0.6	70.8	1.0	4.1	58.0

Phosphorus tended to be hundreds of times less concentrated in water than in the soil. Probably more important than concentration values was the fact that the ratio of nitrogen and phosphorus did not follow the optimal 16:1 ratio for algae (Hillebrand and Sommer 1999).

In the dry period, inorganic nitrogen concentration was again higher in the soil than in periphyton (Figure 11.9). Nitrate (NO₃⁻) was 7 to 30 times higher in soil than in periphyton in sites 1, 3, and 4; in site 2, however, nitrate concentration remained almost the same. Ammonia (NH₃) was 4 to 34 times higher in soil than in periphyton.

Phosphorus (again expressed in terms of orthophosphates, PO₄³⁻) was three to seven times higher in soil than in periphyton, except in site 3. Compared to the flooded period, nitrogen concentration decreased in periphyton, with the exception of site 2. Nitrate in soil was reduced by 50 percent in sites 1 and 4, while remaining almost the same in the other sites. Ammonia (NH₃) also was reduced in sites 2 and 4, but increased in sites 1 and 3 (Table 11.4).

Phosphorus concentration in the soil increased twofold in this period in sites 1 and 4, and in site 3 increased almost eightfold. The increase in site 2 was only 10 percent.

Changes in nutrient concentration are reflected by changes in periphyton biomass (Figures 11.10, 11.11). Simultaneous changes in chlorophyll *a* and

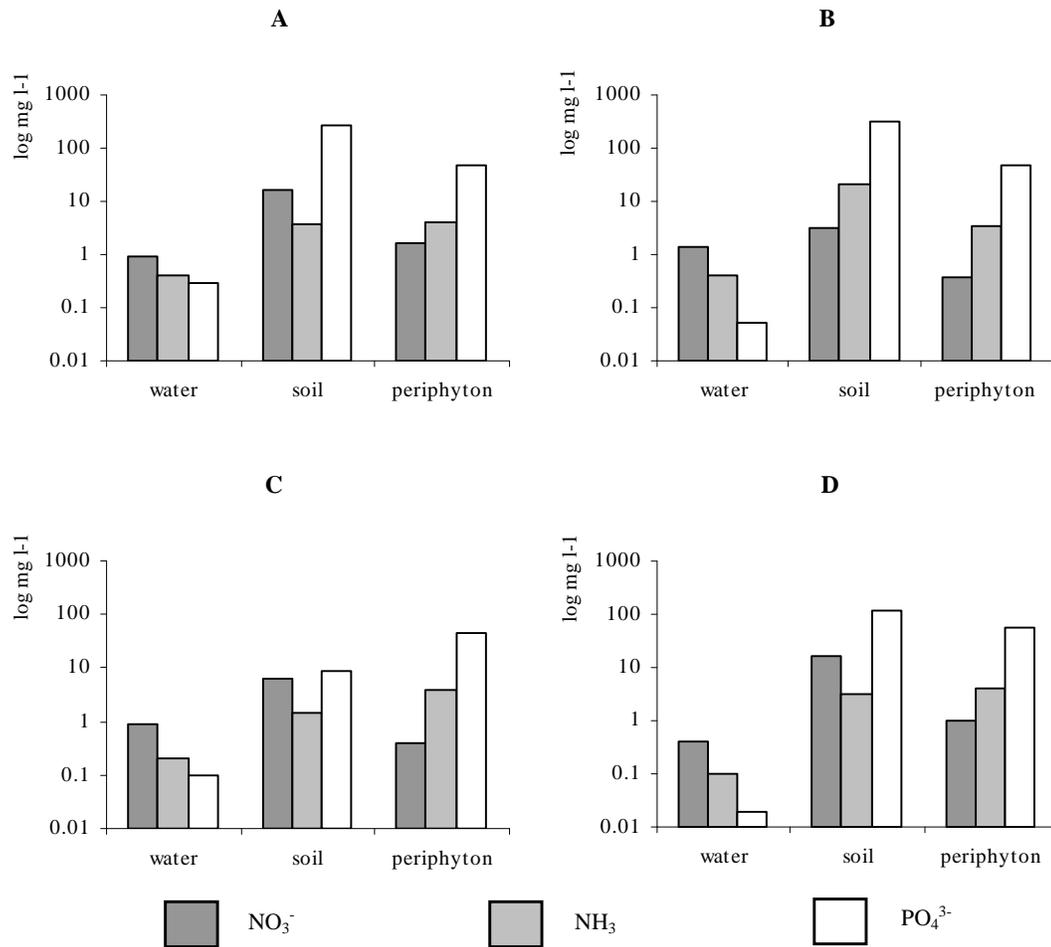


FIGURE 11.8. Flooded period nutrient concentrations in water, soil, and periphyton in sites 1 through 4 during October 1999; A = site 1; B = site 2; C = site 3; D = site 4.

ammonia could be explained by the metabolic utilization of nitrogen-reduced forms, while nitrate could be less important to the metabolic influence of nitrogen on biomass (Figure 11.10). Orthophosphate in periphyton seems to change inversely in relation to biomass, which suggests the direct utilization of the assimilable phosphorus (Figure 11.11). However the biomass value in site 4 in November suggests that further study is necessary to explain its apparent decrease.

DISCUSSION

Periphyton composition and structure

Algal richness in El Edén is considerably high, even when compared to much larger geographical regions such as the Tehuacan–Cuicatlan Valley

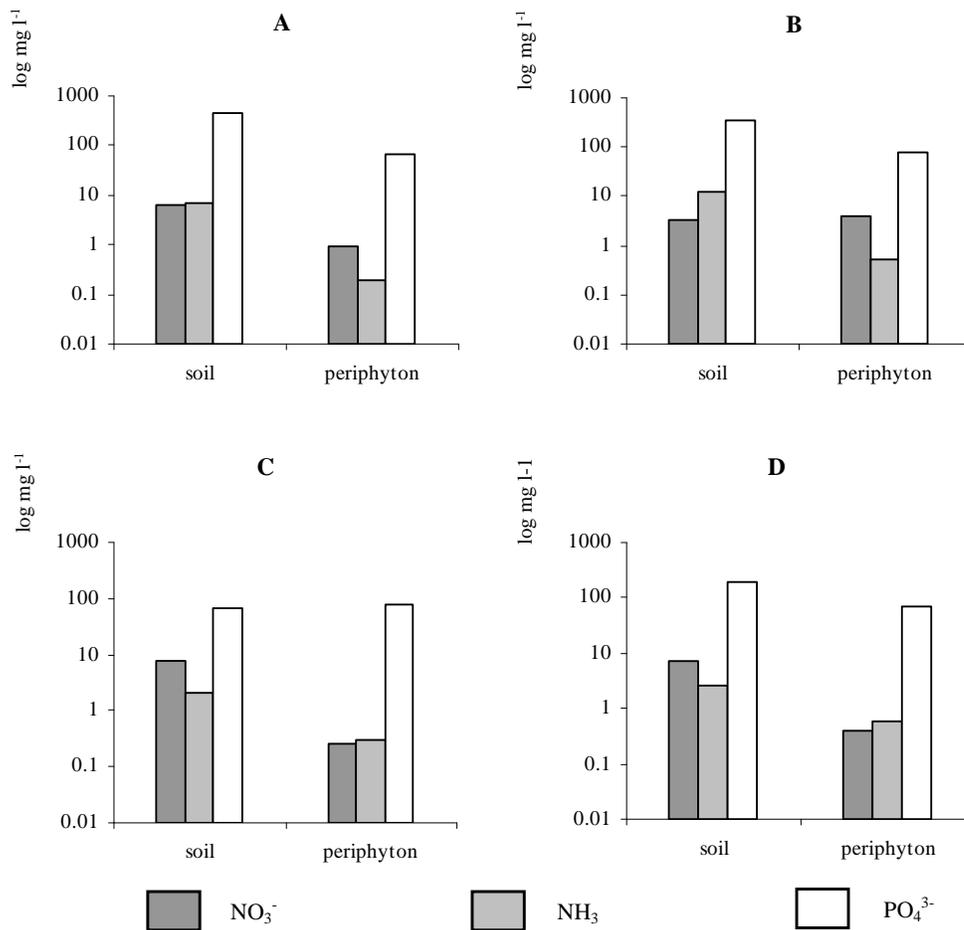


FIGURE 11.9. Dry period nutrient concentrations in water, soil, and periphyton in sites 1 through 4 during April 2000; A = site 1; B = site 2; C = site 3; D = site 4.

(Novelo 1998) or the Huasteca Potosina (Montejano, Carmona-Jiménez, and Cantoral-Uriza 2000). Importance of El Edén's algal flora is based, too, in the predominance of Cyanoprokaryota and the great number of rare or not well-known species. This richness is very important because of the abundance and cover of periphyton in the savanna. Species from other groups are present in the periphyton, but in much less abundance than the cyanophycean algae; still, their presence indicates microconditions whose effects should be evaluated. In the flooded period, water in the savanna is continuous with the ponds and cenotes and could suggest some kind of homogenized flora; the data in Tables 11.2 and 11.3, however, point to a more restricted distribution of species than might be suspected.

Remarkably, nearly 60 percent of the total species that compose the periphyton belong to Cyanoprokaryota and Chlorophyta. The principal structure of all types of periphyton, however, consists only of filamentous Cyanoprokaryota. The compact subaerial and edaphic wefts are formed by members of the family Scytonemataceae, which are responsible for the

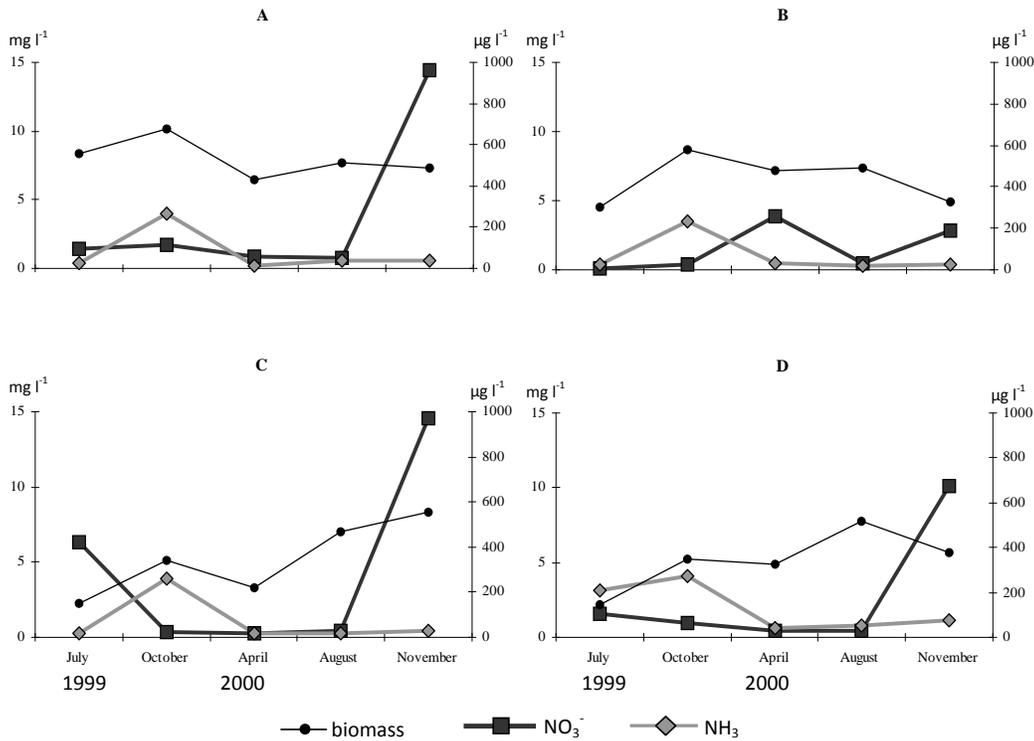


FIGURE 11.10. Changes in NO_3^- , NH_3 , and biomass during the study period. Axis Y_1 = inorganic compounds in $\text{mg}\cdot\text{l}^{-1}$; axis Y_2 = biomass (chlorophyll a in $\mu\text{g}\cdot\text{l}^{-1}$); A = site 1; B = site 2; C = site 3; D = site 4.

consistency and the weave of the mucilaginous sheaths; meanwhile, colonial Chroococcales are intermingled with the filamentous wefts. The organization of species inside the weft is probably linked to a higher production of mucilage by colonial species. Dominance of scytonematalean species at the surface of wefts may be explained by the production of scytonemine-pigments that filter the solar radiation (Garcia-Pichel and Castenholz 1991).

Massive periphyton growths are possible in El Edén because of at least two environmental conditions: (1) complete inundation for an extended period of time (three months or more), and (2) a lack of vascular plant canopy. In zones with a thicker canopy, such as median forest or “acahual,” periphyton is not present at all. Similarly, in areas with dense stands of *Typha* in the savanna, periphyton is not encountered, and even the *Nostoc*-type periphyton grows only along the edges of such stands.

The model proposed by Goldsborough and Robinson (1996) is inadequate to explain the hydrologic cycle at El Edén for two reasons. First, algal crusts are maintained all year long. Second, the periphytic growths block nutrient flux; thus, there is no planktonic community—the lake phase of the model does not exist, and the protected phase is rare. The periphyton structure is built over several years and does not disappear in dry periods. This means that the algal community participates permanently in the ecosystem,

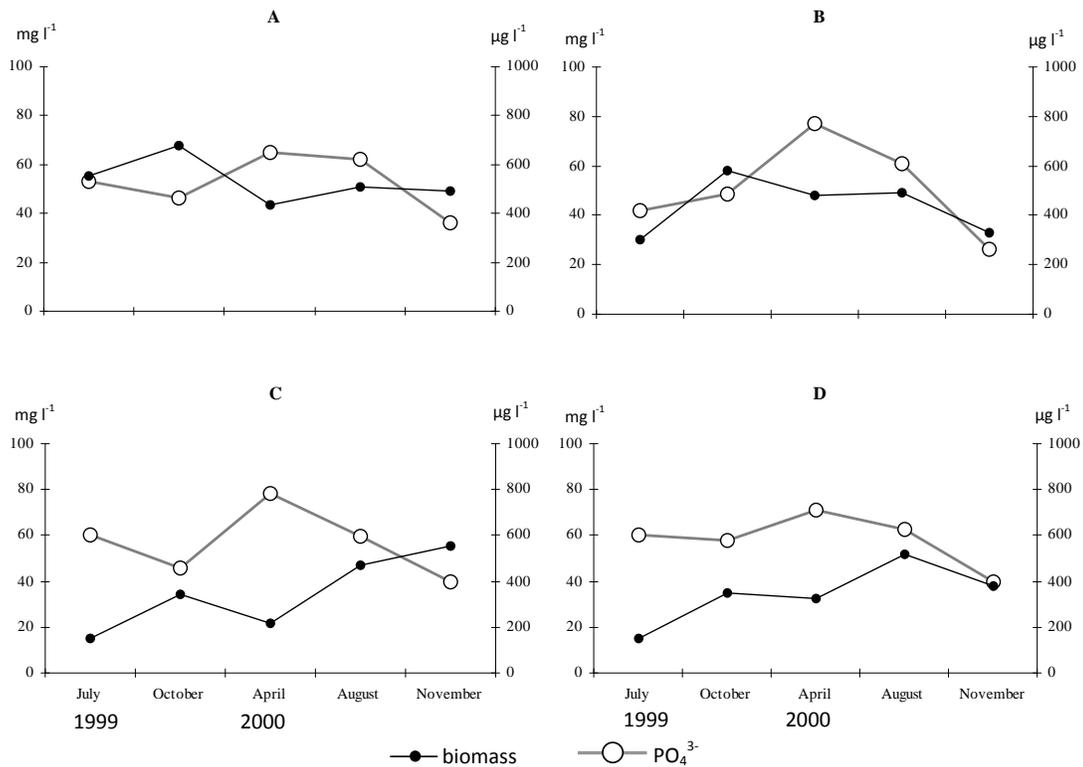


FIGURE 11.11. Changes in PO_4^{3-} and biomass during the study period. Axis Y_1 = orthophosphate in $\text{mg}\cdot\text{l}^{-1}$; axis Y_2 = biomass (chlorophyll *a*) in $\mu\text{g}\cdot\text{l}^{-1}$; A = site 1; B = site 2; C = site 3; D = site 4.

and loss of part of this community would require more than a year to recover.

Algal biomass in the hydrologic cycle

Periphyton biomass (chlorophyll *a*) increased through the flooding of the wetland up to a maximum in October, then decreased through desiccation down to a probable minimum (see Figure 11.7). Biomass recovery in the following period of flooding reached more or less the same level as the previous flooded period, which probably means that biomass fluctuation is constant and likely regulated (perhaps even self-regulated) by the mobilization of nutrients in the ecosystem. This has been observed in constructed freshwater wetlands in the Midwestern United States, when periphyton productivity was measured (Cronk and Mitsch 1994), and high-flow wetland periphyton samples had significantly greater average amounts of chlorophyll *a* per unit area than low, flow wetlands.

Phytoplankton biomass decreased through the hydrologic cycle. Initial values of chlorophyll *a* in water (see Figure 11.7) revealed a high biomass that could be interpreted as typical for any eutrophic body of water (Tavera and Castillo 2000). This could be due to the liberation of inorganic dissolved

nutrients from litter, in response to rain and preliminary flooding. These nutrients then cause the phytoplankton communities to flourish. Later, rapid growth of periphyton removes nutrients from the water and forces the consequent decline of the phytoplankton. As observed in Lake Okeechobee in southeastern Florida, periphyton and plankton coexisting in shallow lakes have similar resource requirements with regard to nutrients and light, and periphyton growing on the sediment surface can affect nutrient dynamics in the overlying water column by direct uptake (Hwang, Havens, and Steinman 1998).

Nutrient flux and algal communities in the wetland

Nitrogen and phosphorus in water were rather low in comparison to those contained in the periphyton and the soil; the nitrogen-phosphorus ratio (N:P) was also low, indicating a possible limitation of nitrogen for phytoplankton. From microscope observations it was clear that the phytoplankton community was indeed very poor in the water column of each studied site when the wetland was flooded. Mesocosm studies (Hwang, Havens, and Steinman 1998) have reported that periphyton rapidly sequester large amounts of phosphorus and reduce soluble phosphorus concentrations, resulting in reduced phytoplankton biomass. Hansson (1990) demonstrated that periphytic algae growing on the sediment reduced total phosphorus concentration by 44 percent in the overlying water, and concluded that periphyton could competitively reduce phytoplankton growth in shallow water. In El Edén, phosphorus in the water column seemed to decrease over the duration of the flooded period—a 2- to 210-fold decrease from August to November, with values of 0.04–0.02 and 2.1–0.01 mg l⁻¹.

Concentration of phosphorus was generally higher in the soil than in the periphyton. Results indicate that the period of phosphorus increase in the periphyton, between the end of the flooded period and the desiccation of the wetland, could be due to the growth of charophycean species, which reaches its maximum at the same time. Once the water disappears and periphyton and charophytes begin to decline, phosphorus is transferred to the soil, producing the increase registered in the dry period. During April in sites 1 and 2, large quantities of white (calcified) fragments of charophytes were observed, lying over the soil. It is thought that these thalli are an important source of phosphorus—one not observed in the other two study sites. This could well explain the higher levels of soil phosphorus in sites 1 and 2.

The low levels of phosphorus observed in the water is surprising. With a soil so rich in phosphorus in the dry period, this nutrient would be expected to enrich the water column through simple dissolution following every flooding of the wetland. Such was not the case in El Edén, and it is suspected that the periphyton, which completely covers the soil, prevent mobilization of oxygen

in the water-sediment interface by producing a thin oxidized layer at the soil surface. This has been demonstrated in Lake Windermere, located in Cumbria, United Kingdom (Carlton and Wetzel 1988); according to investigations there, this oxidized layer need only be between 3 to 5 mm thick to prevent the liberation of phosphorus. Another possibly important factor in the binding of phosphorus to the soil may be the presence of carbonates, common in the limestone substrate of the Yucatán Peninsula.

Thus, trapped phosphorus in the soil is inaccessible even to algae, until sporadic episodes of periphyton removal allow the sediments access to oxygen. Once the released phosphorus is transformed into reactive phosphorus, it could be utilized by mycorrhizae, algae, and other soil organisms. It may be assumed that the ecological role of periphyton in El Edén is the enrichment of phosphorus in the soils through the processes of the hydrologic cycle.

Experimental studies in periphyton mats have shown that periphyton can sequester large amounts of nitrogen (not only phosphorus) from the water column (Havens et al. 1999). Concentrations of ammonia in the soil were almost the same throughout the flooded period. This form of nitrogen increased in sites 1, 3, and 4 while nitrate diminished; the converse occurred in site 2 for unknown reasons. When the wetland is dry, loss of nitrogen is evident, with ammonia decreasing to a greater extent than nitrate. This difference may be due to the microbial and algal preference for reduced nitrogen compounds instead of nitrate (Norton 1981; Vymazal 1995).

Periphyton nitrate levels were maintained throughout the flooded period in site 2. In sites 1, 3, and 4, nitrate showed a 10- to 15-fold increase. As the dry period proceeded, nitrogen levels in the periphyton diminished, most notably due to a decrease in ammonia (4- to 6-fold decrease). Nitrate decreased 30 to 50 percent in sites 1, 3, and 4; in site 2, however, nitrate levels showed a 10-fold increase.

Other unpublished experimental data (not discussed in this chapter) have demonstrates the decrease in nitrogen fixation throughout the flooded period, reaches its lowest values during the dry period. This may be consistent with the previous results on levels of nitrogen and ammonia.

CONCLUSION

Periphyton in El Edén are a rich and complex community, indispensable in the preservation of the wetland as a differentiated ecosystem. In these algal growths, wefts remain throughout the year, later to provide support and rapid hydration for the new growths when the rainy season begins. They contribute to the maintenance of humidity for the lower strata, and serve to protect these strata from heat and desiccation in the dry period by capturing water during

the night. In addition to this function, the accumulated wefts protect vegetative and resistant cells that will serve as propagules in the next phase of vegetative growth. This is important for organisms such as *Chara* and *Nitella*, whose thalli disaggregate during drought, but do form resistant oospores at the end of the rainy season.

In general, when periphyton dehydrate they loses nitrogen—mainly as NH_3 —and the phosphorus concentration is remarkably increased in the soil, probably because some algal material (mainly charophytes) is directly incorporated into the soil through desiccation and pulverization. This process is quite evident in sites 1 and 2. The phosphorus in periphyton decreases at the end of the flooded period; but, given the higher levels of phosphorus during the dry period, it is possible that loss and recovery take place in each hydrologic cycle. Indeed, chlorophyll *a* values seem to point to a rapid metabolic uptake of phosphorus. The lower quantities of reduced forms of nitrogen found in the periphyton at the end of the flooded period can be attributed to the lower rates of nitrogen fixation as the wetland dries out.

Periphyton biomass is constant, although deviations were noted in all four study sites during the study period. Chlorophyll *a* quantities in the dry period were sufficiently high to account for the persistence of vegetative structures inside the dry periphyton crust. On the other hand, growths in the flooded period do not multiply as they do in other environments. In this case, the sequence of sustained exponential growth followed by a stationary phase is not clear. Modifications in species composition surely play an important role in this conservative tendency. However, it could possibly be due to the regulation of nutrient flux by algal growths.

Such structured behavior within the ecosystem obliges a reanalysis of the use of periphyton as an exploitable resource. Crusts sampled from the study sites did not fully recover over the course of the study period. Although the recovery process was not followed systematically, the absence of periphyton in previously collected zones, microscopic observations of mucilaginous wefts of several ages throughout the hydrologic cycle, the conservative trend of biomass, the nitrogen flux from periphyton to soil, and the phosphorus flux from soil to periphyton all serve as evidence that recovery is distinctly retarded. Systematic removal of periphyton could possibly break the nutrient cycles completely, thereby impoverishing the soil and having drastic consequences for the rest of the ecosystem.

If periphyton are to be used as a biofertilizer for agricultural soils because of their high nutrient content, the effects of such extraction upon the ecosystem, as well as the slow recovery of the periphyton, must be taken into account. As is true of any other component of a complex, diverse ecosystem, periphyton cannot be indiscriminately exploited without a better knowledge of their role and importance in the ecosystem.

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Chapter 12

Distribution and Ecology of Myxomycetes in the Forests of Yucatán

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INTRODUCTION

The myxomycetes (plasmodial slime molds) are a group of fungus like organisms usually present (and sometimes abundant) in terrestrial ecosystems. The myxomycete life cycle involves two very different trophic stages—one consisting of uninucleate amoebae, with or without flagella, and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin, Alexopoulos, and Farr 1983). Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies that contain spores. The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by higher fungi, although they are considerably smaller (usually no more than 1–2 mm tall). The spores of myxomycetes are, for most species, apparently wind-dispersed and complete their life cycle by germinating to produce the uninucleate amoeboflagellate cells.

There are approximately 800 recognized species of myxomycetes (Lado 2001). The majority of species are probably cosmopolitan, but a few species appear to be confined to the tropics or subtropics, while others have been

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collected only in temperate regions (Alexopoulos 1963; Farr 1976; Martin, Alexopoulos, and Farr 1983). Myxomycetes appear to be particularly abundant in temperate forests, but at least some species apparently occur in any terrestrial ecosystem with plants (and thus plant detritus) present (Stephenson and Stempen [1994] 2000). Most of what is known about the assemblages of myxomycetes associated with particular types of terrestrial ecosystems has been derived from studies carried out in temperate regions of the Northern Hemisphere. In these forests, myxomycetes are associated with a number of different microhabitats. (As used herein, the term “microhabitat” simply denotes a specific portion of the total forest habitat [Stephenson 1989].) These include coarse woody debris on the forest floor; the bark surface of living trees; forest floor litter; the dung of herbivorous animals; and aerial portions of dead, but still standing, herbaceous plants. Each of these microhabitats tends to be characterized by a distinct assemblage of species (Stephenson 1988, 1989).

The myxomycetes associated with coarse woody debris are relatively well-known because the species typically occurring in this microhabitat tend to be among those that characteristically produce fruiting bodies of sufficient size to be detected in the field (Martin and Alexopoulos 1969). However, much less is known about the myxomycetes associated with such microhabitats as the bark surface of living trees and forest floor litter. The primary reason for this lack of knowledge is that many of the species involved are rather inconspicuous, or sporadic in their occurrence, and thus difficult to detect in the field. However, the moist chamber culture technique as it applies to myxomycetes (Gilbert and Martin 1933) provides a convenient and often very productive method of supplementing field collections when studying such microhabitats as bark and litter. Since its introduction, the technique has been used with considerable success by many researchers (e.g., Keller and Brooks 1976; Härkönen 1981; Blackwell and Gilbertson 1980; Stephenson 1989).

Knowledge of the assemblages of myxomycetes associated with various microhabitats in Neotropical forests is still rather limited (Schnittler and Stephenson 2000). The objective of the study reported herein was to carry out an intensive survey of myxomycetes in the semideciduous tropical dry forests of the El Edén Ecological Reserve on the Yucatán Peninsula. Primary emphasis was placed on analyzing patterns of species composition and diversity of the assemblages of myxomycetes associated with the microhabitats represented by (1) those substrates [mostly coarse woody debris but also including other types of dead plant material] from which specimens of myxomycetes that had fruited in the field under natural conditions were collected, (2) the bark surface of living trees, (3) forest floor litter, and (4) aerial litter [dead but still attached plant parts above the ground]. The data set used for the first of these microhabitat types consisted exclusively of field

collections (FC), whereas the data sets used for the myxomycetes occurring on bark (BK), forest floor litter (FL), and aerial litter (AL) were obtained by means of the moist chamber culture technique. El Edén was selected as the site for our study because data already available from previous studies (Ogata and Andrade-Torres 1998; Andrade-Torres 1997) of myxomycetes in the general study area suggested that it would be particularly suitable for an intensive ecological investigation of these organisms.

STUDY AREA

The El Edén Ecological Reserve is located in the lowlands of northern Quintana Roo, Mexico. This portion of the Yucatán Peninsula has a warm climate, with mean temperatures in the coldest month above 18°C. Average annual precipitation exceeds 1,000 mm, but there is a distinct dry season that lasts from three to five months. Our visit was made during November 1999, which corresponded with the early portion of the dry season.

Semideciduous tropical dry forests represent the predominant vegetation type throughout the entire region. Such forests are dominated by trees up to 15 m in height, including such species as *Manilkara zapota*, *Bursera simaruba*, *Cedrela mexicana*, and *Brosimum alicastrum*. Human activities have had a considerable influence on the structure and composition of vegetation throughout the general study area, which has been inhabited for approximately ten thousand years and was densely populated for several centuries (300 to 900 B.C., the Classic Period).

At El Edén, some areas remain flooded for at least a portion of the year. These seasonally flooded forests (“tintales”) are lower (with trees usually reaching a height of no more than 12 m) and less diverse than those forests not subjected to flooding. A single species of tree (*Haematoxylon campechianum*) is often the overwhelming dominant in seasonally flooded forests.

Primary emphasis of the study described herein was directed at semideciduous tropical dry forests, with limited collecting also carried out in seasonally flooded forests. A number of other vegetation types, including several types of wetlands, occur at El Edén, but these were not included in this study.

METHODS AND MATERIALS

The methods used in carrying out this project were essentially the same as those described by Stephenson (1988, 1989) for a study of the myxomycetes occurring in the upland forests of southwestern Virginia in the eastern United States. Field collections (FC) of myxomycetes were made at a number of different localities throughout the general study area. For the

purposes of the present study, a “collection” was defined as one or more fruiting bodies (sporangia, aethalia, pseudoaethalia, or plasmodiocarps) considered to have originated from a single plasmodium (Stephenson 1988). The method used in making a collection involved removing all of the material represented by a particular fruiting, along with a portion of the substrate upon which fruiting occurred. In addition, notes were made of any unusual fruiting position or substrate. All collections were brought back to the laboratory and glued into small boxes for permanent storage.

Samples of dead outer bark (BK) were collected from larger [usually > 10 cm dbh (diameter at breast height)] individual trees throughout the general study. Ten different species (*Bursera simaruba*, *Byrsonima bucidaefolia*, *Crescentia cujete*, *Gymnopodium floribundum*, *Haematoxylum campechianum*, *Jacquinia aurantiaca*, *Lysiloma latisiliquum*, *Manilkara zapota*, *Metopium brownei*, and *Vitex gaumeri*) were represented among the trees sampled. Bark samples were taken from a convenient trunk height of about 1.0 to 1.8 m.

Samples of forest floor litter (FL) were gathered at regular intervals along a rough transect established at each of the localities examined for field collections of myxomycetes. These samples consisted of mixtures of leaves. Although twigs of sufficient size to be easily noticed in the field were selectively excluded from litter samples, the latter contained various types of plant debris (e.g., seeds, small twigs, and pieces of bark) that typically make up the uppermost layer of litter on the forest floor.

Samples of aerial litter (AL) were obtained from suitable sources (e.g., dead but still attached leaves of vascular epiphytes growing on the trunks of trees) along these same transects. All samples were placed in small paper bags and transported to the laboratory, where moist chamber cultures were prepared in the manner described by Stephenson and Stempen ([1994] 2000).

The moist chambers used consisted of disposable plastic Petri dishes (10 cm in diameter) lined with filter paper. Samples were moistened with distilled water that had been adjusted to pH 7.0 with a 3 percent solution of potassium hydroxide (KOH). After a period of approximately 24 hours, the pH of each culture was measured using a flat-plate electrode and an Orion Model 610 pH meter. After the pH had been determined, excess water in each dish was removed with a pipette (for BK samples), or poured off (for FL or AL samples). Cultures were kept at room temperature (22–25° C) in diffuse daylight and examined with a stereomicroscope on a regular basis for a period of up to three months in order to detect plasmodia and/or fruiting bodies. When necessary, a small amount of water was added to each culture to maintain moist conditions. After several months, cultures prepared with litter (FL or AL) were allowed to dry out completely, after which they were

moistened again and examined at approximately weekly intervals for another four to six weeks.

Myxomycete plasmodia and/or fruiting bodies were noted and recorded each time the cultures were checked. When fruiting bodies of a given species developed more than once in the same culture, they were considered to represent one "collection." As such, some collections consisted of a single fruiting body, whereas others consisted of as many as several dozen fruiting bodies. As soon as fruiting bodies were judged to be fully mature (usually at least one to two days after they were first noticed), the portion of the substrate upon which they occurred was removed from the moist chamber, dried in air, and then glued in a small box for permanent storage.

Identifications of collections were made using the descriptions and keys provided by Martin and Alexopoulos (1969), Farr (1976), Mitchell (1980), and Lado and Pando (1997), or by means of direct comparisons with authentic material of a particular species obtained on loan from the National Fungus Collections (BPI) in Beltsville, Maryland. Voucher specimens of all species reported herein were deposited in the herbarium of the Royal Botanical Garden, Madrid (MA-Fungi), or the herbarium of Fairmont State College (FWVA), with some duplicates in the collections of two of the coauthors (Schnittler and Estrada-Torres) also placed in the herbarium of the Universidad Autónoma de Tlaxcala (TLXM) or the Herbarium Haussknecht, Jena, in Germany (JE).

The assemblages of species associated with each different microhabitat were compared using coefficient of community (CC) and percentage similarity (PS) indices (Mueller-Dombois and Ellenberg 1974; Gauch 1982). The CC index is based solely on a consideration of the presence or absence of species in the two assemblages being compared. CC values range from 0 (when no species are present in both assemblages) to 1.0 (when all species are present in both assemblages). The PS index considers the relative abundance of species and not just their presence in the two assemblages being compared. PS values also range from 0 (for assemblages with no species in common) to 1.0 (for assemblages identical both in species composition and in quantitative values for species). Taxonomic diversity (*sensu* Stephenson et al. 1993) was assessed by calculating the mean number of species per genus (S/G) from the data set for each microhabitat, as well as the pooled data for all microhabitats.

Nomenclature for myxomycetes essentially follows Martin and Alexopoulos (1969) except for the order Stemonitales, where the taxonomic concepts used are those of Nannenga-Bremekamp (1991). Vascular plant nomenclature follows Ogata et al. (1999).

RESULTS

At least 74 species in 27 genera were identified from the 688 collections of myxomycetes considered in this study (Table 12.1). The vast majority (> 95 percent) of the specimens collected could be assigned with a reasonable degree of certainty to a particular species. (The abbreviation “cf.” as part of the name of a species indicates that the identification in question is tentative.) However, it was not possible to identify some specimens beyond genus. This was especially true for those that were old and weathered, excessively moldy, or (particularly for specimens from moist chamber cultures) that had not matured properly. With the exception of a species of *Diderma* (designated as *Diderma* sp. A) that is almost certainly new to science, collections of taxa that could be identified only to genus are included (e.g., as *Arcyria* spp., *Diderma* sp., and *Physarum* spp.) in Table 12.1, but were not considered in comparisons of species diversity among the various microhabitat types. In addition, a number of moist chamber cultures yielded plasmodia that never produced fruiting bodies.

In all, 462 collections were represented by material that fruited in the field under natural conditions, while 226 collections were obtained from the 171 moist chamber cultures prepared with samples of bark or litter (see Table 12.2). The majority of field collections (FC) were associated with coarse woody debris on the forest floor, where a few species (e.g., *Arcyria cinerea*, *A. denudata*, *Hemitrichia calyculata*, and [especially] *H. serpula*) were exceedingly common. In addition to coarse woody debris (i.e., such things as dead stumps, decaying logs on the forest floor, dead branches that had fallen from trees, and fragments of wood), other substrates from which specimens of myxomycetes were collected in the field included decaying palm fronds and dead leaves on the forest floor.

At least 56 different species in 23 genera were identified from the 462 field collections. This total included representatives of all six taxonomic orders recognized for myxomycetes (Martin and Alexopoulos 1969), although the majority (74 percent) of the specimens collected belong to just two orders—the Physarales and the Trichiales. Members of the Trichiales alone accounted for almost 42 percent of all collections. This is due in part to the fact that four of the five most common species we collected belong to the Trichiales. The predominance of the Trichiales is less apparent if numbers of species and not number of collections are considered, because more than half (52 percent) of all species recorded as field collections are members of the Physarales. Members of the Trichiales (16 percent of all species), Stemonitales (16 percent), and Liceales (12 percent) also were relatively common, whereas the Ceratiomyxales and Echinosteliales were each represented by a single species. It should be noted that members of the Ceratiomyxales differ in a number of important respects (e.g., fruiting bodies

TABLE 12.1. Occurrence of myxomycetes in the microhabitats examined in the present study. Data are numbers of collections. FC = field collections, BK = bark surface of living trees, FL = forest floor litter, and AL = aerial litter.

Species	FC	BK	FL	AL
<i>Arcyria cinerea</i>	38	2	14	7
<i>Arcyria denudata</i>	36		3	
<i>Arcyria</i> spp.			1	3
<i>Badhamia ainoae</i>		1		
<i>Calomyxa metallica</i>		1		
<i>Ceratiomyxa fruticulosa</i>	9			
<i>Clastoderma debaryanum</i>	21			1
<i>Collaria arcyrionema</i>	8	1	1	10
<i>Collaria</i> cf. <i>lurida</i>		1		
<i>Comatricha</i> cf. <i>laxa</i>			1	
<i>Comatricha pulchella</i>	2	3		
<i>Comatricha tenerrima</i>	2			1
<i>Comatricha</i> sp.	1			
<i>Craterium leucocephalum</i>	7			
<i>Craterium paraguayense</i>	1			
<i>Craterium</i> sp.	1			
<i>Cribraria cancellata</i>	5			
<i>Cribraria languescens</i>	12	1		
<i>Cribraria microcarpa</i>			5	12
<i>Cribraria tenella</i>	2			
<i>Cribraria violacea</i>	4	4	4	1
<i>Cribraria</i> spp.	2			
<i>Diderma effusum</i>	5	1	1	2
<i>Diderma hemisphaericum</i>	1		9	3
<i>Diderma platycarpum</i>	1			
<i>Diderma rimosum</i>	11		3	
<i>Diderma</i> cf. <i>rugosum</i>	2			
<i>Diderma spumarioides</i>	15			
<i>Diderma</i> sp. A	3			
<i>Diderma</i> sp.	1			

TABLE 12.1. (Continued)

Species	FC	BK	FL	AL
<i>Didymium cf. floccosum</i>	1			
<i>Didymium iridis</i>			2	
<i>Didymium nigripes</i>	5			
<i>Didymium ochroideum</i>			2	
<i>Didymium squamulosum</i>				4
<i>Didymium</i> spp.	3		1	
<i>Echinostelium minutum</i>		3		
<i>Enteridium juranum</i>	1			
<i>Fuligo megaspora</i>	2			
<i>Hemitrichia calyculata</i>	37			
<i>Hemitrichia serpula</i>	57		11	
<i>Lamproderma scintillans</i>			3	
<i>Licea biforis</i>	1			
<i>Licea operculata</i>		1		1
<i>Lycogala exiguum</i>	9			
<i>Macbrideola martinii</i>		7		1
<i>Macbrideola scintillans</i>		4		
<i>Metatrachia horrida</i>	7			
<i>Perichaena chrysosperma</i>	2	1	15	1
<i>Perichaena depressa</i>	4		7	1
<i>Perichaena minor</i>		1	13	1
<i>Perichaena vermicularis</i>		4	1	4
<i>Perichaena</i> sp.				1
<i>Physarella oblonga</i>	5			
<i>Physarum aeneum</i>	1			
<i>Physarum bogoriense</i>	1			
<i>Physarum cinereum</i>	2			
<i>Physarum cf. crateriforme</i>		16		
<i>Physarum flavicomum</i>	4			
<i>Physarum cf. galbeum</i>	1			
<i>Physarum globuliferum</i>	1			
<i>Physarum melleum</i>	2		4	4
<i>Physarum nucleatum</i>	2			

Species	FC	BK	FL	AL
<i>Physarum nutans</i>	9			
<i>Physarum pusillum</i>	1			5
<i>Physarum roseum</i>	3			
<i>Physarum stellatum</i>	36			
<i>Physarum tenerum</i>	4			
<i>Physarum vernum</i>	3			
<i>Physarum viride</i>	6			
<i>Physarum</i> spp.	8	1	2	1
<i>Stemonaria longa</i>	2			
<i>Stemonitis axifera/smithii</i>	17			
<i>Stemonitis fusca</i>	15			
<i>Stemonitis</i> cf. <i>lignicola</i>	1			
<i>Stemonitis nigrescens</i>			4	
<i>Stemonitis</i> sp.	1			
<i>Stemonitopsis hyperopta</i>	2			
<i>Stemonitopsis subcaespitosa</i>		1		
<i>Stemonitopsis typhina</i>	4			
<i>Trichia affinis</i>	9			
<i>Trichia verrucosa</i>	1			
<i>Trichia</i> spp.	1	1		
<i>Willkommlangea reticulata</i>	1			
Total	462	55	107	64

are exosporous instead of endosporous) from members of the other orders, and are considered by most to be more closely related to the protostelids (another group of slime molds) than to the other myxomycetes (Olive 1975). However, they have been included along with the other myxomycetes in virtually all previous studies of the latter group, which is the approach taken in the present study.

In addition to the four species already mentioned, *Physarum stellatum* (36 collections), *Clastoderma debaryanum* (21), *Stemonitis axifera/smithii* (17), *Diderma spumarioides* (15), and *Stemonitis fusca* (15) would be regarded as “abundant” on the basis of each being represented by greater than 3.0 percent of the total number of the collections (Stephenson, Kalyanasundaram, and Lakhanpal 1993). Although recognized as distinct species by Martin and Alexopoulos (1969), *Stemonitis axifera* and *S. smithii* have been considered to be “linked . . . by intergrading forms” by some authors (e.g., Farr 1976).

TABLE 12.2. Summary data on moist chamber cultures

Microhabitat	No. of cultures	pH		Positive (percent)	No. of species
		range	mean		
Bark surface (BK)	46	7.7–8.3	8.0	74	19
Aerial litter (AL)	47	5.5–7.2	6.6	87	17
Forest floor litter (FL)	78	5.5–7.3	6.6	87	19

Specimens collected in the present study included examples of such intergrading forms, and all were combined and listed under a single taxon.

Moist chamber cultures prepared with bark (BK) yielded at least 19 species of myxomycetes in 14 different genera. *Physarum* cf. *crateriforme* was represented by the largest number of collections (16), with *Macbrideola martinii* (7), *M. scintillans* (4), *Cribraria violacea* (4), and *Perichaena vermicularis* (4) the only other species represented by more than 3 collections. Members of the Stemonitales and Trichiales each made up 32 percent of the assemblage of species recorded from bark, whereas the Physarales (35 percent) and Stemonitales (31 percent) were represented by the greatest numbers of collections. Values of pH recorded for these moist chamber cultures ranged from 7.7 to 8.3, with a mean value of 8.0 (Table 12.2).

Nineteen species in 11 genera were collected from moist chamber cultures prepared with samples of forest floor litter (FL), and 17 species in ten genera were recorded from cultures prepared with samples of aerial litter (AL). The most common species of myxomycetes on forest floor litter (FL) were *Perichaena chrysosperma* (15 collections), *Arcyria cinerea* (14), *Perichaena minor* (13), *Hemitrichia serpula* (11), and *Diderma hemisphaericum* (9). The four most common species all belong to the Trichiales, which was clearly the predominant order (with > 60 percent of all collections) in this microhabitat. The Trichiales and the Physarales were represented by the most species. For aerial litter (AL), *Cribraria microcarpa* (12), *Collaria arcyriionema* (10), *Arcyria cinerea* (7), and *Physarum pusillum* (5) were the only species represented by at least 5 collections. Members of the Liceales, Stemonitales, Trichiales, and Physarales were all relatively common in the aerial litter microhabitat, where their respective contributions to the total numbers of collections and species ranged from 19 percent to 30 percent and 18 percent to 29 percent, respectively. Values of pH recorded for these two sets of moist chamber cultures were remarkably similar, and the percentage of positive cultures (87 percent) was the same for both types of litter (Table 12.2).

Coefficient of community (CC) and percentage similarity (PS) indices (Table 12.3) calculated from all possible pairwise combinations of the data sets from the four different microhabitats (Table 12.1) yielded mean values of 0.36 and 0.21, respectively. Consequently, the differences among the microhabitats resulted more from differences in abundances for species shared in common than from differences in actual species composition. The comparison of field collections (FC) and collections from bark (BK) yielded the very lowest values for both indices. A comparison of field collections with a data set obtained from combining the records of species obtained from all 171 moist chamber cultures produced a CC value of just 0.34. This would indicate that the assemblage of species fruiting in the field under natural conditions is distinctly different from the assemblage appearing in moist chamber cultures. Indeed, only 16 species were recorded both as field and moist chamber culture collections, and only a few of these (e.g., *Arcyria cinerea*, *Hemitrichia serpula*, and *Collaria arcyronema*) were fairly common in the two different situations.

The data set for aerial litter (AL) had the highest overall CC value (mean = 0.45) when compared to those for the other microhabitats, and a comparison of the two types of litter microhabitats yielded the very highest value (0.61). However, the PS value calculated for these two microhabitats was much lower (0.35).

The mean numbers of species per genus (S/G) calculated for the four different data sets ranged from 1.36 (bark) to 2.43 (field collections). Combining all of the data sets yielded a value of 2.74.

DISCUSSION

The total number of species (74) recorded for El Edén in our study does not reflect the entire myxoflora of the general study area. Ogata and Andrade-Torres (1996) and Andrade-Torres (1997) recorded 20 species and two genera not encountered by us. The addition of these species (*Arcyria carnea*, *A. incarnata*, *A. nutans*, *A. pomiformis*, *Ceratiomyxa morchella*, *C. sphaerosperma*, *Collaria elegans*, *Cribraria aurantica*, *Cr. intricata*, *Diachea bulbillosa*, *Diderma deplanatum*, *Didymium verrucosporum*, *Lycogala epidendrum*, *Stemonitis flavogenita*, *S. pallida*, *S. splendens*, *S. webberi*, *Trichia floriformis*, *Tubifera ferruginea*, and *T. microsperma*) brings the overall total to 94 species in 29 genera.

Based on these data, the portion of the Yucatán Peninsula represented by the general study area has a moderate to high myxomycete diversity when compared to other regions of the Neotropics for which comparable data exist. For example, the myxoflora of Costa Rica is probably as well known as any area completely within the Neotropics. Alexopoulos and Saenz (1975)

TABLE 12.3. Comparison of assemblages of myxomycetes associated with the four different microhabitats examined in the present study. Coefficient of community and percentage similarity indices are given.

a. Community coefficient

	Field collections (FC)	Bark surface (BK)	Forest floor litter (FL)	Aerial litter (AL)
Field collections	***	0.19	0.27	0.25
Bark surface	0.10	***	0.37	0.50

b. Percentage similarity

	Field collections (FC)	Bark surface (BK)	Forest floor litter (FL)	Aerial litter (AL)
Bark surface	0.10			
Forest floor litter	0.30	0.14	***	0.61
Aerial litter	0.17	0.23	0.35	***

reported 91 species for the entire country, but this total was based almost entirely on field collections. Extensive use of the moist chamber culture technique by Schnittler and Stephenson (2000) increased the number of myxomycetes known from Costa Rica by at least 32 taxa. Several additional taxa are represented among specimens collected as a result of field work carried out in the country since 1995. However, the total number of species now known from all of Costa Rica still seems low when compared to the species totals reported for specific and much smaller study areas in temperate regions of the world (e.g., Stephenson 1988; Stephenson, Kalyanasundaram, and Lakhanpal 1993). This suggests that the assemblages of myxomycetes associated with tropical forests are inherently less diverse (or certainly no more diverse) than those associated with temperate forests, as discussed by Alexopoulos (1970) and Farr (1976).

The myxomycete survey carried out thus far at El Edén is certainly not complete. As Seifert (1981) and others have indicated, one of the most frequently expressed complaints in studying fungal communities is that all of the species present are never known. This same situation undoubtedly applies to myxomycetes, whose life history is rather similar in a number of basic respects (e.g., a vegetative stage that is usually within a substrate and thus not easily studied or even detected in nature) to that of the “true” fungi. An intense sampling effort, especially one carried out over a period of at least several years, would almost certainly yield an appreciable number of additional species. Moreover, myxomycetes are known to occur in several microhabitats not yet examined at El Edén. One important microhabitat for

myxomycetes both in high-latitude regions of the world and in deserts is the dung of herbivorous animals. A few species seem to occur predominantly or even exclusively on dung (Eliasson and Keller 1999). In moist tropical forests, animal dung decomposes very rapidly and usually does not persist long enough to serve as a potential microhabitat for myxomycetes. Although no animal dung of sufficient mass to be noticed easily in the field while at El Edén, was encountered, this does not mean that it does not occur in the general study area. During the dry season, the possibility of dung serving as a microhabitat for myxomycetes cannot be discounted.

Other microhabitats seemingly unique to tropical/subtropical forests, and not known to support myxomycetes until very recently, are the living inflorescences of large tropical herbs, the cover of epiphyllic liverworts on living leaves of understory plants (Schnittler 2000), and the mantle of dead organic matter (literally a “canopy soil”) found at the bases of vascular epiphytes growing on the trunks and larger branches of trees (Stephenson and Landolt 1998). The first of these appears to be especially rich in myxomycetes, and some species (e.g., *Physarum didermoides*, not yet known from El Edén) seem to show a strong preference for this microhabitat. Myxomycetes also are known to occur in forest soils (Kalyanasundaram 1997), but their occurrence in this microhabitat has received very little study (Stephenson and Cavender 1996).

In a given study area, the pH of the substrates potentially available to myxomycetes is regarded as a major factor influencing the distribution of these organisms (Härkönen 1981; Stephenson 1989; Wrigley de Basanta 2000; Mosquera, Lado, and Beltrán-Tejera 2000). Based upon the values obtained for samples used to prepare moist chamber cultures in the present study (Table 12.2), most substrates in Yucatán forests are mildly acidic to moderately basic. Although many myxomycetes appear to have a relatively wide pH tolerance, this is not the case for all species. Härkönen (1981), who measured the pH of substrates upon which fruitings occurred in a study of the distribution patterns of myxomycetes associated with the bark microhabitat in southern Finland, concluded that species of myxomycetes have different pH optima and amplitudes. In her study, some species seemed to prefer an acidic substrate, whereas others never developed under low pH conditions. Stephenson (1989) found the same to be true for both the bark microhabitat and the forest floor litter microhabitat in a study carried out in the eastern United States. In general, members of the Stemonitales developed under more acidic conditions than did members of the Physarales and the Trichiales.

The pH values recorded for the substrates we examined were generally more basic than those reported for the same types of substrates in other studies. This was particularly true for bark. For the study carried out in the eastern United States (Stephenson 1989), values of pH for moist chamber

cultures prepared with samples of bark ranged from 3.3 to 7.4, with a mean value of 6.0 for all cultures. The values recorded for cultures prepared with samples of forest floor litter ranged from 3.6 to 6.5, with a mean value of 5.2. Schnittler and Stephenson (2000), who studied myxomycete biodiversity in four different forest types in Costa Rica, reported mean values for pH ranging from 6.4 to 6.6 for bark and 5.9 to 6.5 for samples of litter, including both aerial litter and forest floor litter. Stephenson, Landolt, and Moore (1999), in a study of the myxomycetes associated with forest floor litter in five different forest types in Puerto Rico, reported mean values that ranged from 4.4 to 5.9.

The number of species (19) recorded from bark in the present study is much lower than the total (47) reported for the temperate forest study site in the eastern United States (Stephenson 1989). Schnittler and Stephenson (2000) also reported relatively low numbers of species of myxomycetes associated with the bark microhabitat in four forest types in Costa Rica, which suggests that this microhabitat is simply less diverse in tropical forests than in temperate forests. In addition to yielding a lower number of species than would be expected from a comparable series of moist chamber cultures prepared with samples of tree bark from a temperate forest, bark cultures in the present study also seemed to produce generally smaller fruitings. In many instances, only one or (at most) a few fruiting bodies appeared in these cultures.

Experience acquired as a result of working with a large number of bark cultures from temperate forests showed that fruitings were noticeably sparse. For example, *Echinostelium minutum* is nearly ubiquitous in moist chamber cultures prepared with bark samples from temperate trees, and cultures containing several hundred fruiting bodies are not uncommon. This was not the case for bark samples from El Edén, where *E. minutum* was uncommon and fruitings small.

A number of as yet determined factors undoubtedly contribute to the differences noted for temperate versus tropical bark, but the high pH values recorded for the latter are likely to represent a factor of some importance. This is almost certainly the case for *E. minutum*, which appeared only on acidified bark in a study of the possible effects of acid deposition on the assemblage of myxomycetes associated with tree bark in the city of Madrid, Spain (Wrigley de Basanta 2000).

Numbers of species recovered from cultures of forest floor litter varied widely in the studies mentioned above. In any event, the number of species (19) we obtained is comparable to or even higher than those reported for particular study sites.

Moist chamber cultures prepared with samples of aerial litter were just as productive as those prepared with samples of forest floor litter, except for the slightly lower number of species recorded (17 for AL versus 19 for FL).

However, as already noted, the assemblages of species associated with the two litter microhabitats were appreciably different. The fact that the fruiting bodies of myxomycetes sometimes occur on substrates located above the ground has long been known, but the use of the moist chamber culture technique to examine aerial litter in tropical forests is a very recent development. As such, data sets comparable to that obtained in the present study are lacking. Clearly, the aerial litter as a microhabitat for myxomycetes warrants further study.

A predominance of members of the Physarales in tropical/subtropical forests has been reported in several other studies (e.g., Stephenson, Kalyanasundaram, and Lakhanpal 1993; Lado, Rodríguez-Palma, and Estrada-Torres 1999b; Schnittler and Stephenson 2000). In the majority of instances, members of the Trichiales were next in abundance, with the Stemonitales the only other order making a significant contribution to the total myxoflora. In general, these three are the predominant orders, regardless of whether numbers of species or number of collections are considered.

The data obtained in this study conform to these general patterns, with two exceptions. First, members of the Trichiales made up a larger proportion of the total number of collections (especially field collections and collections from the forest floor litter microhabitat) than might have been anticipated. Second, the contribution of the Liceales (both in numbers of collections and numbers of species) to the assemblage of myxomycetes associated with aerial litter was greater than has been reported in most other studies of the myxoflora of tropical/subtropical forests.

As Simberloff (1970) and others have pointed out, a biota in which the species are divided among many genera (i.e., a low S/G value) is intuitively more “diverse” than one in which many species belong to only a few genera (i.e., a high S/G value). On this basis, the three microhabitats sampled by means of moist chamber cultures are more diverse (with S/G values ranging between 1.4 and 1.7) than the microhabitat represented by field collections (S/G = 2.4). However, this difference may not be as ecologically meaningful as the values themselves would seem to suggest. Each of the other microhabitats (i.e., the bark surface of living trees, forest floor litter, and aerial litter) is almost certainly ecologically less complex than the microhabitat represented by field collections, which is probably best viewed as a complex of a number of different and somewhat intergrading microhabitats. Presumably, any single component of this complex of microhabitats, if it could be isolated and studied, would be characterized by a subset of the total assemblage of species recorded as field collections. It seems likely that the resultant S/G value calculated for this subset would be comparable to those of the other microhabitats. Both the S/G value for field collections and the value calculated for all collections were somewhat lower than that reported for

tropical/subtropical southern India by Stephenson, Kalyanasundaram, and Lakhanpal (1993).

Three basic types of plasmodia have been described in the myxomycetes (Alexopoulos 1960). The most commonly encountered type is the phaneroplasmodium, which is robust, can achieve considerable size in some species, and appears to tolerate the two extremes of the moisture gradient better than the other types of plasmodia (Kalyanasundaram 1997; Schnittler and Stephenson 2000). A phaneroplasmodium is characteristic of the Physarales and probably almost all members of the Trichiales. Because these were the predominant orders represented among our collections from El Edén, it follows that a very high percentage of the species (and especially records) of myxomycetes to be found in forests of the Yucatán Peninsula are characterized by a phaneroplasmodium.

Stephenson, Landolt, and Moore (1999), as well as Schnittler and Stephenson (2000), reported that overall abundance and numbers of species of myxomycetes decrease with increasing elevation in Puerto Rico and Costa Rica. Cloud forests located at the very highest elevations and characterized by almost daily cloud exposure and a very high annual precipitation supported very few myxomycetes, whereas in lower elevation forests—especially those located towards the xeric end of the moisture gradient—myxomycetes were relatively common.

Studies carried out in deserts (e.g., Blackwell and Gilbertson 1980; Schnittler and Novozhilov 2000) indicate that these organisms are often surprisingly abundant, although only when there is sufficient moisture available to allow their growth and development (Lado, Mosquera, and Beltrán-Tejera 1999a). Such conditions exist (1) during and immediately following a period of rainy weather and (2) on substrates collected from nature and placed in moist chamber cultures.

When considered together, these patterns suggest that myxomycetes are organisms that adapt to highly fluctuating conditions of environmental moisture, but continuously high moisture levels do not favor their growth and development. During the wetter portions of the year, the forest floor at El Edén is almost certainly too moist to be favorable for myxomycetes. Seasonally flooded forests would represent the extreme example of this situation. Under these circumstances, the only microhabitats realistically available for myxomycetes would be aerial microhabitats. In tropical/subtropical forests characterized by a distinct dry season, the experience suggests that myxomycetes are most abundant at the very beginning of the dry season when most substrates on which myxomycetes occur are still moist but not excessively so. Later in the dry season, as these substrates dry out, myxomycetes become much less common.

As noted by Stephenson (1988), myxomycetes would seem to be rather opportunistic or “fugitive” organisms (*sensu* Hutchinson 1951) in that they

have a high reproductive potential, possess effective dispersal mechanisms, and are characterized by rapid development. These attributes allow them to exploit successfully microhabitats that are limited both temporally and spatially in nature. Although a particular microhabitat within which a species of myxomycete has become established may persist for only a short period of time, the species always survives by reestablishing itself in some new microhabitat (which may indeed be the very same microhabitat if conditions once again become favorable). Because of their life-history strategy and inconspicuous nature, myxomycetes provide an immense challenge to anyone who wishes to study their ecology.

The present study was undertaken to add to our knowledge of the distribution and ecology of myxomycetes in Neotropical forests, where they are a very understudied group of organisms. Such knowledge is a basic and necessary prerequisite to a more complete understanding of the relative importance and exact role of myxomycetes in the detritus food chain, as well as the ecological significance of their interactions with other organisms in terrestrial ecosystems.

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Chapter 13

A Preliminary Assessment of the Butterfly Fauna of El Edén Ecological Reserve: Species Richness and Habitat Preferences

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INTRODUCTION

The Yucatán Peninsula is a distinct subregion—not only biologically, but also geologically and climatically. It includes parts of southern Mexico, Belize, and Guatemala. The peninsula was once covered with forest, but at present, this forest does not have the same characteristics before human settlements (Welling 1966). Data from the Yucatán Peninsula indicate that the late Pleistocene and early Holocene epochs were dry (Metcalf et al. 2000). In many cases, lake levels were strongly influenced by lower glacial sea levels and groundwater levels. Lake levels started to rise after 9000 yr. B.P. Moist conditions, possibly wetter than present, were established by about 6800 yr. B.P., but this was followed by a dry period between about 6000 and 5000 yr. B.P. (Metcalf et al. 2000).

The late Holocene was marked by strong variations in water balance, and the driest period of the Holocene was recorded at many sites sometime between 1500 and 900 yr. B.P. This very dry period is of considerable interest as it corresponds with the time of the collapse of the lowland Maya. Wetter conditions were then reestablished. Many sites in this region also provide records of human disturbance throughout the late Holocene (Metcalf et al. 2000), and sometimes deliberate modification of the natural environment.

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Leyden et al. (1998) have suggested that pollen records show a very strong human disturbance signal. Hence, both historical human and natural destructive forces have been influential in greatly decimating the natural forest cover along with the associated fauna in the Yucatán Peninsula. Because the area of primary forest and other semi-natural habitats have suffered dramatic changes in much of the peninsula over the course of its history, it is likely that this has also precipitated changes in animal species composition and diversity.

Compared to other insect groups in the Neotropics, butterflies have become such well-studied species that they have been used as a representative insect group for many regions. Unlike most insects in tropical forests, butterflies are taxonomically tractable, occur at moderate levels of species richness, and are easy to sample (Gilbert 1984; Brown 1991; New 1991; Sparrow et al. 1994; Lewis, Wilson, and Harper 1998). These characteristics have made tropical butterflies a popular group for investigations into the effects of small-scale disturbances (Bowman et al. 1990; Spitzer et al. 1993), selective logging (Hill et al. 1995), and forest fragmentation (Daily and Ehrlich 1995). Several studies have revealed consistent differences in the responses of butterflies with large and small geographical ranges to human disturbance of tropical forest habitats (Thomas 1991). Whereas widespread butterfly species typically become more abundant in human-modified tropical forests, endemic or geographically restricted species decline (Thomas 1991; Spitzer et al. 1993; Hill et al. 1995).

The aim of this paper was to investigate the patterns of species composition and richness, species habitat preferences, and geographic ranges of butterflies from a specific region in the Yucatán Peninsula—namely, the El Edén Ecological Reserve in the northern part of the peninsula. Whether current species composition patterns could reflect historical (and recent) recurrent habitat modifications in the peninsula is the focus of investigation. Can current butterfly species composition tell us something about past and present habitat disturbance in the Yucatán Peninsula? Are geographically widespread butterfly species more common in Yucatán landscapes than elsewhere in Mexico and Central America?

METHODS

Study site

The El Edén Ecological Reserve (hereafter, El Edén) is located in the Mexican State of Quintana Roo, in the northern portion of the Yucatán Peninsula (Figure 13.1). El Edén occupies an area of approximately 1,560 hectares (ha). Medium-height tropical subperennial forest is the main

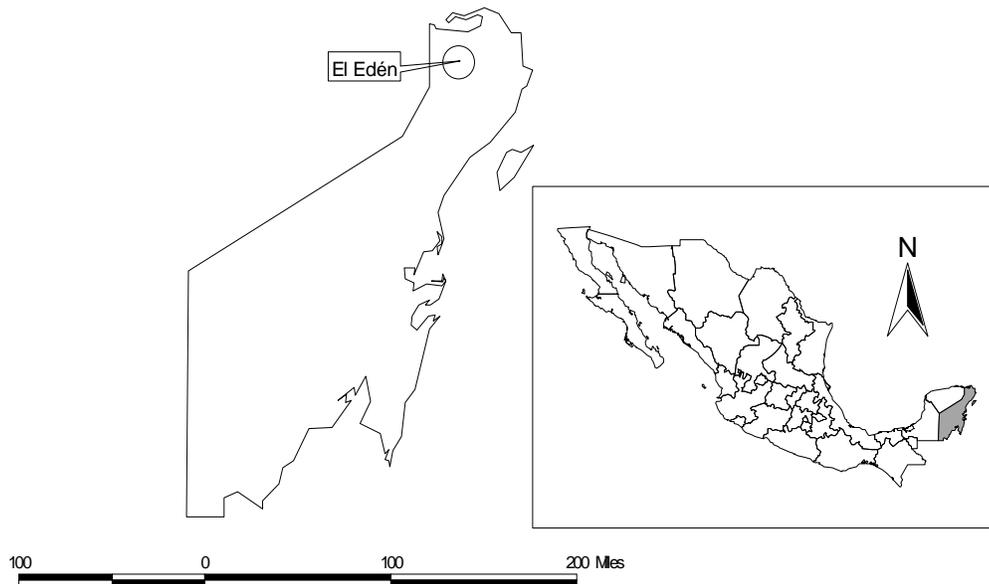


FIGURE 13.1. The Mexican State of Quintana Roo is shown in black in southern Mexico (inset), and the circle shows the location of El Edén Ecological Reserve. The bar scale applies to Quintana Roo.

vegetation type in the region. A variety of habitat types are also present at El Edén, namely secondary forest, inundated mixed forest (“tintal”), savanna, forest gaps, hedges, and forest borders. All major habitat types recognized in the vicinity of El Edén (see as follows).

Sampling protocol and fauna size

During late summer and early autumn 1995, mostly Papilionidae, Pieridae, and Nymphalidae butterflies were caught using direct netting and traps of vertical cylindrical netting (Van Someren-Rydon traps). For other families (e.g., Hesperidae and Lycaenidae), limited sampling efforts were carried out. Van Someren-Rydon traps were baited with decaying fruits and hung above trees near lightgaps, forest margins, and moist trails (DeVries 1987; Raguso and Llorente-Bousquets 1991). Traps were inspected daily for captured specimens. Sampling efforts began at 9:00 a.m. and ended at 6:00 p.m. Sampling was carried out only when conditions were ideal to observe active butterflies (Pollard and Yates 1993). All captured individual butterflies were mounted, labeled as to locality, and deposited at the Entomological Collection of El Colegio de la Frontera Sur (ECOSUR). Specimens were identified using a variety of sources, including De la Maza-Ramírez (1987);

De la Maza-Elvira and De la Maza-Elvira (1993); and DeVries (1987). The reference entomological collection at ECOSUR was also used.

As a way of checking the accuracy of our sampling effort at El Edén, the cumulative number of species versus the number of individuals sampled (see Figure 13.2) was plotted. The species accumulation curve is expected to reach a maximum value when all species at a site have been collected. The faunistic data was fitted to a Michaelis-Menten function type (known in the Entomological literature as Clench's function), which has provided accurate estimates for butterfly faunas in a variety of tropical sites (Clench 1979; Soberón and Llorente 1993; Colwell and Coddington 1994; Raguso and Llorente-Bousquets 1991; León-Cortés, Soberón-Mainero, and Llorente-Bousquets 1998). Clench's equation is expressed as follows:

$$S(t) = \frac{a*t}{(1 + b*t)} \quad (1)$$

In Equation (1), $S(t)$ is the expected size of the list, a is the slope at the beginning of the collection, b is a parameter related to the shape of the accumulation of new species during the collection, and t is the collecting effort (e.g., some unit of time) (Soberón and Llorente 1993; León-Cortés, Soberón-Mainero, and Llorente-Bousquets 1998). Using this method, the size and the amount of effort needed to achieve the total sample size of the El Edén butterfly fauna was assessed.

Habitat distribution and geographic range

The habitat distribution and geographic range data was analyzed for El Edén Papilionidae, Pieridae, Nymphalidae, Hesperidae, and Lycaenidae butterflies from field observations as well as from the information given in the species account in DeVries (1987); Tyler, Brown, and Wilson (1994); and Opler and Wright (1999). Although Hesperidae and Lycaenidae were also considered for the present analysis, some species were excluded because their habitat description was too scant or ambiguous.

The present analysis deals with 76 species of the 86 species reported in this paper. Following Thomas (1991), butterfly species were classified as occupying unmodified vegetation (when no mention was made that they occupy secondary or agricultural habitats), or as occupying modified vegetation (when mention was made that they occupy secondary, agricultural, or other human-modified habitats, although most of these species also occupy unmodified habitats). Some species that were classified as occupying only unmodified vegetation do make some use of modified habitats, but in most cases the latter are used very rarely by these species, and usually only when modified and unmodified habitats are adjacent (DeVries 1987). A habitat

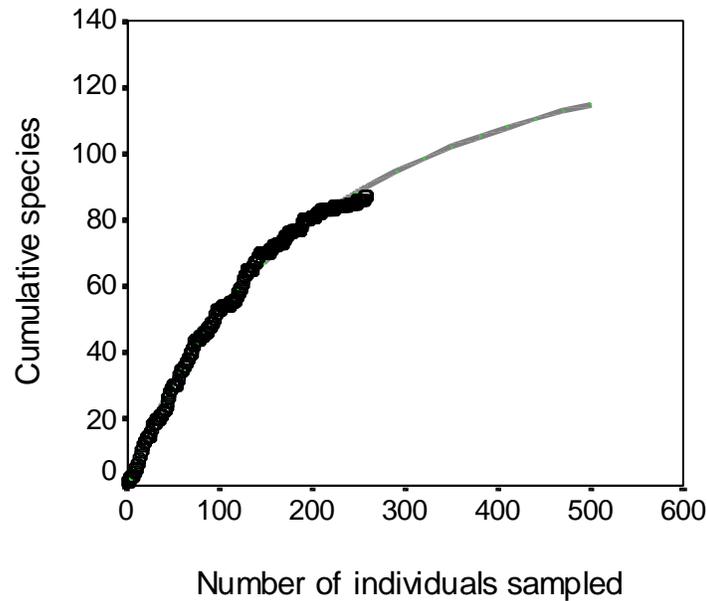


FIGURE 13.2. Plot of cumulative species versus the number of individuals sampled at El Edén. The data for the observed cumulative number of butterfly species are shown as circles on the plot, while the estimates (continuous line) of richness are based on Clench's equation ($R^2 = 0.99$). Asymptotic value for Clench's function is 163 species.

designation to each species before examining its geographic range category. Geographic range categories were consulted in DeVries (1987); Tyler, Brown, and Wilson (1994); and Opler and Wright (1999). The three geographic range categories used were defined as follows:

1. Restricted to southeast Mexico and Central America, but not farther south than Panama
2. North America to Central America, and/or southern Mexico to northern South America
3. Widespread in the Neotropics (at least reaching Brazil or Bolivia)

Although the habitat distribution and geographic range categories were somewhat arbitrary, the general pattern, rather than the habitat-use patterns of a particular species. We also wanted to examine a possible overall association between habitat use and geographic range within each subfamily was also examined. Because the sample size for each subfamily was rather small, samples were collated to examine the overall trend. The proportion of species in each geographic range category that was restricted to unmodified habitats only was calculated. Thus, the whole sample had up to three values. Values were examined according to a declining or increasing proportion of species restricted to unmodified (or primary) habitats with increasing geographic range.

RESULTS

Butterfly richness

Eighty-six species of butterflies were collected during a 35-day sampling period at El Edén (see Appendix 1). Nymphalidae was the richest family with 53 species (62 percent), followed by Pieridae with 13 species (15 percent), Hesperidae with 12 species (14 percent), Papilionidae with 5 species (6 percent), and Lycaenidae with 3 species (3 percent).

The plot of cumulative species versus the number of individuals sampled for the El Edén data is shown in fig. 2. Using Equation (1), the estimated richness at El Edén is 163 species. If this estimate is accurate, then we sampled 53 percent of the El Edén butterfly fauna in 35 days. Although the regression line is a reasonably close match to the observed data points ($R^2 = 0.99$, Norusis [1994], Figure 13.2), the collections were conducted over a consecutive 35-day period during portions of two seasons (late summer and early autumn). Therefore, model predictions may be biased due to natural changes in the seasonal patterns and abundance of butterfly species. An important number of butterfly species remains to be recorded, mostly for Lycaenidae, Riodinidae, and Hesperidae families, which are extremely rich in Central America.

Habitat use and geographic range categories

The habitat use and geographic range categories assigned to each of the species included in the analysis are shown in Appendix 1. Fifteen species were placed in the unmodified habitats category, and 61 species were placed in the modified habitats category. A significant association between habitat use and geographic range for 76 butterfly species at El Edén (Table 13.1, $\chi^2 = 17.23$, d.f. = 2, $p < .001$). Species with narrow geographic ranges were usually grouped in unmodified habitats, whereas widespread species were much more likely to make some use of human-modified habitats.

A declining proportion of species restricted to unmodified habitats with increasing geographic range (Figure 13.3, Table 13.2). Thus, the general trend at El Edén suggested that widespread butterfly species were more likely to make some use of modified habitats.

TABLE 13.1. Association between habitat use and geographic range for Nymphalidae, Pieridae, Hesperidae, Papilionidae, and Lycaenidae butterfly species at El Edén^a.

Habitat use at El Edén	Geographic range categories		
	1	2	3
Unmodified habitats	6	2	7
Modified habitats	2	13	46

^aAssociation between habitat use and geographic range: chi square = 17.23, d.f. = 2, $p < .001$.

1 = Restricted to southeast Mexico and Central America, but not farther south than Panama; 2 = North America to Central America, and/or southern Mexico to northern South America; 3 = Widespread in the Neotropics (at least reaching Brazil or Bolivia).

DISCUSSION

Species richness

The butterfly inventory reported here represents a preliminary list of the butterfly fauna of El Edén. The faunistic data closely fit the model (see Figure 13.2) but, as mentioned previously, the data were collected over a consecutive 35-day period during portions of two seasons (late summer and early autumn) of 1995. Thus, the estimate of 163 species at El Edén is tentative. A species that is rare or absent one day is likely to be rare or absent the next, but may be common in another season or during the same season in a different year. For this reason, we expect a greater increase in the number of new species, particularly for largely unknown butterfly families such as Lycaenidae, Riodiinae, and Hesperidae. More conspicuous butterfly species (e.g., Papilionidae, Pieridae, and Nymphalidae) were sampled vigorously during the course of this study. Therefore, we would not expect to add many more new species for these families.

Habitat preferences and geographic ranges

Habitat availability (and the disturbance of it) may influence a species' abundance and its distribution (e.g., Hughes 2000). Although disturbance may be brought about by human activities, natural events such as hurricanes, fires, and falling trees may also cause ecological disturbance of comparable magnitude. Depending on its historical scale and frequency, habitat modification may elicit a variety of responses from the members of a given Neotropical butterfly community (Raguso and Llorente-Bousquets 1991).

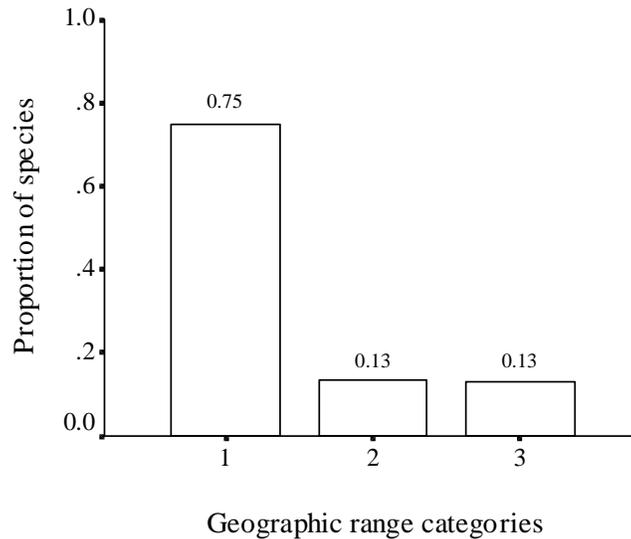


FIGURE 13.3. The proportion of butterfly species at El Edén, using unmodified habitats with increasing geographic range (see Table 13.2). For a description of geographic range categories, see text.

For instance, recent evidence supports the hypothesis that historical climate variations have had a great effect on British butterfly species assemblages (Dennis 1977; Thomas 1994). Janzen (1988) has emphasized that the resulting mosaic of habitats and successional stages of vegetation can accommodate more species of Lepidoptera than a pristine tropical dry forest (either past or future) could realistically support.

The prevalence of weedy, cosmopolitan species at El Edén conform well to the pattern observed by Welling (1966) for *Papilio*, *Euptoieta*, *Zerene*, and *Phoebis* species in patches cut into dense thorn forests of the Yucatán Peninsula. Nearly 20 percent of the species reported here have been considered as a fauna characteristic of disturbed habitats (see Raguso and Llorente-Bousquets 1991). Some of these butterflies are migratory habitat generalists with nonspecialized host plant requirements and wide distributions throughout the Neotropics, and could rapidly invade disturbed rainforest patches in the Yucatán Peninsula (e.g., *Papilio toas*, *Ascia monuste*, *Phoebis sennae*, *P. Argante*, *Dannaus gilippus*, and *Marpesia chiron*).

From a habitat point of view, there are important differences between cosmopolitan species that can exploit disturbed forest habitat and organisms that are adapted to undisturbed primary forests. When examining a species' abundance and distribution across many habitat types, one must consider the availability of the habitats (MacNally 1989). It is possible to have a species that can only use one habitat type, but is relatively abundant in that habitat. If the habitat type is widespread, then the species will be distributed across a large range; conversely, if the habitat is rare, then the species will be narrowly

TABLE 13.2. Association between habitat use and geographic range for butterflies in each subfamily of Nymphalidae, Pieridae, Hesperidae, Papilionidae, and Lycaenidae at El Edén.

Habitat	Geographic range categories					
	1		2		3	
	U	M	U	M	U	M
Nymphalidae Apaturinae	0	0	0	0	0	1
Nymphalidae Brassolinae	0	0	0	0	0	2
Nymphalidae Charaxinae	2	0	0	0	1	6
Nymphalidae Danainae	0	0	0	1	0	1
Nymphalidae Heliconiinae	0	0	0	0	0	4
Nymphalidae Melitaeinae	0	0	0	1	0	1
Nymphalidae Morphinae	0	0	0	1	0	0
Nymphalidae Nymphalinae	3	1	1	6	5	12
Nymphalidae Satyrinae	0	0	0	0	1	0
Pieridae Coliadinae	0	0	0	3	0	8
Pieridae Pierinae	0	0	0	0	0	2
Hesperidae Pyrginae	0	0	1	1	0	5
Papilionidae Papilioninae	1	1	0	0	0	3
Lycaenidae Polyommatainae	0	0	0	0	0	1
Number of species	6	2	2	13	7	46

U = unmodified habitats; M = modified habitats

1 = Restricted to southeast Mexico and Central America, but not farther south than Panama; 2 = North America to Central America, and/or southern Mexico to northern South America; 3 = Widespread in the Neotropics (at least reaching Brazil or Bolivia).

distributed. Thus, abundance-distribution relationships can change depending on the geographic extent of the habitats in which species' densities are measured (e.g., Gaston and Lawton 1990).

Few forest species that possess relatively narrow geographic ranges were classified as making use of modified habitats. These included: *Achalarus toxeus*, *Dynamine talassina*, *Hamadryas februa ferentina*, *H. guatemalena guatemalena*, *H. iphite*, *Memphis morvus boisduvali*, *Pyrrhogyra neaerea hypsenor*, *Taygetis virgilia rufomarginata*, and *Temenis laothoe agatha*. Geographically restricted or endemic butterfly species are often regarded as biotope specialists, although they can be among the most abundant species at

sites where they occur. Some biotope specialists might occupy disturbed habitats, but in most cases the latter are used very rarely by these species, and usually only when modified and unmodified habitats are adjacent (Thomas 1991). For instance, many savanna and tropical dry forest butterflies appear to congregate in mesic habitats, such as gallery forests, or migrate to higher elevations in the dry season (e.g., DeVries 1987). The microdistribution of butterflies in a habitat is influenced by a variety of abiotic and biotic factors such as the distribution of food, shelter, microclimatically favorable spots, or intraspecific and interspecific interactions (Loertscher, Erhardt, and Zettel 1995). Furthermore, many species may be specialists on naturally occurring successional habitats and so be able to occupy human-modified areas that provide the same successional conditions.

If the relationship between habitat use and geographic range reported here is repeated elsewhere in Mexico and Central America as past surveys suggest it is (e.g., Thomas 1991; Raguso and Llorente-Bousquets 1991), an increasing proportion of secondary vegetation throughout the Neotropics will produce a decreasing difference between the faunas of different regions (i.e., endemic species will be exterminated with the loss of primary forest, and the same widespread species will be left inhabiting secondary vegetation in each region). If unmodified habitats continue to be lost, local (alpha) diversity may not noticeably decrease—and may sometimes increase (e.g., Raguso and Llorente-Bousquets 1991)—but regional (beta) diversity will decline.

Although our conclusions are preliminary, the relatively equal time and effort we spent at different habitats within El Edén produced results that support this conclusion. It would be desirable to establish uniform biodiversity-monitoring protocols at a wide range of spatial scales and for different regions in the Yucatán Peninsula. These protocols would build on the results presented here and attempt to generalize the present status of butterfly diversity in the peninsula with the factors that are affecting changes in species composition.

**APPENDIX:
CHECKLIST OF THE BUTTERFLIES
AT EL EDÉN ECOLOGICAL RESERVE,
QUINTANA ROO, MEXICO.**

Taxon	Habitat use	Geographic range
HESPERIOIDEA		
HESPERIIDAE		
Pyrginae		
<i>Proteides mercurius</i> (Fabricius)	2	3
<i>Polignus leo</i> Gmelin	2	3
<i>Chioides zilpa</i> (Butler)	2	2
<i>Urbanus proteus</i> (Linnaeus 1758)	2	3
<i>Urbanus dorantes</i> (Stoll 1790)	2	3
<i>Urbanus tanna</i> Evans	NA	NA
<i>Astraptus aulensis</i>	NA	NA
<i>Achalarus toxeus</i> (Plötz 1782)	1	2
<i>Xenophanes tryxus</i> (Stoll 1780)	2	3
<i>Heliopetes arsalte</i> (Linnaeus 1767)	NA	NA
<i>Oligoria maculata</i>	NA	NA
<i>Spathilepia clonius</i>	NA	NA
PAPILIONOIDEA		
PAPILIONIDAE		
Papilioninae		
<i>Battus polydamas polydamas</i> (Linnaeus 1758)	2	3
<i>Papilio thoas</i> Rothschild & Jordan 1906	2	3
<i>Eurytides protesilaus</i> (Rohschild & Jordan 1906)	2	3
<i>Mimoides ilus branchus</i> (Doubleday 1846)	2	1
<i>Mimoides phaon</i> (Boisduval 1836)	1	1
PIERIDAE		
Pierinae		
<i>Appias drusilla</i> (Cramer 1777)	2	3
<i>Ascia monuste</i> (Linnaeus 1774)	2	3

Taxon	Habitat use	Geographic range
Coliadinae		
<i>Anteos clorinde</i> Godart 1823	2	3
<i>Anteos maerula</i> Fabricius 1775	2	3
<i>Phoebis argante</i> (Fabricius 1775)	2	2
<i>Phoebis sennae</i> Linnaeus 1758	2	3
<i>Aphrissa statira</i> (Cramer 1777)	2	3
<i>Eurema proterpia</i> (Fabricius 1775)	2	3
<i>Eurema boisduvaliana</i> (Felder 1865)	2	2
<i>Eurema dina westwoodi</i> (Boisduval 1836)	2	2
<i>Eurema albula</i> (Cramer 1775)	2	3
Coliadinae		
<i>Eurema nise</i> (Cramer 1775)	2	3
<i>Eurema दौर</i> (Godart 1819)	2	3
LYCAENIDAE		
Theclinae		
<i>Pseudolycaena damo</i> (Druce 1785)	NA	NA
<i>Thereus zebina</i>	NA	NA
Polyommatainae		
<i>Hemiargus ceraunus</i> (Butler & Druce 1872)	2	3
NYMPHALIDAE		
Charaxinae		
<i>Prepona omphale octavia</i> Fruhstorfer 1904	2	3
<i>Archaeoprepona demophon centralis</i> Fruhstorfer 1905	2	3
<i>Archaeoprepona demophoon gulina</i> Fruhstorfer 1904	2	3
<i>Siderone marthesia</i> (Cramer 1777)	2	3
<i>Consul electra</i> (Westwood 1850)	1	1
<i>Anaea aidea</i> (Guérin-Ménéville 1844)	1	1
<i>Memphis morvus boisduvali</i> (Comstock 1961)	1	3
<i>Memphis oenomais</i> (Boisduval 1870)	2	3

Taxon	Habitat use	Geographic range
<i>Memphis pithyusa</i> (Felder 1869)	2	3
<i>Memphis</i> sp.	NA	NA
Apaturinae		
<i>Doxocopa laure</i> (Drury 1773)	2	3
Nymphalinae		
<i>Colobura dirce</i> (Linnaeus 1764)	2	3
<i>Historis odius</i> (Fabricius 1775)	2	3
<i>Smyrna blomfieldia datis</i> Fruhstorfer 1908	2	2
<i>Biblis hyperia</i> (Cramer 1782)	2	3
<i>Mestra amymone</i> Menetries 1857	2	2
<i>Hamadryas februa ferentina</i> (Godart 1824)	1	3
<i>Hamadryas glauconome glauconome</i> (Bates 1864)	1	1
<i>Hamadryas feronia farinulenta</i> (Fruhstorfer 1916)	2	3
<i>Hamadryas guatemalena guatemalena</i> (Bates 1864)	1	3
<i>Hamadryas iphtime</i> (Bates 1864)	1	3
<i>Hamadryas</i> sp.	NA	NA
<i>Dynamine thalassina</i> Boisduval 1870	1	2
<i>Dynamine mylitta</i> (Cramer 1782)	2	3
<i>Marpesia petreus</i> (Cramer 1778)	2	3
<i>Marpesia chiron</i> (Fabricius 1775)	2	3
<i>Marpesia alcibiades</i> (Staudinger 1876)	1	1
<i>Eunica tatila caerulea</i> Godman & Salvin 1887	2	2
<i>Eunica monima modesta</i> Bates 1864	2	3
<i>Temenis laothoe agatha</i> (Fabricius 1787)	1	3
<i>Pyrrhogyra neaerea hypsenor</i> Godman & Salvin 1884	1	3
Nymphalinae		
<i>Diaethria astala</i> (Guérin-Ménéville 1844)	2	2
<i>Adelpha basiloides</i> (Bates 1865)	1	1
<i>Adelpha iphiclus</i> (Linnaeus 1758)	2	3
<i>Adelpha fessonia</i> Hewitson 1847	2	1
<i>Siproeta stelenes biplagiata</i> (Fruhstorfer 1907)	2	3
<i>Anartia fatima</i> Godart 1820	2	2

Taxon	Habitat use	Geographic range
<i>Anartia jatrophae</i> (Linnaeus 1763)	2	3
<i>Junonia evarete</i> Cramer 1782	2	3
<i>Junonia coenia</i> Hübner	2	2
Heliconiinae		
<i>Agraulis vanillae</i> (Linnaeus 1758)	2	3
<i>Dryas iulia</i> (Fabricius 1775)	2	3
<i>Heliconius charitonius</i> (Linnaeus 1767)	2	3
<i>Heliconius erato petiverana</i> Doubleday 1847	2	3
Melitaeninae		
<i>Chlosine lacinia</i> (Geyer 1837)	2	3
<i>Thessalia theona</i> (Menétries 1855)	2	2
Danainae		
<i>Danaus gilippus thersippus</i> Bates 1863	2	2
<i>Danaus eresimus montezuma</i> Talbot 1943	2	3
Morphinae		
<i>Morpho peleides limpida</i> Butler 1872	2	2
Brassolinae		
<i>Opsiphanes cassina fabricii</i> (Boisduval 1870)		
<i>Opsiphanes cassina chiriquensis</i> Stichel 1904	2	3
<i>Caligo memnon memnon</i> (Felder & Felder 1866)	2	3
Satyrinae		
<i>Taygetis virgilia rufomarginata</i> Staudinger 1888	1	3
<i>Cissia</i> sp.	NA	NA

Note: Habitat use: (1) unmodified habitats only; (2) some use of modified habitats. *Geographic range:* (1) Restricted to southeast Mexico and Central America but not farther south than Panama; (2) North America to Central America and/or southern Mexico to northern South America; (3) Widespread in the Neotropics (at least reaching Brazil or Bolivia). *NA:* Taxon for which habitat use and/or geographic information was not available; these species were excluded from habitat analyses. For taxonomic authorities see DeVries (1987); Raguso and Llorente-Bousquets (1991); Tyler, Brown, and Wilson (1994); and Opler and Wright (1999).

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Chapter 14

Diversity of Chalcidoidea (Hymenoptera) at El Edén Ecological Reserve, Mexico

John Heraty
Michael Gates

INTRODUCTION

Animal diversity is declining worldwide, and efforts to document this change are hampered by inaccurate estimates of the true number of species. The number of described (i.e., formally named) animal species has been estimated to be 1.2 million to 2.2 million (Stork 1988; Grove and Stork 2000), with insects by far the most dominant group (751,012 species, according to Arnett Jr. 1985). As groups are revised and types reexamined, many of the names proposed are placed as synonyms of other species. This leads to as much as a 25 percent decrease in estimates of the number of described species (May 1997), but not, however, in the tremendous number of species that remain to be discovered.

One of the first accurately quantified estimates of the total number of insect species was 30 million (Erwin 1982). This figure was derived by extrapolation from the number of canopy beetle (Coleoptera) species feeding on *Luhea seemanii* (Tileaceae) in Panama relative to the proportions of described Coleoptera and Insecta. This estimate has been continually revised, but without a real consensus, and we are left with figures that range from

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3 million to 80 million species of insects (Erwin 1982; Wilson 1985; May 1988; Stork 1988; Godfray, Lewis, and Memmott 1999; Grove and Stork 2000). Lower estimates of between 5 million and 10 million species are usually considered a conservative baseline for comparison (Stork 1988; Gaston 1991; Gaston, Gauld, and Hanson 1996; Grissell 1999; Noyes 2000).

Hymenoptera (ants, bees, and wasps) are one of the few megadiverse insect orders. Approximately 115,000 species have been described, and anywhere from 300,000 to 2.5 million species are estimated to be extant (LaSalle and Gauld 1992 [1991], 1993; Gauld and Gaston 1995; Stork 1988; Grissell 1999). Parasitic insects, of which most are Hymenoptera, account for approximately 25 percent of all arthropods in both temperate and tropical ecosystems (Stork 1988).

Among the parasitic Hymenoptera, wasps in the superfamily Chalcidoidea are ecologically and economically the most important insects for the control of other insect populations (Noyes 1978; LaSalle 1993). Chalcidoids are small to minute wasps, ranging from 0.11 to 45 mm (rarely more than 10 mm), but usually averaging 2 to 4 mm in body length. Species are distributed in 19 families and 89 subfamilies, and estimates of the number of species have ranged between 60,000 and 100,000 (Noyes 1978; Gordh 1979; Gibson, Heraty, and Woolley 2000). Most species are parasitoids of other insects, with females depositing their eggs into the eggs, larvae, pupae or rarely adults of almost every group of insect. Relatively few species are phytophagous. Among the most commonly encountered and economically important families are Eulophidae and Pteromalidae, which attack a wide variety of insects, primarily the larval stages of Coleoptera, Lepidoptera, and Hymenoptera; Encyrtidae, which parasitize mostly Euhemiptera; Aphelinidae, which are primarily parasitoids of aphids, scales and whiteflies; and Trichogrammatidae, which are egg parasitoids of primarily Lepidoptera (Goulet and Huber 1993; Hanson and Gauld 1995; Gibson, Heraty, and Woolley 2000).

The importance of Chalcidoidea in sustainable agricultural systems cannot be underestimated. When chalcidoids are removed through the use of pesticides, or the introduction of a new pest into an area without its complement of parasitoids, the results can often be drastic, resulting in the explosion of pest populations (DeBach and Rosen 1991). Chalcidoidea also includes some of the most important species used for the biological control of pest insect populations (Noyes 1978; Noyes and Hayat 1984; Greathead 1986; LaSalle and Gauld [1991]1992; LaSalle 1993). Although Trichogrammatidae are important for augmentative control measures, Aphelinidae, Encyrtidae, and Eulophidae are used primarily for the classical biological control of pests such as the cassava mealybug, olive scale, citrus blackfly, and purple scale (DeBach 1971). Tremendous long-term economic savings have resulted from the introduction of a few beneficial species (Noyes and Hayat 1984; LaSalle

and Gauld [1991]1992; LaSalle 1993). In Africa, control of the cassava mealybug alone is estimated to have saved \$250 million and allowed for the continued production of a staple food item that is very important to a large proportion of the population (Norrgard 1988).

For such an important group of insects, what do we know about Chalcidoidea? Their taxonomy is a nightmare. Original descriptions are poor and often not diagnostic; in addition, identification keys are available for only a few taxa. Most descriptions are based on only a single specimen, thus ignoring intrataxon variation. Indeed, much of the original taxonomic work has been (or often must be) repeated. Fewer than 5 percent of the described species can probably be named without comparison to the type specimen (LaSalle and Gauld 1993). Far less is known of their biology, which is often based on relatively few representative species.

Can such a group be ignored in studies of taxonomy and biodiversity? Most species are very small (May 1988; Stork 1988). In animals in general, the proportion of morphospecies (unnamed species) is inversely proportional to the logarithm of their body length (Lawton et al. 1998, but see Dial and Marzluff 1988). Because of their small size, smaller organisms require more time for proper mounting and curating, and this lag time means they are often not included in the initial estimates of species richness (Lawton et al. 1998). Lawton et al. 1998 suggested that current estimates of tropical forest diversity would be 10 to 100 times higher if inventories of smaller species were ever completed. Earlier studies suggesting that the diversity of Hymenoptera actually decreased from temperate to tropical regions focused almost entirely on larger Ichneumonoidea (Owen and Owen 1974; Gauld 1986). Ultimately, it was pointed out that competition in tropical systems would likely favor species attacking earlier and smaller stages of host insects, and that these forms would likely be more diverse in tropical regions (Hespenheide 1979; Noyes 1989a, b). The question of whether smaller parasitic Hymenoptera are more diverse in tropical regions forms a testable hypothesis that, to date, has not been thoroughly examined.

Systematists often are interested only in overall species richness (Godfray, Lewis, and Memmott 1999), while trying to answer one basic question: What species are present? This is, perhaps, a myopic perspective for sampling because it essentially ignores the qualitative aspects of developing species accumulation curves or other such measures that could better estimate the total number of species (Coddington et al. 1991; Collwell and Coddington 1994; Godfray, Lewis, and Memmott 1999). However, there is only so much time to collect and process the material at hand, and most studies are not comparable because they are biased by sampling time, sampling effort, and collector experience or preference.

Even when techniques are very close (e.g., pesticide fogging of the forest canopy), differences in the apparatus, method of application, and type of

pesticide used means that results are not comparable statistically (Erwin 1995). As well, studies of beta (i.e., between places) diversity are often hampered by site differences. Regional comparisons (faunal lists of named species), built up over a long period of time, may ultimately be the most important measures of shared diversity (Bartlett et al. 1999). Quantitative resampling methods can always be reapplied to the data once processed (Kerr 1996; Grove and Stork 2000). For now, our questions are simple: (1) Given the amount of time and methods used, how many species can be collected? and (2) How does this relate to the overall accumulation of data for species richness in Mexico and in neighboring countries?

HOW MANY SPECIES OF CHALCIDOIDEA?

Parasitic Hymenoptera probably account for between 6.5 percent and 20 percent of insect species, and a range of between 170,000 and 6 million species of parasitic Hymenoptera has been proposed on the basis of various estimates of the number of insect species (2.65 million to 30 million) (LaSalle and Gauld 1992[1991]). Approximately 21,000 species of Chalcidoidea have been described (Noyes 1998, 2000). If Chalcidoidea represent about 33 percent of described parasitic Hymenoptera (LaSalle and Gauld 1992), their estimated number of species could range between 56,000 and 2 million.

Using the British fauna as a benchmark, Noyes (2000) estimated that Chalcidoidea represent about 8 percent of all British insects and proposed that, given a conservative estimate of 5 million insect species, there could be as many as 400,000 chalcidoid species worldwide. Noyes purposefully chose to ignore the ramifications of an increase in diversity at lower latitudes. However, higher proportions of tropical Chalcidoidea are more likely. For example, in canopy fogging samples from Borneo, 26 percent of about 2,800 species of the arthropods collected were chalcidoids (Stork 1988). In Costa Rica, Chalcidoidea represented 28 percent of 17,065 morphospecies of Hymenoptera collected in Malaise traps (Gaston, Gauld, and Hanson 1996). Proportions may be even higher for islands. In the Galapagos Islands, Chalcidoidea comprise 44 percent of the 243 species of Hymenoptera collected (Heraty and Peck unpublished); on Norfolk Island, 42 percent of 189 morphospecies of Hymenoptera (I. Naumann personal communication) were chalcidoids.

Other examples reinforce ideas of the large number of chalcidoid species yet to be discovered. In the Galapagos Islands, only 55 species of Hymenoptera were known prior to 1985; of these, seven species were Chalcidoidea. From 1985 to 1990, an additional 101 species of Chalcidoidea were sampled (Heraty and Peck unpublished), which represents a 14-fold

increase in the number of known species. In a canopy fogging sample in Sulawesi (an Indonesian island east of Borneo), one family of Chalcidoidea (Aphelinidae) represented 82 percent of the 1,073 species of Hymenoptera collected, while one genus (*Encarsia*) was partitioned into 156 morphospecies, or almost as many species as have been described (Noyes 1989a, b). When it is considered that Sulawesi is not taxonomically as rich as other tropical countries such as Costa Rica (Noyes 1989a), the potential exists for discovering a tremendous number of new species.

In Costa Rica, only 278 species of Chalcidoidea are currently recognized in published accounts (Table 14.1), only 6 percent of the 4,705 morphospecies that were sampled (Gauld and Gaston 1995; Gaston, Gauld, and Hanson 1996) which is a 17-fold increase in the number of species. If this last figure is applied to the total number of described species (21,000), the estimated number of Chalcidoidea is 357,000, a value similar to the 400,000 number proposed by Noyes (2000).

HOW MANY SPECIES IN MEXICO?

Numbers of described species of Chalcidoidea in Mexico were obtained from two sources (Noyes 1998; González-Hernández 2000). Noyes' catalogue is a CD-ROM database of all published records for Chalcidoidea worldwide (approximately 35,000 references and 21,248 species names). From these published records, 716 described species in 18 families are known to occur in Mexico (Figure 14.1; numbers adjusted for duplicate species and genus records).

Using a different approach, González-Hernández (2000) surveyed specimens in five different museum collections: the Florida State Collection of Arthropods (FSCA); Texas AandM University (TAMU); Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (CIBE); University of California, Riverside (UCR); and the National Museum of Natural History (USNM). From the 4,547 specimens entered into his database (of 9,488 examined), González-Hernández found 276 morphospecies in 16 families of Chalcidoidea (Figure 14.1). Only Agaonidae and Elasmidae, both reported as being present in Mexico (Noyes 1998), were not encountered in these collections. Of the 276 morphospecies, only 176 (64 percent) were identified to a described species name. Of these named species, only 49 were not in common with Noyes' list.

After combining their results, 765 named species are known from Mexico (Table 14.1). With the addition of the 95 morphospecies from the González-Hernández survey, the number rises to 860 species. These numbers provide a baseline for comparison, but this knowledge must be tempered by the fact that most specimens of Chalcidoidea in these collections are not

TABLE 14.1. Number of described species of Chalcidoidea in the United States, Central America, and Colombia. Numbers are gathered from Noyes (1998), with figures for Mexico modified by additional data (parentheses) from described species records listed by González-Hernández (2000).

Family	United States			El Salvador					Costa Rica			Panama		Colombia
	United States	Mexico	Guatemala	Honduras	Belize	Salvador	Nicaragua	Rica	Panama	Colombia				
Agaonidae	15	16	0	1	0	1	0	34	10	1				
Aphelinidae	211	57 (1)	1	5	0	15	1	10	9	11				
Chalcididae	129	115 (5)	18	18	8	6	12	80	38	59				
Elasmidae	20	5	0	0	0	1	0	1	0	0				
Encyrtidae	449	94 (8)	3	3	0	2	2	43	17	27				
Eucharitidae	30	10	2	0	0	0	5	4	6	3				
Eulophidae	679	148 (12)	12	12	6	7	7	30	11	35				
Eupelmidae	103	22 (4)	12	0	0	2	4	10	25	6				
Eurytomidae	271	57 (2)	6	3	1	3	4	8	7	6				
Leucospidae	7	16	4	3	0	2	1	4	5	8				
Mymaridae	142	35 (1)	1	1	1	1	1	11	7	5				
Ormyridae	17	4 (2)	1	0	0	0	0	0	0	0				
Perilampidae	35	17	1	0	1	0	4	1	1	0				
Pteromalidae	465	77 (13)	12	3	3	8	4	20	15	26				
Rotoitidae	0	0	0	0	0	0	0	0	0	0				
Signiphoridae	19	10	2	1	0	0	0	1	1	3				
Tanaostigmatidae	15	23	0	0	0	0	1	7	2	2				
Tetracampidae	2	0	0	0	0	0	0	0	0	0				
Torymidae	181	32 (1)	4	2	0	1	5	1	1	9				
Trichogrammatidae	89	27	6	3	2	1	2	13	3	13				
Total	2,879	765	85	55	22	50	53	278	158	214				

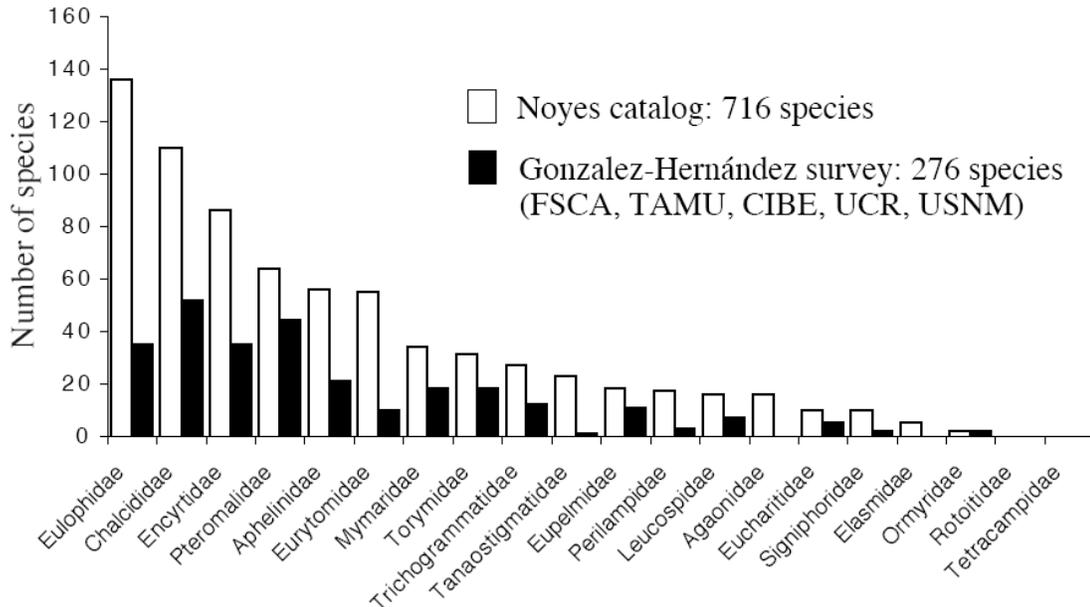


FIGURE 14.1. Described species of Chalcidoidea in Mexico based on published records (Noyes 1988) and a survey of five museum collections (González-Hernández 2000). Acronyms for museum collections are listed in the text.

sorted to species and remain as miscellaneous unsorted material; furthermore, some important collections such as the Canadian National Collection (CNC) have not yet been surveyed. On the basis of figures derived from the Galapagos and Costa Rican surveys, about a 15-fold increase in the number of species expected to occur in Mexico, which would translate to about 13,000 species of Chalcidoidea. At the very least, the number of species should exceed the approximately 5,000 species known from Costa Rica.

SPECIES RICHNESS AT EL EDÉN

Sampling of Hymenoptera, with an emphasis on Chalcidoidea, was conducted in the subtropical savanna of the Yucatán Peninsula at the El Edén Ecological Reserve in Quintana Roo, Mexico. The reserve is located 25 km NNE of Leona Vicario and consists of lowland, subtropical savanna, primary and secondary forest, and several lagoons in marshy areas. The area is subject to monsoon rains in the summer and is periodically inundated with precipitation during the fall and winter.

Numbers of Chalcidoidea from El Edén Ecological Reserve are based on a four-month sampling program from 1998. During an initial intensive collecting period in August 1998, active sampling (sweep-netting) and passive

insect sampling traps (Malaise traps, yellow pan traps, and aquatic pan traps) were established in six microhabitats in the Reserve. Sweep-nets were made of a very fine mesh fabric to focus sampling on minute insects. Malaise traps are essentially vertical tents of fine mesh netting with open sides that funnel flying insects into a collecting head filled with 75 to 80 percent ethanol (Townes 1972). Pan traps are small (20 cm diameter) yellow plastic bowls filled with water, salt (acting as a preservative), and a few drops of detergent (surfactant) to trap flying insects. Pan and Malaise traps were maintained on a casual basis through December 1998 by a resident parataxonomist. All specimens were collected in 75 to 80 percent ethanol and point mounted after being dried with use of hexamethyldisilazane (Heraty and Hawks 1997). Hymenoptera were mounted, labeled, and sorted to morphospecies by students at CIBE, UCR, and Universidad Autónoma de Querétaro (UQT). Specimens will be housed in collections at CIBE and UCR.

Fifteen of 19 families of Chalcidoidea were sampled; from the 656 specimens processed to date, 192 morphospecies (Figure 14.2) have been sorted. Of the 19 families, three families were not expected to be collected: Rotoitidae are known only from New Zealand and Chile; Tetracampidae are Holarctic; and Ormyridae are inquilines in oak galls, which are usually encountered only at higher elevations (Gibson, Huber, and Woolley 1997). Both Agaonidae (fig-pollinating wasps) and Signiphoridae (parasitoids of whiteflies, mealybugs, and small Diptera) should have been encountered, and their absence probably reflects inadequate sampling procedures.

The number of morphospecies is 25.1 percent of the described species recorded from Mexico. The species richness across families coincides with the most commonly encountered groups elsewhere, with a predominance of Eulophidae (54 species), Encyrtidae (32 species), and Pteromalidae (36 species). Chalcididae (18 species) and Aphelinidae (3 species) were underrepresented as compared to the number of described species in Mexico (fig. 2). At least for Aphelinidae (and probably for Signiphoridae), more species would be represented in the survey if collections were focused on rearing armored scale and whitefly hosts. The 192 species is a substantial increase in the known fauna, as only 5 genera and species of Chalcidoidea were known to occur in the State of Quintana Roo on the basis of museum records (González-Hernández 2000).

The next logical step for assessing the collections of Chalcidoidea from El Edén is to provide species names. Only by this means can the distribution be compared to that of the rest of Mexico, or to similar habitat types in Central America. Do these studies add to the regional list of species or merely extend the distribution of known species? Unfortunately, there are almost no identification keys available for the Chalcidoidea of Mexico (cf. González-Hernández 2000), and few species are described. At best, species can be

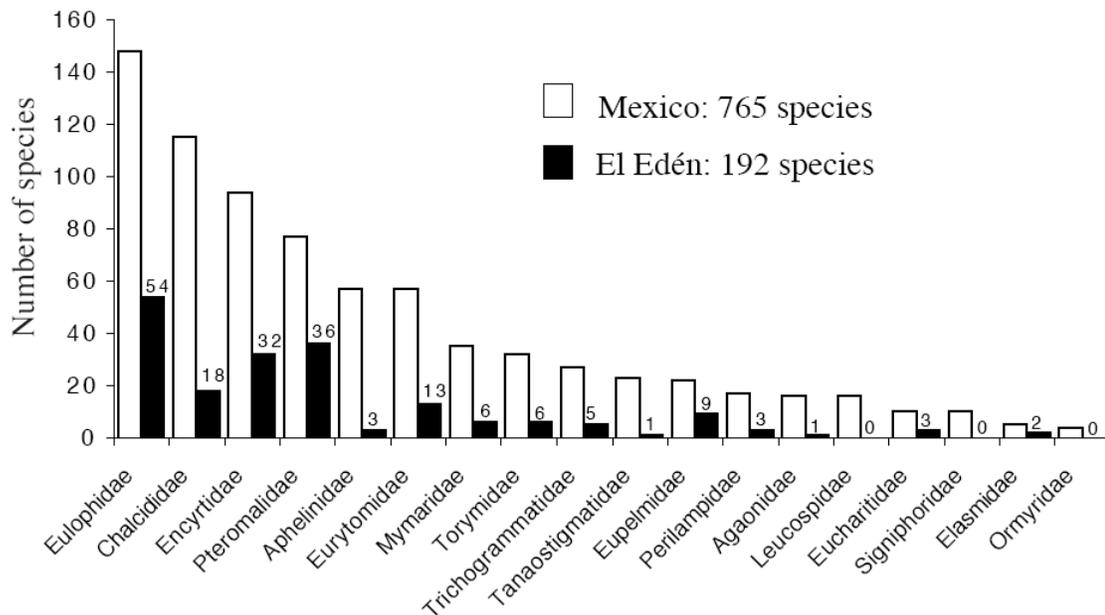


FIGURE 14.2. Species richness of Chalcidoidea, ranked by number of species described from Mexico (Noyes 1988; González-Hernández 2000). Numbers for El Edén Ecological Reserve are based on morphospecies (Heraty and Gates unpublished).

sorted to genus, but otherwise most will remain as morphospecies and thus be unavailable for beta-level comparisons for the foreseeable future.

SPECIES RICHNESS IN CENTRAL AMERICA

The species richness of Chalcidoidea in the United States, Central America, and Columbia was compiled using Noyes (1998) CD-ROM database, with estimates for Mexico adjusted as discussed (Table 14.1). For the Nearctic region (which would include parts of Mexico), Gibson, Huber, and Woolley (1997) estimated a total of 706 genera and 2,757 described species of Chalcidoidea. This is within 5 percent of the report of 2,879 described species for the United States taken from Noyes (1998) (Table 14.1).

Gaston (1993) estimated that only about 50 percent of North American species of Hymenoptera are named, which suggests a total of about 6,000 species of Chalcidoidea. Mexican species are probably better known than species of other countries because many would be included in revisionary studies of North American genera. However, even including Mexico, the numbers of chalcidoid species drop precipitously for all of the Central American countries and Colombia (Table 14.1).

Initially these lower values suggest a pattern of decreased tropical diversity, or possibly area relationships (smaller countries with fewer species). But these area relationships are not uniform: Colombia, which has access to the entire northern biota of South America, has fewer species than Costa Rica. Admittedly, the large number of North American species represents the extensive land mass and habitat diversity, but it is also a product of a larger number of collectors and systematists, as well as a history of descriptive taxonomy.

The lower numbers for Central and South America are more likely representative of the lack of taxonomic focus on collecting in these regions. Two examples support this concept. In El Edén, which is a relatively uniform lowland habitat, 192 species were collected over four months. This exceeds the number of species in all bordering countries to the south, each of which has a more diverse habitat. Secondly, in the example cited above, 4,705 morphospecies of Chalcidoidea have been recognized in Malaise trap samples in Costa Rica (sampled (Gauld and Gaston 1995; Gaston, Gauld, and Hanson 1996). This suggests that Costa Rica has a species diversity that is roughly equivalent to that of the United States, which, given the much smaller area of Costa Rica, supports the notion of increased tropical diversity.

WHERE DO WE GO FROM HERE?

The values presented provide a baseline for examining the diversity of described species for Mexico and surrounding countries. However, especially for Central America, richness values for Chalcidoidea ranging from 50 to 765 species are simply not realistic. If 4,705 morphospecies are found in Costa Rica, then similar numbers should be expected in surrounding countries. We can expect to find 5,000 to 13,000 species of Chalcidoidea in Mexico alone. These numbers are not exclusive. Tropical species should overlap a great deal between countries throughout Central America, and temperate Nearctic species should occur across much of Mexico.

For pimpline ichneumonids in Malaise traps set in lowland tropical forests in Panama and Belize, the overlap in species with the well-known Costa Rican fauna was 96.6 percent and 84 percent, respectively (Bartlett et al. 1999). Overlap between all three sites was only 39 percent, but this lower value was likely because of habitat differences among sites. Tropical lowland species are expected to show lesser degrees of endemism than those at higher altitudes (Gaston, Gauld, and Hanson 1996). However, without valid names, any beta-level comparisons between sites, habitats, or regions are nearly impossible beyond a few representative taxa.

CONCLUSION

In this paper, we have focused on three aspects of understanding diversity in tropical countries. Each area is summarized in detail below.

1. *Use of Published Information.* For Chalcidoidea, there now exist one of the most complete literature databases (Noyes 1998). It is crucial that this time-intensive project be ongoing if we are to keep abreast of changes in new species, new distributions, and the synonymy of taxa. Each of these aspects affects the ability to make future estimates of the number of species within and between areas.

For examining the diversity of broad groups in this manner, errors inherent in the data must be accepted, since not all literature is trustworthy and not all synonymies are updated. Literature surveys also tend to be broad in their geographical scope and do not take into account state or exact locality differences in distribution. Only by intensely focusing on limited taxa can these problems be addressed, although this places obvious limitations on the scope of the taxa to be included in diversity assessments.

2. *Survey of Collections.* The survey of species in collections across North America by González-Hernández (2000) (through the Comisión Nacional de Biodiversidad [CONABIO]), as well as the placement of these records into a progressive database, is commendable. On the basis of 639,867 specimens input into CONABIO's all-species database, about 80 percent of all specimens collected in Mexico are currently located in museums in developed countries (Soberón, Llorfente, and Benítez 1996). For birds, 86 percent of all specimens are held in collections in the United States (Soberón, Llorfente, and Benítez 1996). Information mined from these collections is an important resource for any developing nation. Measures of diversity and other information can be gathered and monitored effectively, but the costs of curation and maintaining collections should ultimately be placed on those countries that can best afford these long-term investments. The resources needed to continue updating and expanding these databases are critical and beneficial at an international level.

On the positive side, information from data-based collections can be recorded more exactly to include explicit information on date of collection, locality (latitude and longitude), elevation, and other relevant data. Use of this basic data (3,991 museum records of 421 species) were used in a Geographic Information System (GIS) analysis of Amazonian species to conceptualize regions of highest diversity and endemism (Kress et al. 1998). Similar analyses were applied to tracking the diversity and distribution of pierid and papilionid butterflies in Mexico extracted from specimens housed in 15 museums in Canada, Mexico, the United States, and Europe (Soberón, Llorfente, and Benítez 1996). Increasingly, exact specimen data is being

excluded from publications (Snow and Keating 1999), and a return to searching for information found only in the primary collections may be necessary.

Significant problems associated with data mining involve the accuracy of current identifications and whether collections have been updated to reflect nomenclatorial changes. Twenty-two (12.5 percent) of the named species reported by González-Hernández (2000) did not include updates in generic or species level synonymies, which makes it difficult to compare names in other lists (e.g., Noyes' database) that are developed for different collections, or from different databases. To address these problems, databases should be integrated with electronic taxonomic catalogues, and information on the authority (identifier) and year of identification must be included for verification purposes. Unfortunately, this form of data collection and the integration of this information into a database is expensive, largely because the same museums must be continually revisited to survey for new material or revised determinations.

3. *Sampling and Curation of New Material.* The survey of Chalcidoidea at El Edén illustrates the importance of new collections. More than 192 species were discovered in a state that previously had records for only five species. This collection forms a groundplan for future surveys and comparisons within El Edén, but on its own does not say much about the diversity in lowland tropical forests in Mexico or Central America.

After all, we only have numbers for morphospecies, which cannot be compared with other areas until names are made available. Identification keys are generally not available. Specimens can be distributed to specialists for accurate identification, but, because most species undescribed, names may not be available. The absence of names hampers our efforts to make meaningful conclusions surrounding comparisons among sites or regions. For these minute, mostly unnamed specimens, the lag time before they can become incorporated into current studies of biodiversity becomes enormous (Stork 1988). Yet, as parasitoids, Chalcidoidea occupy the tertiary trophic levels—controlling outbreaks of primary herbivores as well as acting as indicators of the health (diversity) of the primary trophic levels (LaSalle and Gauld 1992[1991], 1993). The need to include this group in biodiversity studies is great.

Two approaches can be taken to increase the value of site collections. First, effort should be expended to identify and describe all of the species. If it is assumed that most species are undescribed, then primary descriptions need to be developed for most of the 192 species. Estimates from the Costa Rican inventory program suggest that, for every species description, \$1,000 is necessary to cover investigator time, artist support, scanning electron microscopy, miscellaneous supplies, and publication costs (J. LaSalle personal communication). For El Edén, this would amount to approximately \$190,000,

but the investment would provide quick access to reliable information at all levels.

Second, if the lag time in collating information is accepted, then steps should be taken to ensure that specimen data and progress of curation is available for updating the various databases. This is easily accommodated by the use of unique specimen code numbers (i.e., unique numbers or barcodes) linked to a database (e.g., BIOTA [Collwell 1997]) that includes all of the detailed collection information. This does not mean that accurate label information on specimens should be abandoned. Unique identifiers are just a means to track a specimen as it is resorted, loaned, named, or described, even if the process takes several years to complete. Database records can (and should) be made universally accessible over the World Wide Web. Problems of single data models for exchange of information have not been resolved, but locality coordinates, date, and species name are basic fields that should be easily exchanged. In this way, specimen databases such as that developed by González-Hernández (2000) could be updated on a regular basis without revisiting collections, or possibly even adding information from previously unvisited collections.

Each of the three categories of information listed above are ultimately based on field-collected material. Well-labeled and curated specimens form the basis of local collections, published accounts, and specimen databases. An accurate description or identification key make the information available across all platforms. Developing programs and electronic databases that link taxonomic and specimen catalogues, and curating specimens in a manner that make the information accessible, should be a priority of all collections (Janzen 1993; Soberón, Llorfente, and Benítez 1996; Kress et al. 1998). Use of this information to provide better estimates of alpha and beta diversities in tropical species-rich countries will ultimately be useful for making more informed decisions on conservation and habitat management issues.

The current focus on biodiversity has unfortunately had a negative impact on sampling efforts (Wheeler 1995). By extolling the virtues of biodiversity, politicians interpret this in economic terms; although this can be good, the associated protectionism has had a major impact not only on scientific collecting, but also with the loan and exchange of museum specimens. Many countries now impose restrictions on the collection and exportation of insect specimens. In the United States, restrictions are even placed on the importation of preserved, non-endangered insects from other countries (Lacey Act Amendments of 1981). Ultimately, this leads to further decline in tropical collecting and a decline in the understanding of diversity. Shared information, without restrictions to access, is crucial to understanding biodiversity as it is today, as well as how it changes in the future.

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Chapter 15

Diversity and Habitat Associations of the Ants (Insecta: Formicidae) of El Edén Ecological Reserve

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INTRODUCTION

Seasonally dry tropical forests are being recognized as ecosystems of high biodiversity in Mexico because they contain elevated levels of endemic flora and fauna (Rzedowski 1993). Although these drier forests are generally not as species-rich when compared with the more highly publicized tropical rain forests, they have been of greater use to humans in the past and are now generally being more impacted by human activities (Mooney, Bullock, and Medina 1995; Janzen 1988). The Yucatán Peninsula contains one of the largest and least disturbed expanses of tropical dry forests in Mexico and Central America. The bioregion known as Yalahau is located in the extreme northeast portion of the peninsula, in the state of Quintana Roo, Mexico.

The seasonally dry forests and other vegetation types of the Yucatán Peninsula are the product of a complex disturbance regime. Hurricanes are common events in the area and often greatly alter forest structure and composition. Fires are also relatively common, and their intensity and

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frequency is apparently related to the quantity of fallen timber left after hurricanes and to the number of fires started during each dry season by farmers for land-clearing purposes. The Yalahau bioregion is seasonally flooded, creating macrohabitats and microhabitats for numerous species of aquatic and semi-aquatic organisms in subterranean caves and canals. Baseline data are needed of the region's species composition in order to aid future studies of the community structure and successional patterns involved in the complex disturbance regime of the peninsula, as well as for comparison with similar ecosystems in the Neotropics, and elsewhere in the world.

Given species diversity calculations from other tropical forests (Erwin 1982; Stork 1994), it is reasonable to assume that insects are the most species-diverse taxonomic group of the Yucatán Peninsula. However, the region has been very poorly collected in the past. Researchers from the Universidad Nacional Autónoma de México made an insect collecting expedition to the Yucatán Peninsula more than 12 years ago, but logistic problems resulted in very little material being mounted and labeled. Previously, Kissinger (1962) reported that a limited collection of weevils (57 species) was obtained from one expedition to the central Yucatán Peninsula; specimens were apparently deposited in the American Museum of Natural History. It is possible that other entomologists have collected in this region, but there is no record of these groups or where any collected insect specimens might be located.

To address the magnitude and nature of insect diversity in the Yalahau bioregion, ants were selected as an indicator group for study. This family was chosen because ants are invariably common in tropical terrestrial ecosystems, are among the most important predators of arthropods, and are significant seed predators and herbivores (Hölldobler and Wilson 1990). The study was conducted at the El Edén Ecological Reserve in Quintana Roo, Mexico, where comparisons were made of the abundances and diversity of ants within four distinct vegetation types, as discussed below.

MATERIALS AND METHODS

Study site

All portions of this study were carried out within El Edén, which is located 25 km NNE of the small town of Leona Vicario in the municipality of Lázaro Cárdenas. El Edén is situated within the Yalahau bioregion, which includes the extreme northeastern portion of the Yucatán Peninsula. The mean annual temperature of the area is 24.7°C, and the mean annual precipitation is 1,511.4 millimeters (mm). The climate is classified as hot and subhumid with summer rains and classified as Aw2(i') by García (1981). The soil is generally

thin and rocky with little organic material or limestone bedrock. The vegetation at El Edén is composed of four principal elements: (1) semideciduous tropical forest; (2) secondary forest (acahual); (3) savanna; and (4) inundated mixed forest (tintal).

Collection methods

The sample period began in July and continued through the first week of October 1997. Samples were taken from the four dominant vegetation types described above. Within each vegetation type, two collection methods were used: manual collection and trapping. Forceps were used for manual collections, and individual specimens were captured from the substrate. Five trap types were used: (1) pitfall, (2) surface, (3) subsoil, (4) arboreal, and (5) leaf litter. Within each trap, two types of attractants were used: protein (fish) and carbohydrates (oatmeal and honey).

Pitfall traps were plastic cups (approximately 250 milliliters [ml] in volume) filled halfway with 60 percent alcohol as a preservative; these traps were sunk into the soil until their edges were flush with the soil surface. Surface traps were petri dishes [9 centimeters (cm) in diameter] containing various small holes in the dish wall; these traps were placed on the soil surface. Subsoil traps were cylindrical plastic containers (9 cm x 4 cm in diameter) with several holes in the sides; a label was secured with string to the neck of the container, and the label left exposed on the soil after burying the trap, thereby allowing for easy relocation and removal of specimens from the trap. Arboreal traps were constructed of the same container as the subsoil traps, but affixed to trees by string. Leaf litter samples were made by collecting all leaf litter within a 0.25-square meter (m²) quadrant, hand-sweeping the litter into a plastic bag kept at soil level, and then placing the samples in a Berlese funnel (Borrer, Triplehorn, and Johnson 1989) with a 25-watt light bulb in the funnel above the sample. Ants within the sample would fall down the funnel and into a vial of alcohol placed at the mouth of the funnel.

Sampling design

Samples were taken in transects at eight localities, with two transects for each of the four vegetation types. For each vegetation type, two 45-meter (m) transects were delineated with a rope marked at 5 m intervals, representing ten sample points/transect. For each transect, traps were arranged in the following manner: (1) one pitfall trap for each 5 m sample point (10 traps total); (2) five subsoil traps at each of the 5 m sample points (25 total traps/transect); (3) five surface traps at each of the 5 m sample points (25 total traps/transect); and (4)

five arboreal traps at each of the 5-m sample points when trees were present (25 total traps/transect).

Pitfall traps were checked every three to four days after placement. Subsoil traps were checked the day following placement, whereas surface and arboreal traps were checked several times a day. Specimens were placed in alcohol in 8-dram vials and labeled with sample number, sample period, type of trap, date, and any additional observations (color of individual, interactions, etc.).

Statistical analysis

The means and frequency procedures of the SAS software package (SAS Institute 1985) were used for general statistics of ant densities for the various vegetation types and sampling methods. The general SAS linear models program was used to analyze differences in total ant densities, as well as the various taxonomic categories among the vegetation types and strata, by using the following model: $\log \text{ mean number of ants trap (+1) = vegetation + transect + trap location + sample period}$. Mean separation of factors affecting the densities of total ants and various taxonomic groups were compared using Tukey's studentized range test (Steel and Torrie 1980).

RESULTS

Ants were present in all vegetation types and strata within El Edén. A total of 5,173 individuals were collected, representing 6 subfamilies, 24 genera, and 42 species (Appendix). The subfamily with the greatest number of species was Myrmicinae (17), followed by Pseudomyrmecinae (5), Dolichoderinae (6), Ponerinae (6), Formicinae (5), and Ecitoninae (3), respectively. The genera with the most species collected were *Pseudomyrmex* (5), *Pheidole* (5), and *Camponotus* (4). Based on Rojas (1996), three ant species are apparently new records for Mexico: *Crematogaster erecta* (Mayr), *Camponotus novogranadensis* (Mayr), and *Anocheus micans* (Brown).

The army ants, *Labidus praedator* Smith and *Eciton burchelli* Westwood, were the species with the greatest number of collected individuals with totals of 1,819 and 997 individuals, respectively. Because these ant colonies are large (often containing more than one million individuals) and nomadic, with no permanent nest site, their distribution was highly aggregated [i.e., Index of dispersion (ID) = variance/mean ratio: 11.37 and 19.39 for *L. praedator* and *E. burchelli*, respectively]. The myrmecines were the next most commonly collected ants, with 420 collected individuals for *Monomorium ebeninum* Smith, 301 for *Crematogaster opaca*, 170 for *Crematogaster* sp. 1, and 147 for *Crematogaster erecta*. These species were encountered more

frequently than army ants, but in lower numbers as indicated by their dispersion indices (i.e., ID = 4.26 for *M. ebeninum*, 7.67 for *Crematogaster opaca*, 7.01 for *Crematogaster* sp. 1, and 7.65 for *Crematogaster erecta*). Twenty-three of the remaining species were collected in numbers ranging from 20 to 100 individuals, and 11 species were represented by ten or fewer collected individuals.

The species accumulation curve for ant species at El Edén indicated that few new ant species would be predicted to be found employing the same collection methods used in this study during the months of July, August, September, and October. However, the sample period was relatively brief (four months), and several important habitats (e.g., the higher forest canopy) were not within the scope of this study, nor feasible given our available resources.

Vegetation and habitat associations

The numbers of ant species, the total individuals collected, and values for Shannon's Index of Diversity are presented in Table 15.1. As expected, the semideciduous tropical forest had greater numbers of both ant species and total individuals collected than the secondary forest (acahual), savanna, or inundated mixed forest (tintal). The secondary forest (acahual) had relatively high species diversity, but almost seven-fold fewer total individuals than the semideciduous tropical forest. Both the savanna and the inundated mixed forest (tintal) had similar species numbers and individuals.

Trap catches of ants also followed this same trend (Table 15.2). Significantly more ants were captured in the semideciduous tropical forest than in the secondary forest (acahual), and both had greater mean trap catches than the savanna or the inundated mixed forest (tintal).

For the large predatory ants Ectoninae and Ponerinae, mean trap catches were not significantly different from semideciduous tropical forest and secondary forest (acahual) traps, and both of these vegetation types were significantly greater than those for savanna and inundated mixed forest (tintal) densities. These large predators were most common in leaf litter traps and in surface traps than in tree traps, although the difference was not significant.

Despite the greater species richness of ants in the semideciduous tropical forest, the diversity index (Shannon's) calculated for this vegetation type was less than that of the secondary forest (acahual), savanna, and inundated mixed forest (tintal). This is because well over half of the ants collected in the semideciduous tropical forest (63.3 percent) were represented by the army ants, *L. praedator* and *E. burchelli*; therefore, the evenness of the species' abundances was low. Excluding these two species from the calculations results in a calculated diversity index similar to that of the secondary forest (acahual) (see Table 15.1).

TABLE 15.1. Comparison of species richness and diversity of ant species between habitats and strata in El Edén Ecological Reserve, Quintana Roo, Mexico

Vegetation Type or Strata	Number of Species	Number of Individuals	Shannon's Index of Diversity
Vegetation Types			
Semideciduous tropical forest	37	4,322	0.934 (1.228)*
Secondary forest (acahual)	29	635	1.223
Savanna	14	110	0.991
Inundated mixed forest (tintal)	13	146	0.948
Strata in Vegetation			
Arboreal	28	1,055	1.136
Surface (Pitfall and surface traps)	17	138	0.932
Leaf litter	2	19	0.933
Subsoil	22	815	0.271

* Shannon's diversity index calculated without inclusion of army ants (*Eciton burchelli* Westwood and *Labidus praedator* Smith).

Several ant species were restricted to one or more of the vegetation types (see Appendix). Eight species were only collected in the semideciduous tropical forest, whereas 15 were restricted to the semideciduous tropical forest and the secondary forest (acahual). Only five species were found in all vegetation types, and no species was found in the savanna or inundated mixed forest (tintal) that wasn't also collected in the semideciduous tropical forest or secondary forest (acahual).

Traps caught significantly more ants in trees than in other habitats. The trap catches values for surface and leaf litter were not significantly different, and both were intermediate between those recorded for the other trap types, whereas subsoil traps caught very few ants (see Table 15.2). Of the ant genera collected, 26.6 percent were recorded in tree traps; not surprisingly, those species were categorized as arboreal (*Pseudomyrmex*, *Dolichoderus*).

TABLE 15.2. Comparison of mean trap catches of ant species between habitats and strata in El Edén Ecological Reserve, Quintana Roo, Mexico.

Vegetation Type or Strata	Mean Number per Trap \pm SD*	
	Total Ants	Ecitoninae and Ponerinae
Vegetation Types		
Semideciduous tropical forest	8.28 \pm 20.55 A	1.87 \pm 17.22 A
Secondary forest (acahual)	1.78 \pm 3.99 B	0.52 \pm 2.81 A
Savanna	0.26 \pm 1.12 C	0.08 \pm 0.88 B
Inundated mixed forest (tintal)	0.34 \pm 1.42 C	0.00 B
Strata in Vegetation		
Arboreal	5.27 \pm 11.24 A	0.29 \pm 1.28 A
Surface (pitfall and surface traps)	2.91 \pm 14.93 B	1.39 \pm 14.34 A
Leaf litter	1.75 \pm 4.20 B	0.30 \pm 0.70 AB
Subsoil	0.095 \pm 0.95 C	0.00 B

*Means with the same letter within a variable group not significantly different using one way analysis of variance (log transformed): $F = 129.11$, d.f. = 3, $p < .001$; $F = 70.13$, d.f. = 3, $p < .001$, respectively for the variable vegetation and strata of all ants; $F = 13.72$, d.f. = 3, $p < .001$; $F = 5.30$, d.f. = 3, $p < .001$, respectively for the variable vegetation and strata.

A considerable percentage of species were found both on vegetation and along the ground surface (37.7 percent); the remainder were found on various combinations of the four strata.

DISCUSSION

Ants are among the most ubiquitous animals of virtually all terrestrial ecosystems; they are also among the most important predators of arthropods (Hölldobler and Wilson 1990). The diversity and number of ants found in this study indicates that the role of ants is significant in the terrestrial ecosystems at El Edén. Although comparisons of ant densities with insect densities was not part of this study, a small series of sweep-net samples of forest vegetation was conducted in 1994. In six series of insect samples captured with a sweep net (roughly 1 hr. each), 18.4 percent of all insects were ants ($N = 391$

insects). This seems a reasonably rough estimate of the proportion of individual insects that are represented by ants at El Edén.

Several types of evidence attest to the evolutionary importance of ants on other organisms in Yucatán terrestrial ecosystems. One of these is the mutualistic associations that have evolved between plants and ants. One of the simplest forms by which plants interact with ants is through extrafloral nectaries, which are found on a wide assemblage of plant species. Extrafloral nectaries have adaptive significance to plants because they attract predators (especially ants), which, in turn, attack injurious herbivorous insects on the secreting plant (Bentley 1977). These plant-ant associations are generally a generalist defense mechanism for the plant, in that there is no specific attractions or associations with a particular ant species. However, the benefits to both plants and ants have led to the evolution of specific obligate mutualism in several species of plants and ants in the tropics. Two of the most well-known and extensively studied examples of this type of mutualism between plant and ant are that between the *Acacia* trees and *Pseudomyrmex* ants, and the invader plant species *Cecropia* and *Azteca* ants (Janzen 1966; Andrade and Carauta 1982). Both *Acacia* and *Cecropia* and their resident ants are a common component in the forest and secondary vegetation of El Edén. Hölldobler and Wilson (1990) list 28 other plant-ant associations that have apparent specific plant-ant mutualisms in the American tropics.

If ants are one of the principal predators of arthropods in northern Yucatán, are they more important as competitors or prey for insectivorous birds? A compelling argument that ants are not a preferred prey item for birds is the large number of insects and other arthropods (Salticid spiders, in particular) that mimic ants. This is also supported by field observations of army ant swarms, where birds have been observed to eat the insects flushed up from the army ant swarm while generally ignoring the ants (Willis and Oniki 1978). The lack of fatty reproductive tissues in worker ants, as well as their proficient ability to defend themselves and fellow workers (Hölldobler and Wilson 1990), are probably the principal reasons that birds avoid feeding on ants.

These arguments would suggest that ants are competitors of insectivorous birds; thus, their diversity, densities, and movements (particularly the army ants) may affect the feeding behavior and habitat preferences of resident and migrant land-birds. This would also suggest that insects developing in immature stages in aquatic habitats where ants are absent may be an important alternative component of the diet of insectivorous birds in areas such as El Edén. Further study is needed of the importance of

interactions among ants and resident and migrant birds of northern Yucatán, and whether insect densities can become a limiting resource for migrant insectivorous birds.

Results from this study indicate that ant density falls sharply with disturbance, even in areas where vegetation has had several years to recover. This suggests that the greater the impact of agricultural practices—especially soil disturbance and tillage—the greater the reduction of ant densities and their importance as predators of insect pests. Comparisons of insect pest densities between diversified traditional systems and modern cultivation practices in the tropics indicates that traditional systems not only have greater diversity and densities of biological control agents (Risch, Andow, and Altieri 1983; Gliessman and Altieri 1982), but also more ants (Cook 1904; Letourneau 1983). Ants were almost certainly an important biological control component in the agricultural systems of the indigenous populations of Mexico and Central America. Ant diversity apparently remains relatively high in existing indigenous farming systems, but are generally reduced to a few opportunistic colonizing species in modern agroecosystems (Sterling 1978).

APPENDIX:
LIST OF ANT SPECIES COLLECTED
AT EL EDÉN ECOLOGICAL RESERVE,
QUINTANA ROO, MEXICO.

Subfamily	Genera	Species	Vegetation				Strata			
			TF	SF	MF	SV	TR	SR	LL	SS
Myrmicinae	<i>Glomyromyrmex</i>	sp. 1	X						X	
	<i>Monomorium</i>	<i>ebeninum</i> Forel	X	X	X	X	X	X	X	
	<i>Crematogaster</i>	<i>opaca</i> Mayr	X	X			X	X	X	
	<i>Crematogaster</i>	sp. 1	X	X		X	X	X	X	
	<i>Crematogaster</i>	<i>erecta</i> Mayr	X	X	X	X	X	X	X	
	<i>Cephalotes</i>	sp. 1	X	X	X	X	X	X	X	
	<i>Cephalotes</i>	<i>cristatus</i> (Emery)	X	X			X	X		
	<i>Wasmannia</i>	<i>auropunctata</i> (Roger)	X			X	X			
	<i>Pheidole</i>	sp. 1	X	X	X	X	X	X		
	<i>Pheidole</i>	sp. 2	X	X	X		X	X	X	

Subfamily	Genera	Species	Vegetation				Strata			
			TF	SF	MF	SV	TR	SR	LL	SS
	<i>Pheidole</i>	sp. 3		X	X	X	X	X		
	<i>Pheidole</i>	sp. 4		X	X	X	X	X		
	<i>Pheidole</i>	sp. 5		X	X	X		X		
	<i>Solenopsis</i>	<i>geminata</i> (Fab.)	X	X	X	X	X	X		
	<i>Cyphomyrmex</i>	<i>rimosus</i> (Spinola)	X		X			X	X	
	<i>Atta</i>	<i>mexicana</i> (Smith)		X				X		
	<i>Trachymyrmex</i>	sp. 1	X	X			X			
Dolichoderinae	<i>Dorymyrmex</i>	<i>flavus</i> McCook	X	X	X		X	X	X	
	<i>Dorymyrmex</i>	sp. 1	X				X			
	<i>Dolichoderus</i>	<i>bispinosus</i> (Olivier)	X	X			X			
	<i>Dolichoderus</i>	<i>diversus</i> Emery	X				X		X	
	<i>Liometopum</i>	<i>apiculatum</i> Mayr	X		X	X	X	X		
	<i>Azteca</i>	sp. 1		X						
Pseudo myrmecinae	<i>Pseudomyrmex</i>	<i>cubaensis</i> (Forel)	X	X			X			
	<i>Pseudomyrmex</i>	<i>gracilis</i> (Fabr.)	X	X			X			
	<i>Pseudomyrmex</i>	<i>elongatulus</i> (Mayr)	X	X			X		X	
	<i>Pseudomyrmex</i>	<i>boopis</i> (Roger)	X						X	
	<i>Pseudomyrmex</i>	<i>pupa</i> (Forel)	X	X			X		X	
Ecitoninae	<i>Neivamyrmex</i>	sp. 1	X							
	<i>Labidus</i>	<i>praedator</i> (F. Smith)	X	X		X		X	X	
	<i>Eciton</i>	<i>burchelli</i> (Westwood)	X	X		X		X		
Formicinae	<i>Camponotus</i>	<i>sericeiventris</i> (Guerin)	X	X						
	<i>Camponotus</i>	<i>novograndensi</i> s (Mayr)	X							
	<i>Camponotus</i>	<i>atriceps</i> (Smith)	X	X			X			
	<i>Camponotus</i>	<i>planatus</i> Roger	X		X	X	X	X		

Subfamily	Genera	Species	Vegetation				Strata			
			TF	SF	MF	SV	TR	SR	LL	SS
Ponerinae	<i>Brachymyrmex</i>	sp. 1	X							
	<i>Odontomachus</i>	<i>laticeps</i> Roger	X							X
	<i>Pachycondyla</i>	<i>villosa</i> (Fabr.)	X	X						X
	<i>Pachycondyla</i>	<i>apicalis</i> (Latr.)	X	X					X	X
	<i>Pachycondyla</i>	<i>harpax</i> (Fab.)	X	X			X	X	X	
	<i>Anochetus</i>	<i>micans</i> (Brown)	X	X			X	X	X	
	<i>Ectatomma</i>	<i>tuberculatum</i> (Olivier)	X	X			X	X		

Note: Vegetation types: TF= Semideciduous tropical forest; SF = secondary forest (acahual); MF = inundated mixed forest (tintal); and SV = savanna. **Strata abbreviations:** TR = tree; SR = surface; LL = leaf litter; and SS = subsoil.

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Chapter 16

The ‘Nonmarine’ Mollusks of the Yucatán Peninsula: A Review

Edna Naranjo-García

INTRODUCTION

The nonmarine mollusks of scattered places in Mexico (e.g., Baja California, Sonora, Veracruz, Chiapas, and Yucatán) are fairly well understood (Olivera and Polaco 1991) even though explorations throughout the region began more than 150 years. Records of the nonmarine mollusks of the Yucatán Peninsula began just before the mid-1800s with explorations by Linden, Morelet, and Dyson. These findings were published in major works, such as those by Fischer and Crosse (1870-1878), and by von Martens (1880-1901), in which species checklists, collections, and sites sampled for Mexico and Central America were recorded.

Linden collected in the Peninsula of Yucatán (Fischer and Crosse 1870–1878) as well as in Venezuela (Pfeiffer 1846). Arthur Morelet traveled across Tabasco, Chiapas, Campeche state, Yucatán state, and throughout Guatemala; he published his own findings (Morelet 1851). In his 1851 work, Morelet described three species from Yucatán state, three species from Campeche state, and several other species throughout Mexico and Central America; in all, Morelet described a total of 22 species for Yucatán state (Bequeart and Clench 1933). Dyson explored mainly Belize, and also collected in Honduras (Pfeiffer 1846, 1849), although his research extended into a few select localities in the Peninsula of Yucatán; between 1846 and 1851, Louis Pfeiffer

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published Dyson shell collections (Fischer and Crosse 1870–1878; Pfeiffer 1846, 1849).

F. D. Godman explored Yucatán state from roughly 1887 to 1889 (cited in von Martens 1890–1901). In 1890, Angelo Heilprein explored the region under the financial support of the Academy of Natural Sciences of Philadelphia (Pilsbry 1891); Heilprein's exploration was the most formal of any research conducted in Yucatán state to that point (Bequaert and Clench 1933).

León J. Cole did some collecting in 1904 (cited in Bequaert and Clench 1933). Later, Bequaert explored the area around Chichén Itzá; along with W. Clench, he prepared a set of publications for Yucatán state that also included information for the entire peninsula (Bequaert and Clench 1931, 1933, 1936, 1938). Additional material used in the studies done by Bequaert and Clench came from several collectors (e.g., J. Sandground, G. C. Shattuck, G. M. Saunders, B. L. Bennett, and F. M. Gaige) as well as from the Peabody Museum of Harvard University (cited in Bequaert and Clench 1933). More detail and specific notes pertaining to each state are given as follows.

YUCATÁN

Before the published work of Bequaert and Clench, no comprehensive account of the molluscan fauna was known for Yucatán state. Their work also brought together information on the mollusks of the other two states that form the Yucatán Peninsula: Campeche and Quintana Roo.

In their 1933 publication, Bequaert and Clench related the history of the explorations of Yucatán state to that time. Their work (Bequaert and Clench 1933, 1936, 1938) comprised the synonymy of the species as well as previous records from the peninsula, and included notes on specimen variations, relative abundance of specimens, distinctive characters among species and their distribution, physical condition of the specimens, and specific descriptions of new species.

Under the financial support of the Zoology Department of Louisiana State University, Harry (1950) went to Yucatán state to study bird migrations. During his research, he set aside some time to search for nonmarine mollusks, and finally reported 29 species on his annotated list.

In 1998, Naranjo-García and Castillo-Rodríguez studied the nonmarine mollusks found in Mayan pyramids. Although they brought together all the species recorded for the Yucatán Peninsula and updated scientific names, no new species were added.

QUINTANA ROO

The study by Richards (1937) on the island of Cozumel is the first publication for Quintana Roo, which was elevated to state status in 1902. His publication was later followed by that of Rehder (1966).

The Bredin–Smithsonian Expedition (Rehder 1966) to Quintana Roo and Grand Cayman was sponsored by Mr. and Mrs. Bruce S. Bredin of Wilmington, Delaware, who also funded several other scientific expeditions throughout the world. The diverse collections made by the various Bredin explorations were deposited at the United States National Museum (Rehder 1966). The main objective of the Bredin–Smithsonian Expedition was “the collection of marine organisms and insects” (Rehder 1966) on the shores of Quintana Roo and Grand Cayman. Rehder and other members of the Bredin–Smithsonian Expedition collected some mollusks in Quintana Roo from around the northeastern shores of the state, as well as from the island of Cozumel. Rehder (1966) then gathered the information available for the nonmarine mollusks up until that date, added new collected material, and then published the most recent record known for the state. Rehder’s publication also is noted for including an annotated list of species.

Several decades passed before Negrete Yankelevich (1998) conducted her research at the El Edén Ecological Reserve. In her work, Negrete Yankelevich studied several biological aspects of *Pomacea flagellata* (Say 1829): the species size in relation to water body size; the influence of factors such as day, night, water temperature, and the environment to the population density of species; the depth and type of the water body (and whether or not it was permanent); and vegetation types. She also investigated the diet of snails, both as to the variety and abundance of the diverse materials eaten.

On five collecting sites at El Edén, Cózatl Manzano (1999) later found a total of 11 species of freshwater mollusks. He studied species richness, species composition per site and between seasons, as well as variations on species composition per site. Cózatl then made cumulative graphs, and calculated the Shannon–Wiener, Czekanowski, and Jaccard indexes. Among his findings were five new records for the state (Quintana Roo) and for the Yucatán Peninsula: *Drepanotrema cimex* (Moricand 1837), *Biomphalaria havanensis* (Pfeiffer 1839), *Planorbella trivolvis* (Say 1817), *Planorbula armigera* (Say 1821), and *Sphaerium transversum* (Say 1829). The three new records of *Physella cisternina* (Morelet 1851), *Physella impluviata* (Morelet 1849), and *Physella* sp. are in controversy. The new research being done by Dr. Paraense (personal communication), and my own findings, seem to indicate that all three could be placed in one very variable species.

Gómez Espinosa (1999) produced distribution maps of the 20 land molluscan species she found in three different habitats present at El Edén, Quintana Roo: tropical subdeciduous forest (“selva mediana

subperennifolia”), savanna, and wetland. She also calculated the relative abundance and species abundance of various rare and common species, and then compiled cumulative graphs to summarize and organize her findings. Gómez Espinosa’s research showed that the relative abundance varies between seasons and among habitats, while rare and common species abundance vary depending on habitat. The new records for Quintana Roo are *Choanopoma gagei* Bequaert and Clench 1931, *Bothriopupa variolosa* (Gould 1848), and *Cecilioides consobrina prima* (de Folin 1870); new records for both Quintana Roo and the Peninsula of Yucatán include *Vertigo ovata* (Say 1822) and *Leptinaria interstriata* (Tate 1869–1870).

CAMPECHE

In 1967, Thompson (1967) published the single comprehensive work known on the nonmarine mollusks of Campeche state. For this work, Thompson compiled reports on previous species records for the state that had been scattered throughout other publications. Thompson reported 59 species, added 21 new records for the state, and also produced an annotated list of species.

For the sake of comparison, all the records available for the nonmarine mollusks of the Yucatán Peninsula (including the states of Campeche and Quintana Roo) were combined along with those of Tabasco and Chiapas states in Mexico, as well as with those of Guatemala and Belize. A summary is shown in Table 16.1. Of all the places summarized in Table 16.1, Guatemala is the best known, Chiapas comes second, the state of Yucatán is third, and the rest are considered poorly understood.

With the information available so far, and the results shown above, the fauna closest to the Peninsula of Yucatán are those from Guatemala, Belize, Tabasco, and Chiapas, in that order. The shared species are highest with Guatemala, and equal with Belize, Tabasco and Chiapas. The calculated similarity index relates Guatemala and Belize to the Yucatán Peninsula more than with Tabasco and Chiapas. These findings agree with the ideas proposed earlier by Bequaert and Clench (1933). Comparisons among faunas are limited because their study has been limited.

Figure 16.1 shows the localities reported in the literature for the nonmarine mollusks of the Yucatán peninsula. From the map, it is apparent that localities in Yucatán state are more scattered than in Campeche, except for a band around the southern borders of the state and on the northeast corner; nonetheless giving us a better idea of the nonmarine mollusks found there. Although the central west part of Campeche state has been explored, the East, South and SW have not. Quintana Roo has been explored on the northeastern shore: Puerto Morelos, Tulum, and Ascension Bay (Rehder

TABLE 16.1. Species summary and Sorenses Index calculation.

Number of species of non-marine mollusks per states/countries:

YCQ	Y	C	Q	T	Ch	B	G
106	80	62	54	51	100	33	154

Shared species among states/countries:

YCQ	YC	YQ	CQ	PYT	PYCh	PYB	PYG
32	18	6	5	15	15	15	31

Sorensen Index (SI) calculated between the Yucatán Peninsula and states/countries:

PYT	PYCh	PYB	PYG
0.19	0.14	0.21	0.23

B = Belize; C = Campeche; Ch = Chiapas; G = Guatemala; Q = Quintana Roo; T = Tabasco; Y = Yucatán; PY = Peninsula of Yucatán; $SI = 2s/(N_1 + N_2)$, where SI = Sorensen Index; s = number of shared species; N_1 = number of species of locality 1; and N_2 = number of species of locality 2.

1966), as well as around the shores of Cozumel Island (Richards 1937; Rehder 1966). More recent mainland records were reported by Negrete Yankelevich (1998), Cózatl Manzano (1999), and Gómez Espino (1999) at El Edén Ecological Reserve, and two more localities are located on the central portion and in the south, as well as at Cozumel Island.

***LOW SPECIES RICHNESS VERSUS
HIGH SPECIES RICHNESS***

Bequaert and Clench (1933) have considered Yucatán state (then with 78 species and now with 80 species) a low diversity region. One can consider the diversity low if Yucatán is compared with regions like Los Tuxtlas in Veracruz, Mexico, which possesses 83 species (Naranjo-García 1997–1998; Naranjo-García and Polaco 1997); a region in San Luis Potosí, Mexico, which reports 87 species (Correa-Sandoval 1997); a site in Jamaica, which has 66 known species (Rosenberg and Muratov 1997–1998); or even a site in Cameroon, in which 97 species have been recorded (de Winter and Gittenberger 1998). In spite of the relative low species number so far reported

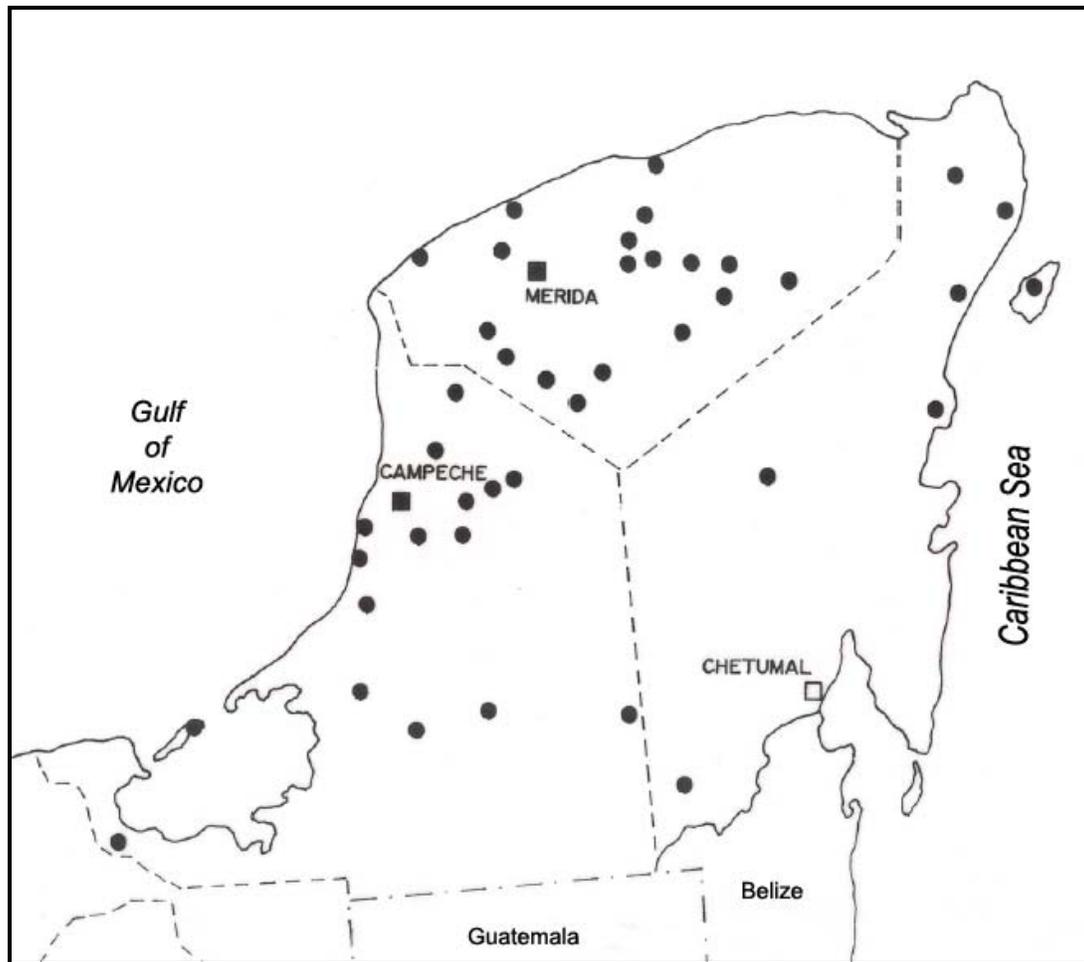


FIGURE 16.1. The localities reported in the literature for the nonmarine mollusks of the Yucatan Peninsula.

in the state of Yucatán, it is highly possible that several new species are waiting to be discovered and described in unexplored areas throughout the peninsula.

The diversity of mollusks is related to the vegetation type and to the climate. Perhaps the low number is explained because only those mollusks that adapt to that variable climate can survive there. The climate might have been a very important factor in the collapse of the Maya (Hodell, Curtis, and Brenner 1995; Curtis, Hodell, and Brenner 1996); climatic changes also could play a very important role in determining whether or not mollusks can adapt to their environment.

SUBSISTENCE STUDIES IN THE MAYA REGION

There are no known subsistence studies performed relative to nonmarine mollusks of the Maya region. Dr. Scott Fedick (from the University of

California–Riverside) thought (as cited by Negrete Yankelevich 1998), that it is possible that the Maya had cultivated and managed *Pomacea flagellata* in the area (cited in Negrete Yankelevich 1998), where it is the only edible freshwater mollusk and thus susceptible to farming; it could also be a valuable source of calcium. Species of *Pomacea* possess several good attributes for farming: they are herbivores, highly fertile, have a high growth rate, and are amphibious; under controlled cultivation, they are also devoid of parasites or other harmful organisms (Mendoza et al. 1999).

Crushed shells of *Pomacea flagellata* could potentially be useful as an additive to enrich artificial animal foods (i.e., as a source of calcium, but a chemical analysis would be necessary first), while whole shells could be used as a resource for the production of art crafts such as lamps and other decorative items. Nonmarine shells are generally brittle and fragile so that very few of them have been used to produce handcrafts (Berry 1946). *Orthalicus princeps* and *Helicina spp.*, however, are other nonmarine mollusks whose shells are hard enough to be used potentially in art crafts as well.

Leidyula moreleti (Fischer 1871), a slug, is a potential intermediate host of human parasites. On the other hand, other slugs such as *Sarasinula dubia* (Semper 1885) and *S. plebeia* (Fischer 1868) (Naranjo-García et al. 1997), which are located near Merida (Yucatán), are potential intermediate hosts as well as possible plagues for agricultural crops as seen in Central America and South America (Caballero et al. 1991; Andrews and Huezo de Mira 1983; Graeff et al. 1993).

SUMMARY

The aim of this chapter is to bring together the information known to date on the nonmarine mollusk of the Yucatán Peninsula.

The main source of information on this fauna are 12 papers published between 1891 and 1999 that discuss the nonmarine mollusks of this area. Large, comprehensive publication dealing with nonmarine mollusks in broader areas provided additional information.

Pilsbry (1891), Bequaert and Clench (1931, 1933, 1936, and 1938), and Harry (1950) for Yucatan state; Richards (1937) Rehder (1966), Cózatl Manzano (1999), and Gomez Espinosa (1999) for Quintana Roo; and Thompson (1967) for Campeche state provided information dealing mainly with taxonomy, distribution of species, and synonymies, but also summarized the knowledge of the time in their respective states. In the late 1990s, studies of nonmarine mollusks included the biology and diet of one species (*Pomacea flagellata*) in Quintana Roo (Negrete Yankelevich 1998) and their habitat,

distribution, and diverse ecological aspects within El Edén Ecological Reserve (Cózatl Manzano 1999; Gómez Espinos 1999).

The first studies ever done on the nonmarine mollusks in El Edén were by Negrete Yankelevich (1998), Cózatl Manzano (1999), and Gómez Espinos (1999). Thompson's (1967) work on the nonmarine mollusks of Campeche state continues to be the first and only comprehensive publication on that state's fauna.

A comparison of the total number of species within Yucatán Peninsula, other states of southern Mexico, Guatemala, and Belize shows that the highest richness is found in Guatemala, Chiapas state, and Yucatan state, respectively. The Yucatán Peninsula shares the largest number of species with Guatemala than with any other of the areas compared.

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Chapter 17

Fungi in the Maya Culture: Past, Present and Future

Gastón Guzmán

INTRODUCTION

Fungi are strongly connected with the indigenous cultures in Mesoamerica. Fungi have been used in rituals; for medical purposes; or as food, as observed in the Mazatec, Nahuatl, Purepecha, Raramuris, and Zapotec cultures, among others in Mexico (Heim and Wasson 1958; Guzmán 1984, 1997; Lowy 1972a, 1974, 1977; Mapes, Guzmán, and Caballero 1981; Sahagún 1569–1582; Schultes and Hofmann 1979; Wasson and Wasson 1957; Wasson 1980). However, the information available is often sketchy because, at the beginning of the Spanish Colony following the Conquest, the indigenous cultures were languishing to extirpate their religious ceremonies (Lowy 1972b; Wasson 1980). The work of Sahagún (1569–1582), with his *Magliabecchiano* and *Florentino Codices*, is a good expression of the Nahuatl Culture concerning the knowledge of fungi. In the *Magliabecchiano Codex*, for instance, it is possible to see an Aztec eating a sacred mushroom with a personage at his back. For the Catholic Church, this personage is the devil; but, for the Indians, it is the god of the mushroom, *Teonanácatl*, who takes the Indian to his sacred and hallucinogenic world (Heim and Wasson 1958; Guzmán 1984; Wasson and Wasson 1957; Wasson 1980).

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Wasson (1980) observed that we know virtually nothing about the fungi of the Maya Culture despite its great interest. Considered that the Maya area encompasses the whole of the Yucatán Peninsula; almost all of the Mexican states of Chiapas and Tabasco; and the Central American countries of Guatemala, Belize, El Salvador, and Honduras, the extent of the problem is apparent. The lack of information is not due to the absence of fungi use among the Maya, but to the great destruction that the Spanish Conquest inflicted on Maya Culture. Diego de Landa (1560) freely admitted that he burned codices and destroyed numerous idols in Yucatán; in his defense, de Landa stated that their destruction was necessary because those things contained nothing but superstitions and devils (Lowy 1972a, b; Wasson 1980). There are, however, many studies on the Maya Culture. In 1990, for example, an international symposium was held at Wakayama University in Japan; the main subject of this symposium was the Maya Culture (Guzmán 1992; Miyanishi 1992). Sadly, numerous mushroom stones and a few codices are the only information that we have on the culture of fungi among the past Maya Culture. Although we have evidence of the use of fungi as food or medicine in the Maya region, it seems that the practice of using ceremonial fungi has long since disappeared.

This paper summarizes the available information on mushroom use among the Maya, both in the past and present. This work is divided into three sections: (1) an historical examination of what we know about past Maya fungi use; (2) an overview of current mycological and ethnomycological studies in the Maya region; and (3) the first results of the fungi inventory at El Edén Ecological Reserve, which are currently being carried out.

KNOWLEDGE IN THE PAST

In spite of the destruction effected by de Landa (1560) in Yucatán, Lowy (1972a, b) noted that it is still possible to study the numerous mushroom stones and four important codices (i.e., Madrid, Paris, Dresden, and Galindo) remaining from the Maya Culture. The Galindo Codex was named by Lowy after he found it in the house of Mr. José Galindo (now deceased), a Guatemalan Indian in Huehuetenango.

Lowy (1972a, b) deduced that the Galindo Codex is a copy of the Madrid Codex after observing a similar image in both codices, in which an Indian painted in black is seen making an offering to an important seated personage. According to Lowy, the special object in the Indian's right hand is a stylized fruit body of *Amanita muscaria* (L. : Fr.) Hook., with typical wart-like patches on the cap. Lowy based his interpretation on the fact that this mushroom is now common in pine forests in both Guatemala and Chiapas, where it is

surrounded in some mystery for the Indians. At present, they call this mushroom by the common Quiche names of “kaquiljá” (or “thunderbolt”) and “itzel ocox” (or “evil mushroom”).

Lowy (1974) noted the connection between the Thunderbolt Legend and *A. muscaria*. According to him, the Indians in Guatemala and Chiapas link this fungus with the thunderbolt because of its strong, rare power (the next section, however, presents another interpretation of the fungus and its relationship to the Thunderbolt Legend). Lowy (1974) also observed that the common name “yuyo” (from the name of a red common wild fruit) was applied both to the edible *Amanita caesarea* (Scop. : Fr.) Grev. as well as the poisonous *A. muscaria*; the latter is also called “yuyo del rayo” or “yuyo del trueno” (“rayo” and “trueno” mean thunderbolt). Guzmán and Ramírez-Guillén (2001) found that *A. caesarea* in Chiapas is a complex of four species: *A. jacksonii* Pomerleau, *A. laurae* Guzmán and Ramírez-Guillén, *A. tullossii* Guzmán and Ramírez-Guillén, and *A. yema* Guzmán and Ramírez-Guillén — all of them named “yuyo.” *A. caesarea* s. str. is confined only to the central and northern portions of Mexico.

It seems that the Quiche Indians of Guatemala consider *A. muscaria* to be a sacred fungus because, according to Wasson and Wasson (1957), the name “holom-ocox” in the ancient religious pre-conquest book “Popol Vuh” means *A. muscaria*. Interestingly, in both Mexico and Guatemala, *A. muscaria* is now considered to be a “diabolical” mushroom because it is “very poisonous”; at the same time, however, the Indians treat it with respect as a special fungus. In 1977, Villacorta and Villacorta (cited in Torres 1984) postulated that the ancient Maya used sacred mushrooms in their Chichén Itzá sacrifices; in fact, they believed that the victims ate toxic mushrooms before their deaths.

Referring to the Dresden Codex (Dresden Codex Reproduction 1981), Lowy (1980) observed four men (displayed on two pages—two men per page) falling through space, with special leaves on their bodies. Lowy believed that these leaves were stylized mushrooms that related to *A. muscaria*. Other authors believe that those leaves belong to the hallucinogenic plants *Turbina corymbosa* (L.) Raf. (a Convolvulaceae) or *Salvia divinorum* Epl. and Jativa-M. (a Lamiaceae) (Ott 1993; Schultes and Hofmann 1979; Torres 1984), which are now used as narcotic plants by other Indians in Mexico. Another interpretation of the Dresden Codex “falling men” lies in their relationship with the god of rain (Chak) and the fungus *Ustilago maydis* (DC.) Corda, which will be discussed later in the chapter.

All of the above observations on the use of sacred mushrooms have a connection with the ancient mushroom stones found in the Maya highlands. Wasson and Wasson (1957) and Wasson (1980) presented these mushroom stones as evidence of the ritual involving hallucinogenic mushrooms among the Maya. Sapper, was the first to find a mushroom stone in El Salvador in

1898 (Heim and Wasson 1958; Wasson and Wasson 1957). Sapper's original discovery is now in a museum in Zurich.

Kobayasi, who was very interested in the ethnomycology of Mexico, made several facsimiles of the Sapper mushroom, which he presented in 1983 at the Third International Mycological Congress in Tokyo, Japan. At present, there are more than 300 known pieces of mushroom stone, the majority of them the Maya area in Guatemala, although a few are from other cultures in Mexico (de Borhegyi 1961; Lowy 1971; Mayer 1977).

Guzmán (in Mapes, Guzmán, and Caballero 1981) and Guzmán (1984) reported the existence of a small mushroom stone (34 mm high) from an archaeological site of the Purepecha Culture in Patzcuaro, Michoacán, México, which he identified with a button of *A. muscaria*. The Maya mushroom stones are figures 28 to 38 cm high, with a standing man or animal represented below the cap of a mushroom. Torres (1984) and Ohi and Torres (1994) discussed these figures from Guatemala. Along with the little mushroom stone from the Purepecha region, de Borhegyi (1961) found miniature mushroom stones in Guatemala that are 10 to 19 cm high.

Although standing figures are represented in the above stones, Wasson (1980) and Lowy (1980) mentioned two other interesting figures, where men are falling or plunging into a dreamlike state. These figures show a man with his feet supporting the cap of the mushroom. These falling figures have a strong relationship with the hallucinogenic effects of the sacred mushrooms, because and a person flying in space. According to Lowy (1980), these figures relate to the falling human figures represented in the Dresden Codex, where the falling men are plunging gods—floating or falling from the sky. In fact, anyone who eats hallucinogenic mushrooms feels as if he or she is flying in space; when the effects subside, he or she falls back to earth. According to Wasson (1980) and Lowy (1980), these falling men in the Guatemalan mushroom stones are strong evidence of the ceremonial use of hallucinogenic fungi in the Maya Culture. However, as noted with the Dresden Codex “falling men,” another interpretation of these figures (i.e., in relation to Chak, the god of rain, and *Ustilago maydis*) will be discussed later in this paper.

The use of hallucinogenic mushrooms belonging to *Psilocybe* is unknown in the entire Maya region, in spite of the fact that *P. mexicana* Heim, *P. cubensis* (Earle) Singer, *P. subcubensis* Guzmán, and *P. zapotecorum* Heim emend. Guzmán have been reported (Sommerkamp in Ohi and Torres 1994; Torres 1984; Wasson 1980). The first report on a hallucinogenic *Psilocybe* from the Maya region was made by Lowy (1977) in Guatemala. Close to the Yucatán Peninsula in the Tehuantepec Isthmus region (Uxpanapa zone), Guzmán (1979) described the following hallucinogenic species of *Psilocybe*: *P. naematoliformis* Guzmán, *P. singerii* Guzmán, *P. uxpanapensis* Guzmán,

and *P. weldenii* Guzmán. It is possible that the use of *A. muscaria* was replaced a long time ago by species of *Psilocybe*, which is what happened in other parts of Mexico. However, at present, there is no evidence of the use of any sacred mushrooms in the Maya area.

MYCOLOGICAL AND ETHNOMYCOLOGICAL STUDIES IN THE MAYA AREA

In spite of the great diversity of fungi not only in the Maya area, but in all the tropical regions, as noted by Guzmán (1998), there are few reports on the fungi of the Maya region. Guzmán (1998) established that although there are more than 200,000 species of fungi in Mexico, we know only about 6,000 of them. As there are more than 70 percent of all fungi in tropical regions, and we only study a few species every year, it would take more than 200 years (at the present pace) to know all the fungi of Mexico. This slow progress is especially disturbing as tropical vegetation is being destroyed at an alarming rate.

The first records of fungi in the Maya area were made by Millspaugh (1896, 1898), who reported relatively few fungi (among them, *Agaricus yucatanensis* Ellis and Everhart) in his study of Yucatán flora. Standley (1930) researched the same area; in his study, Standley presented a checklist of the 22 fungi species recorded from Yucatán. Hedrick (1935) recorded some lichens from Yucatán, while Guzmán (1982, 1983); Guzmán and Johnson (1974); Guzmán and Madrigal (1967); Guzmán-Dávalos and Guzmán (1982); Mata (1987); Pérez-Moreno and Villarreal (1988); Pérez-Silva, Herrera, and Valenzuela (1992); and Ulloa (1974) studied the fungi of the Maya area of Mexico. Of these works, Ulloa (1974) is the only one confined to molds, although Guzmán (1982) described a few micromycetes.

Ulloa (1974) studied the molds that form pozol—a Mayan beverage that was also recorded by de Landa (1560). Guzmán (1982, 1983), and Guzmán-Dávalos and Guzmán (1982), discussed more than 250 species of fungi from 66 localities on the Yucatán Peninsula; some of them were new records, and others were new species. The papers of Guzmán (1983) and Mata (1987) also deal with the ethnomycology of Yucatán. Related to this latter ethnomycological point, Laughlin (1975) presented several Tzotzil names on fungi, while Barrera-Vázquez, Bastarrachea, and Brito-Sansores (1980) considered some few names on fungi in their respective dictionaries of the Maya Region (also transcribed by Guzmán 1997). However, neither Barrera-Vázquez, Bastarrachea, and Brito-Sansores (1980) nor Laughlin (1975) presented any names related with the sacred mushrooms.

Sommerkamp (1991) and Sommerkamp and Guzmán (1990) presented a discussion of the 21 known edible species from the popular markets in Guatemala, and a checklist of the fungi in the Herbarium of the University of San Carlos of Guatemala; Sommerkamp (1994) discussed the known hallucinogenic species of *Psilocybe*. Guzmán, Torres and Logemann (1985) described *Morchella guatemalensis* Guzmán, Torres, and Logemann from Guatemala. Guzmán (1987) discussed *Pseudofistulina radicata* (Schw.) Burdsal from Yucatán, Guatemala, and El Salvador, this latter report being based on Escobar and Toledo (1977). Logemann et al. (1987) reported a fatal case of poisoning with *Amanita magnivelaris* Peck in Guatemala. There are at present more than three hundred species of fungi known from the Maya area.

Important species of fungi used at present in Yucatán are *Geastrum saccatum*, *Clathrus crispus*, *Pleurotus djamor*, and *Ustilago maydis*, among others (Guzmán 1983). *Geastrum saccatum* is named “looi lu um” (or “flower of the earth”), and is used to stop diarrhea in children known as “mal de ojo.” *Clathrus crispus* is known as “chaaha quai” (i.e., colander of the medicine man or wizard), and is used to control some eye infections using the liquid that is obtained when the mushroom is squeezed. *Pleurotus djamor* is a common pantropical edible fungus known as “xikin che” (or “ear of the woods”); in the present tourist resort of Xcaret (which is close to Cancun, Quintana Roo), employees have a laboratory and greenhouses to cultivate this fungus and cook it in their restaurants. Furthermore, the University of Yucatán, in Merida, has a program on the cultivation of this fungus to teach the technology to the farmers.

There are some important ethnomycological observations to be made regarding *Ustilago maydis*, the edible fungus of the Nahuatl culture known as “huitlacoche”, which is a parasitic fungus on corn. This fungus is called “ta chaak,” “ta chak ixim,” “ixim chaak,” and “nal chaak,” among other names, all of which are related to Chak, the god of rain. It is believed that this fungus falls on the corn from rain, and that the fungus has concentrated the violence of the thunderbolt (Guzmán 1983; Mata 1987). These interesting observations on the fungus that falls from the sky with all the violence of the thunderbolt are strongly related, and demonstrate the connection of *Ustilago maydis* with the Thunderbolt Legend, the Dresden Codex, and the mushroom stones portraying “falling men,” as discussed earlier. Lowy (1974, 1980) stated that the Thunderbolt Legend—which related the thunderbolt with a fungus, and the falling men in both the Dresden Codex and the mushroom stones—are related to the ingestion of *A. muscaria*. Why, then, is all this information not connected with the important edible fungus *Ustilago maydis*, which is also

said to fall from the sky? This is a new interpretation, and may be the most proper way of relating “falling men” and the Thunderbolt Legend. As long as different interpretations exist, it is clear how much study is still needed on the Maya Culture in relationship with the fungi.

**THE PROJECT ON THE FUNGI OF EL EDÉN
ECOLOGICAL RESERVE, QUINTANA ROO**

To cope with the high destruction of vegetation on the Yucatán Peninsula, Arturo Gómez-Pompa (University of California, Riverside) founded a private ecological reserve in the north of Quintana Roo, called “Reserva Ecologica El Edén,” to conserve and study the biodiversity of this site. Two explorations took place in 2000—one in July, and the other in November—to gather all the fungi possible.

More than 400 specimens of fungi, mainly macromycetes, were gathered, as well as some lichens and myxomycetes. A preliminary checklist of studied species was prepared (Table 17.1) noting 65 species, of which *Leucopaxillus gracillimus* is first reported in Mexico. This species was only previously known in Florida, U.S.A., Brazil, and the Antilles (Dennis 1970; Pegler 1983). Moreover, *Fomitopsis rosea*, *Panellus stypticus*, and *Trogia cantharellus* were also first reported on the Yucatán Peninsula.

New species will be described from the material that is now being studied. The ultimate plan is to publish articles and descriptions of any new or interesting species. The main objective of this project is to prepare an illustrated book with color plates of the main fungi of El Edén.

TABLE 17.1. A preliminary checklist of the fungi of El Edén Ecological Reserve

Ascomycotina	<i>Cookeina sulcipes</i> (Fr.: Fr.) Dennis <i>C. tricholoma</i> (Mont.) Kuntze <i>Daldinia eschscholzii</i> (Ehenb.: Fr.) Rehm <i>Hypoxylon rubiginosum</i> (Pers.: Fr.) Fr. <i>Phillipsia domingensis</i> (Berk.) Berk. <i>Phylacia globosa</i> Lév. <i>P. poculiformis</i> (Mont.) Mont. <i>Xylaria bomboensis</i> Lloyd sesu San Martin & Rogers <i>X. cocoophora</i> Mont. <i>X. phyllocharis</i> Mont. <i>X. polymorpha</i> (Pers.:F.) Grev.
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TABLE 17.1. (continued)

Basidiomycotina

Agrocybe retigera (Speg.) Singer
Auricularia fuscusuccinea (Mont.) Farlow
A. mesenterica Pers.
A. polytricha (Mont.) Sacc.
Clathrus crispus Turpin
Coprinus radians (Desm.) Fr.
Coriolopsis byrsina (Mont.) Ryv.
C. polyzona (Pers.) Ryv.
Dacryopinax elegans (Berk. & M.A. Curtis) Martin
Daeladea sprucei Berk.
Dictyopanus pusillus var. *rhpidium* (Berk.) Singer
Earliella scabrosa (Pers.) Gilbn. & Ryv.
Fomitopsis feel (Fr.) Kreisel.
Ganoderma curtisii (Berk.) Murrill
Geastrum campestre Morgan.
G. saccatum Fr.
Gloeophyllum striatum (Sw.: Fr.) Murrill
Hexagonia papyracea Berk.
H. tenuis Fr.
Lepista singeri Guzmán
Leucocoprinus birnbaumii (Corda) Singer
Leucopaxillus gracillimus Singer & A.H. Smith
Mycenoporella clypeata (Pat.) R. Heim
Panaeollus antillarum (Fr.) Dennis
Panus badius (Berk.) Singer
P. crinitus (L.: Fr.) Singer
Phellinus extensus (Lév.) Pat.
P. gilvus (Schw.: Fr.) Pat.
P. linteus (Berk. & M.A. Curtis) Teng
P. pectinatus (Kl.) Quél.
Phylloporia spathulatha (Hook.) Ryv.
Pleurotus djamor (Fr.) Boedijn
P. hygrophanus (Mont.) Dennis
Pogonomyces hydnoides (Sw.: Fr.) Murrill
Polyporus tenuiculus (Beauv.) Fr.
P. tricholoma Mont.
Pycnoporus sanguineus (L.: Fr.) Murrill
Rigidoporus microporus (Fr.) Overeem
Schizophyllum commune Mont.
S. fasciatum Pat.
Scleroderma sinnamariense Mont.
Trametes maxima (Mont.) David & Rajch.
T. villosa (Fr.) Kreisel
Trichaptum perottettii (Lév.) Ryv.
Tremella rubromaculata Lowy.
Trogia cantharellus (Mont.) Pat.
Volvariella volvacea (Bull. : Fr.) Singer

Lichens

Coenogonium linkii Ehrenb.
Graphis librata (L.) Anch.
Strigula complanata Mont.

Myxomycota
(*Myxomycetes*)

Arcyria denudata (L.) Wettst.
Ceratiomyxa fruticulosa (Müll.) Macbr.
Stemonites splendens Rostafineski

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Chapter 18

Moss Distribution in the Yucatán Peninsula

Claudio Delgadillo M.

INTRODUCTION

Mosses are represented by a small number of species in the Yucatán Peninsula. According to Millspaugh (1895, 1896, 1898), Standley (1930), and Steere (1935), there were 39 species in the area. However, studies by Delgadillo and co-workers (Delgadillo, Cárdenas, and Sharp 1982; Delgadillo and Cárdenas 1982; Delgadillo 1984) identified a total of 69 moss species and varieties. The number of species remained essentially unchanged in *The Moss Flora of Mexico* (Sharp, Crum, and Eckel 1994), but recent field work has served to add precision to the floristic data.

Despite the number of moss species, the peninsular moss flora is of interest because it maintains important floristic connections with mainland Mexico, Central America, and the West Indies. From the phytogeographic point of view, study of the peninsular moss flora may identify routes of migration in the Caribbean basin while, from a strict biological perspective, it illustrates the morphological diversity and adaptive strategies that merit further investigation. Delgadillo (1984) described the main patterns of distribution and made reference to the occurrence of phenotypic convergent features among the peninsular mosses. This paper offers additional comments on the distribution of the peninsular moss flora.

Thanks are extended to Dr. Kenneth D. McFarland, University of Tennessee, for assistance with herbarium records. Dr. Ronald A. Pursell, Pennsylvania State University, identified all *Fissidens* specimens. Angeles Cárdenas assisted in the identification of specimens and in field and herbarium work. Field work in eastern Quintana Roo in October 2000 was made possible by Dr. Arturo Gómez-Pompa, Reserva Ecológica El Edén and by Project "A Biodiversity Survey of Poorly-Known Taxa from Quintana Roo, Mexico" supported by UC Mexus. Field assistance by El Edén personnel is greatly appreciated.

METHOD

A list of moss species in the Yucatán Peninsula was compiled from herbarium and bibliographic sources. Field work conducted at the El Edén Ecological Reserve in the state of Quintana Roo (21°12' N to 87°11' W) in October 2000 yielded additional data on local moss distribution. A complete set of specimens was deposited at MEXU, the Bryophyte Collection at the National University of Mexico, where herbarium materials collected in 1980–1981 were also available. The nomenclature was updated according to recent treatments (see Delgadillo, Bello, and Cárdenas 1995), and the latitudinal distribution (expressed as geographical coordinates) was obtained for further analysis.

Following a previous study (Delgadillo 1984), the Yucatán Peninsula was divided into four latitudinal areas: (1) 17°48' to 19° S (southern); (2) 19°01' to 20° (S-C or south-central); (3) 20°01' to 21° (N-C or north-central); and (4) 21°01' to 21°33' (N or northern). The presence or absence of all known species was recorded in an OGU (Operational Geographical Units) data matrix that served first as the basis for the computation of Jaccard's index of similarity, and then to obtain the UPGMA (unweighted pair-group method, arithmetic average) dendrograms that show the relationships among OGUs (states and latitudinal subdivisions) in the peninsula. An NTSYS-PC software package, version 2.0 (Exeter Software, New York), facilitated the analyses.

RESULTS

The moss flora of the Yucatán Peninsula contains 70 species and varieties (table 1). Three additional species have been mentioned elsewhere for the area. Sharp, Crum, and Eckel (1994) recorded *Bryum procerum* Schimp. from the state of Yucatán, but this is based on a mistaken citation by Ochi (1981) that refers to a Venezuelan locality. *Squamidium nigricans* (Hook.) Broth., cited from Quintana Roo (Sharp, Crum, and Eckel 1994) with no reference to any specimen, remains unconfirmed. The presence of *Didymodon rigidulus* Hedw., originally cited as *D. acutus* (Brid.) Saito, is still questionable as examination of the supporting specimen has not been possible.

Among the mosses of the Yucatán Peninsula, 20 species are locally frequent and broadly distributed, as shown by their presence in the four latitudinal subdivisions. Such species as *Calymperes afzelii*, *Entodontopsis leucostega*, *Henicodium geniculatum*, *Leucobryum incurvifolium*, *Octoblepharum albidum*, and others in Table 18.1, illustrate this pattern among the epiphytes while *Barbula agraria*, *Barbula indica*, *Hyophila involuta*, and

TABLE 18.1. Moss species and their state and latitudinal distribution in the Yucatan Peninsula

C	Y	QR	Species	1	2	3	4
x	x	x	<i>Acroporium longirostre</i>	x	x	x	-
-	x	-	<i>Anoetangium aestivum</i>	-	-	x	-
x	x	x	<i>Barbula agraria</i>	x	x	x	x
x	-	x	<i>Barbula indica</i>	x	x	x	x
x	-	x	<i>Brachymenium globosum</i>	-	x	-	x
x	-	-	<i>Brachymenium klotzschii</i>	x	-	-	-
-	x	-	<i>Bryoerythrophyllum recurvirostrum</i> var. <i>aeneum</i>	-	-	x	-
x	x	x	<i>Bryum apiculatum</i>	x	-	x	x
x	x	x	<i>Bryum coronatum</i>	x	x	x	-
x	-	x	<i>Calymperes afzelii</i>	x	x	x	x
-	-	x	<i>Calymperes erosum</i>	-	-	-	x
-	-	x	<i>Calymperes lonchophyllum</i>	-	x	-	x
x	x	x	<i>Calymperes palisotii</i>	x	x	x	x
-	-	x	<i>Calymperes tenerum</i>	-	-	x	-
x	-	x	<i>Chryso-hypnum diminutivum</i>	x	x	x	x
-	x	x	<i>Cryphaea filiformis</i>	-	x	x	x
-	x	-	<i>Cryphaea patens</i>	-	-	x	x
x	x	x	<i>Cyrto-hypnum involvens</i>	x	-	x	-
x	x	x	<i>Cyrto-hypnum schistocalyx</i>	x	-	x	-
-	x	-	<i>Didymodon rigidulus</i> var. <i>gracilis</i>	-	-	-	x
x	x	x	<i>Entodontopsis leucostega</i>	x	x	x	x
x	-	-	<i>Entodontopsis nitens</i>	x	-	-	-
x	x	x	<i>Erpodium domingense</i>	x	-	x	x
-	x	-	<i>Eulacophyllum cultelliforme</i>	-	-	-	x
x	x	x	<i>Fissidens pallidinervis</i>	x	-	x	-
x	x	x	<i>Fissidens radicans</i>	x	x	x	-
x	x	x	<i>Fissidens santa-clarensis</i>	x	x	x	x
x	-	-	<i>Fissidens serratus</i>	x	-	-	-
-	x	-	<i>Fissidens steerei</i>	-	-	x	-
x	x	x	<i>Fissidens yucatanensis</i>	-	-	x	-

TABLE 18.1 (Continued)

C	Y	QR	Species	1	2	3	4
X	X	X	<i>Fissidens zollingeri</i>	X	-	X	-
X	X	-	<i>Funaria hygrometrica</i> var. <i>Calvescens</i>	-	-	X	-
X	X	X	<i>Groutiella tumidula</i>	X	X	X	X
X	-	X	<i>Henicodium geniculatum</i>	X	X	X	X
-	X	-	<i>Hyophila bartramiana</i>	-	-	X	-
X	X	-	<i>Hyophila involuta</i>	X	X	X	X
-	-	X	<i>Isopterygium tenerum</i>	X	-	X	-
X	-	-	<i>Jaegerina scariosa</i>	X	-	-	-
X	X	X	<i>Leucobryum incurvifolium</i>	X	X	X	X
X	X	-	<i>Luisierella barbula</i>	-	-	X	-
X	-	X	<i>Neckeropsis undulata</i>	X	-	-	-
X	X	X	<i>Neohyophila sprengelii</i>	X	X	X	X
-	X	-	<i>Neohyophila sprengelii</i> var. <i>stomatodonta</i>	-	X	-	-
X	X	X	<i>Octoblepharum albidum</i>	X	X	X	X
-	-	X	<i>Orthostichopsis tetragona</i>	X	X	-	X
X	X	X	<i>Papillaria nigrescens</i>	X	-	X	X
-	X	X	<i>Philonotis uncinata</i> var. <i>uncinata</i>	X	X	-	-
-	-	X	<i>Pilosium chlorophyllum</i>	-	X	-	-
X	X	X	<i>Pireella cymbifolia</i>	X	X	X	X
X	X	-	<i>Pireella pycnothallodes</i>	X	-	X	-
X	X	X	<i>Pseudocryphaea domingensis</i>	X	X	X	X
X	X	X	<i>Racopilum tomentosum</i>	X	X	X	-
X	-	X	<i>Schlotheimia rugifolia</i>	X	-	-	X
X	X	-	<i>Schoenobryum concavifolium</i>	X	-	X	-
X	X	X	<i>Sematophyllum adnatum</i>	X	X	X	X
-	-	X	<i>Sematophyllum cuspidiferum</i>	-	X	-	X
-	X	-	<i>Sematophyllum galipense</i>	-	-	-	X
X	X	X	<i>Sematophyllum subpinnatum</i>	X	-	-	X
X	X	X	<i>Splachnobryum obtusum</i>	X	-	X	-
X	X	X	<i>Stereophyllum radiculosum</i>	X	X	X	X
X	X	X	<i>Syrrhopodon incompletus</i> var. <i>incompletus</i>	X	X	X	X
X	X	X	<i>Syrrhopodon parasiticus</i>	X	X	X	X

C	Y	QR	Species	1	2	3	4
x	x	x	<i>Taxithelium planum</i>	x	x	x	x
-	-	x	<i>Taxithelium portoricense</i>	-	x	x	-
-	-	x	<i>Trichosteleum sentosum</i>	x	x	x	-
x	x	x	<i>Trichostomum crispulum</i>	x	-	x	-
x	x	-	<i>Trichostomum portoricense</i>	x	-	x	-
-	x	-	<i>Vesicularia vesicularis</i> var. <i>rutilans</i>	-	-	x	-
x	x	x	<i>Weissia jamaicensis</i>	x	-	x	-
-	-	x	<i>Zelometeorium patulum</i>	x	-	-	-
48	49	50	TOTAL	48	34	52	35

C = Campeche; Y = Yucatán; QR = Quintana Roo; 1 = 17°48' -19°S; 2 = 19°01' - 20° S-C; 3 = 20°01' - 21° N-C; 4 = 21°01' - 21°33' N.

Neohyophila sprengelii are apparently obligate calcicolous species whose distribution is linked to limestone formations (Breen 1963; Serrano 1996).

The moss flora in all peninsular states is similar in size, with nearly half (31 species) of their mosses common to all of them (table 1). The remaining 39 species are either known from state pairs or are restricted to single states in the Yucatán Peninsula (Table 18.2). As the number of shared species among the states is large, the overall similarity values are close to one another (0.56–0.63), but cluster analysis indicates that Campeche (C) and Quintana Roo (QR) are closer to each other than to the state of Yucatán (Figure 18.1).

The distribution of mosses along a latitudinal gradient shows the absence of a peninsular effect—that is, there is no progressive reduction of the number of species from the base to the tip of the peninsula (Figure 18.2). Cluster analysis indicates closer similarity between the northern and south-central sections, and between the southern and north-central sections (Figure 18.3). These similarities, however, may be an artifact induced by a better exploration record in those sections.

DISCUSSION

Compared to other tropical areas, the peninsular moss flora includes a small number of species. For an area nearly 140,000 km², the number of species is considerably smaller than that of neighboring Chiapas, which has an area of 74,211 km² and a moss flora of about 327 species. The Valley of

TABLE 18.2. Number of species shared among states and size of the peninsular moss flora

States	Campeche	Quintana Roo	Yucatán	TOTAL
Campeche	4	---	---	48
Yucatán	6	2	10	49
Quintana Roo	7	10	---	50
Species shared by all states				31
Species restricted to one or two states				39
Total number of species in moss flora				70

Mexico, with an area of about 7,500 km² has some three hundred moss species (Cárdenas 1999); Cuba, with a land area of 115,000 km², has a moss flora containing more than 370 species.

Several factors explain, at least in part, the reduced size of the peninsular moss flora. Most of the Yucatán Peninsula is a lowland limestone area characterized by an undulating topography and the near absence of surface waterways (Beltrán 1959; Miranda 1958b). Precipitation in the southernmost section (outside the area of study) may reach 5,000 millimeters (mm), and 1,000 to 1,100 mm elsewhere in the peninsula; in the northern part, it may reach only 500 mm (Miranda 1958b). With these values, rainfall may not be a limiting factor, but the rapid drainage through the limestone may produce a comparatively dry environment that would limit the number of moss habitats.

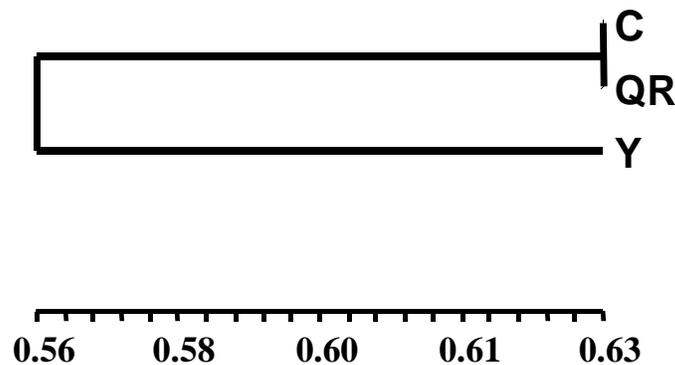


FIGURE 18.1. Floristic relationship among the states of the Yucatán Peninsula, based on a cluster analysis of Jaccard's index of similarity values (C = Campeche; Y = Yucatán; QR = Quintana Roo).

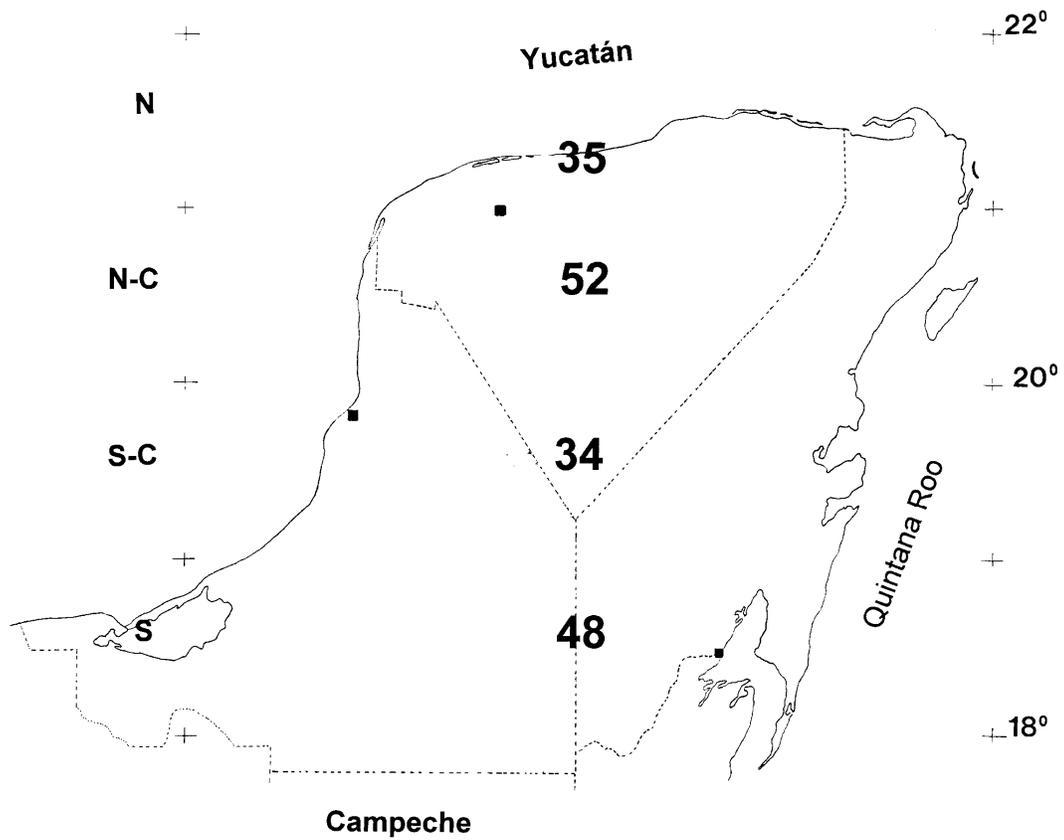


FIGURE 18.2. Number of moss species per latitudinal subdivision in the Yucatan Peninsula.

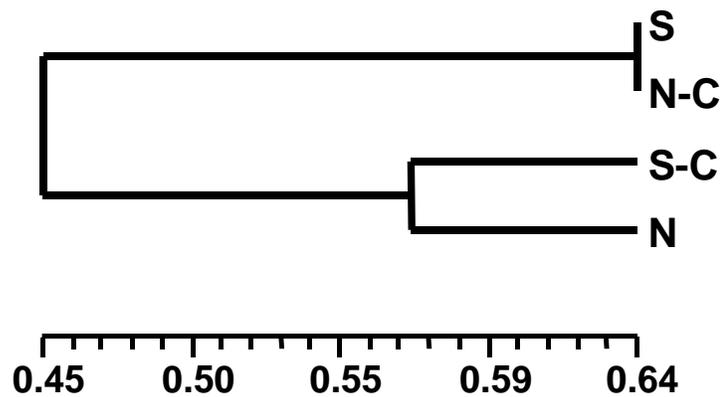


FIGURE 18.3. Floristic relationship among the latitudinal subdivisions of the Yucatán Peninsula, based on a cluster analysis of Jaccard's index of similarity values. (S = southern [17°48' – 19°]; N-C = north central [20°01' – 21°]; S-C = south-central [19°01' – 20°]; N = northern [21°01' – 21°33']).

The area of study is mostly covered by subdeciduous forests (Miranda 1958a) that become smaller in stature northwards. Fire, hurricanes, and a long history of human occupation have altered the original vegetation and increased near-ground solar radiation and evaporation. The edge effect resulting from forest fragmentation and other natural causes, as well as anthropogenic disturbance, has led to the disappearance of habitats and the impoverishment of moss flora since historic times. [Such recurrent climatic changes such as the driest period in the last eight thousand years, dated between 1300 and 1100 yr. B.P. (~A.D. 800–1000 yr.; Hodell, Curtis, and Brenner 1995), must have especially affected mosses from the moister habitats in the Yucatán Peninsula.

The effect of human activities deserves special notice as a force that reduces moss diversity. Agriculture and cattle raising have been major disturbances in the Yucatán Peninsula. According to García and Falcón (1984), from 3 to 24 percent of the surface area of each state is used for agriculture, and 14 to 17 percent is reserved for cattle raising. It is not clear whether these figures include areas where, through the traditional agricultural methods, land is abandoned after a period of cultivation. Along with wood extraction, the use of fire in land clearing practices, and such natural disturbances as Hurricane Gilbert in 1988, have caused extensive damage to vascular flora and have certainly depleted moss populations.

Diversity was perhaps higher in the past. The geographical ranges exhibited by the peninsular mosses suggest that the Yucatán Peninsula has been the pathway of tropical floras (Delgadillo 1984) and that the interchange with neighboring areas is still in progress. With about ninety percent of the mosses shared with the West Indies, the near absence of endemics, and with no peninsular effect in evidence, this hypothesis seems acceptable. A larger number of endemics would signify strong selective pressures and insufficient time for dispersal of the products of speciation. The recognition of a peninsular effect, on the other hand, would show a progressive trend toward fewer species from the base toward the tip of the peninsula; the number of species observed in the four areas do not correspond to those resulting from a peninsular effect. However, the closer similarity between the moss floras of Campeche and Quintana Roo with respect to Yucatán (see Figure 18.1) indicates that the distribution of taxa is not entirely homogeneous throughout the peninsula and that the interchange between the continent and the islands has not been uniform.

Whether at the state level or by latitudinal subdivision, there is a conspicuous group of moss species that are widespread in the Yucatán Peninsula (see Table 18.1). Their occurrence may be attributed to the ubiquitous limestone substrate, a widespread vascular flora, and to gradual climatic variation in the area. Ibarra-Manríquez, Villaseñor, and Durán (1995) indicate that about 50 percent of the arboreal species are shared among the

peninsular states, and Wendt (1993) described several distribution patterns of rain forest species that are common in the peninsula. Wendt (1993:616) noted that among rainforest species restricted to northern Mesoamerica in their continental distribution (excluding the Mexican endemics), “the 43 species that occur in the Peninsula of Yucatan (Yucatan and widespread groups) have a much higher percentage also occurring in the Greater Antilles” than the 61 nonpeninsular species. No evidence exists of a common history between the vascular species and the widespread epiphytic mosses cited in this contribution, but this range similarity calls for a closer look at the geographic distribution of mosses and their phorophytes in the Yucatán Peninsula.

Knowledge of the peninsular moss flora is far from complete. Several areas may still yield new moss records for the area, and this will require the reevaluation of the proposed hypotheses. From the geographic point of view, the mosses from Belize and the Petén region of Guatemala are part of the Yucatán Peninsula and should be included to have a better view of the size and distribution of flora. Certain other features of the peninsular landscape are floristically important. The so-called “Petenes” and the Sian ka’an National Park in eastern Quintana Roo have not been explored for mosses. The former represents a unique environment where mosses from the mainland may be associated with freshwater habitats in the sea.

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PART IV:
AGRICULTURE

Chapter 19

Archaeological Evidence for Ancient and Historic Resource Use Associated with the El Edén Wetland, Northern Quintana Roo, Mexico

Scott L. Fedick

INTRODUCTION

Since the early 1970s, an increasing amount of evidence has indicates that the ancient Maya of southern Mexico and Central America (Figure 19.1) made use of wetlands for agricultural production (e.g., Siemens and Puleston 1972; Gliessman et al. 1983; Turner and Harrison 1983a; Culbert, Levi, and Cruz 1990; Pohl 1990; Pohl et al. 1996; Culbert et al. 1997). The kinds of wetland cultivation strategies employed by the ancient Maya ranged from the simple planting of crops in the moist soils left behind by receding waters to the labor-intensive transformation of wetland landscapes through channelization and the construction of raised planting platforms (Turner 1983; Siemens 1996). It has been suggested that the earliest pioneer settlers of the

I would like to thank Arturo Gómez-Pompa for his initial invitation to conduct research at the El Edén Ecological Reserve, and for the many years of assistance and inspiration he has provided before and since then. The work at El Edén was greatly facilitated by Marco Lazcano and the assistance of the other staff members. Many students and volunteers worked on the El Edén survey, and I thank them all for their hard labor and good company, with special appreciation to Field Directors Bethany Morrison and Bente Juhl Andersen. Funding for the project was provided by grants from the UC MEXUS and the University Research Expeditions Programs, both of the University of California, and by the Foundation for the Advancement of Mesoamerican Studies. Financial support for the final analysis and write-up of the project was provided by a generous donation from Michael Baker, owner of Rancho Santa Maria and good neighbor to the south of the El Edén Ecological Reserve.

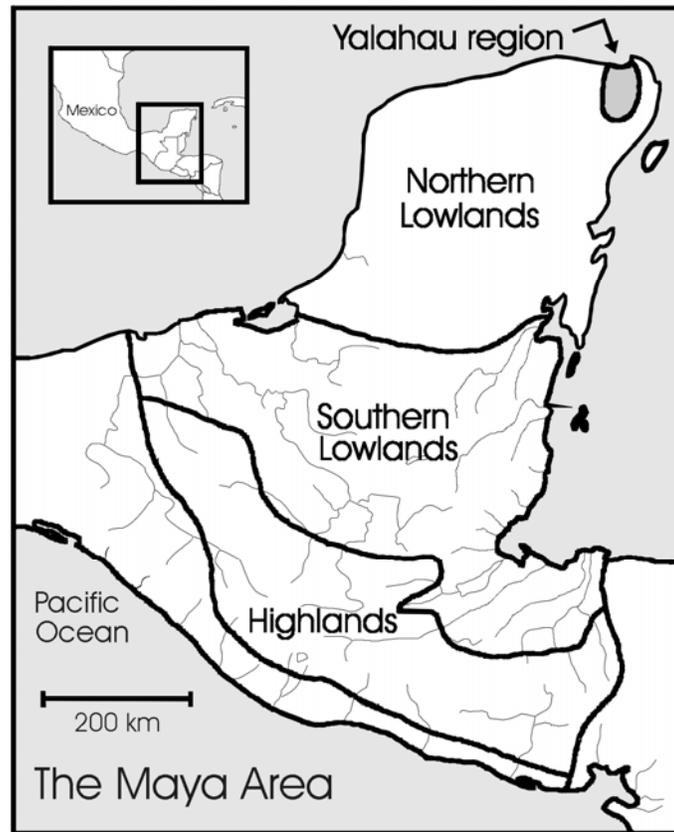


FIGURE 19.1. Location of the Yalahau region within the Maya area of Mexico and Central America.

interior lowlands practiced nonintensive dry-season cultivation of riverine wetlands, combined with wet season slash-and-burn cultivation of adjacent uplands, as they moved up river courses from the coastal margins (Puleston and Puleston 1971; Wilk 1985; Pohl et al. 1996). The largest labor investment in wetland landscape engineering, and the greatest extent of wetland cultivation, is often attributed to the Late Classic period (ca. A.D. 600–900) when population levels reached their pre-Hispanic maximum (Turner and Harrison 1983b). There is, however, a great deal of debate concerning the chronology of wetland cultivation, the economic significance of wetland food production, and the amount of labor invested in the construction of agricultural engineering features such as raised planting platforms. The geographic distribution of wetland manipulation, and the range of wetland ecosystems that were used for agricultural production, are also topics of disagreement. (To understand more about the wetland debate, see Pope and Dahlin 1989; Fedick and Ford 1990; Turner 1993; Fedick 1996a,b.)

Evidence for ancient Maya cultivation of wetlands has previously been restricted to the southern Maya lowlands, where wetlands comprise a

significant portion of the landscape. The Yalahau region, located in the extreme northeast corner of the Maya lowlands (Figure 19.1), is a unique environmental region containing numerous freshwater wetlands. An archaeological survey conducted in one of the Yalahau wetlands (contained within the El Edén Ecological Reserve in northern Quintana Roo, Mexico) has provided evidence for a previously unreported form of ancient wetland manipulation in a little-known region of the northern Maya lowlands. The survey also provides archaeological evidence for forest-resource extraction in the region during the Historic period (after European contact).

WETLANDS OF THE YALAHAU REGION

The Maya lowlands consist of a vast limestone shelf that tilts downward to the north (Figure 19.1). The northern Maya lowlands, located above lat 19° N latitude, is an area that is generally characterized as lacking rivers or surface water except where the water table is exposed by sinkholes or natural wells referred to locally as cenotes. In comparison with the southern lowlands, the north also receives significantly less rainfall, has lower elevation and more level terrain, less soil cover, and a lower forest canopy (Isphording 1975; Wilson 1980; Gómez-Pompa 1998). The Yalahau region of northern Quintana Roo, Mexico, stands in sharp contrast to the rest of the northern lowlands, receiving substantially more precipitation due to a localized rainfall anomaly that contributes to the formation of wetlands along a north-south oriented system of linear karstic solution features which follow a geological fault system (Weidie 1982, 1985; Southworth 1985; Tulaczyk 1993; Tulaczyk et al. 1993).

Wetlands cover about 40 percent of the terrain in the southern Maya lowlands, but are very rare in the northern lowlands. In the north, brackish-water wetlands dominated by mangrove forest are found along the coast, reaching farthest inland in southern Quintana Roo within what is now the Sian Ka'an Biosphere Reserve (Morales Barbosa 1992). The Yalahau region contains the largest area of freshwater wetlands in the northern Maya lowlands.

The Yalahau region contains about 300 separate wetlands that cover a total area of approximately 134 square kilometers (km²) (Figure 19.2). In general, the Yalahau wetlands are seasonally inundated, with only small areas containing open water throughout the year. In the eastern and southern portions of the Yalahau region, the wetlands tend to be relatively steep sided, with very narrow transitional zones separating the wetlands from upland areas that are not subject to flooding. In the eastern and northern areas, there tends to be a much wider transitional zone of land between the wetlands and the uplands which is subject to occasional flooding during years of particularly

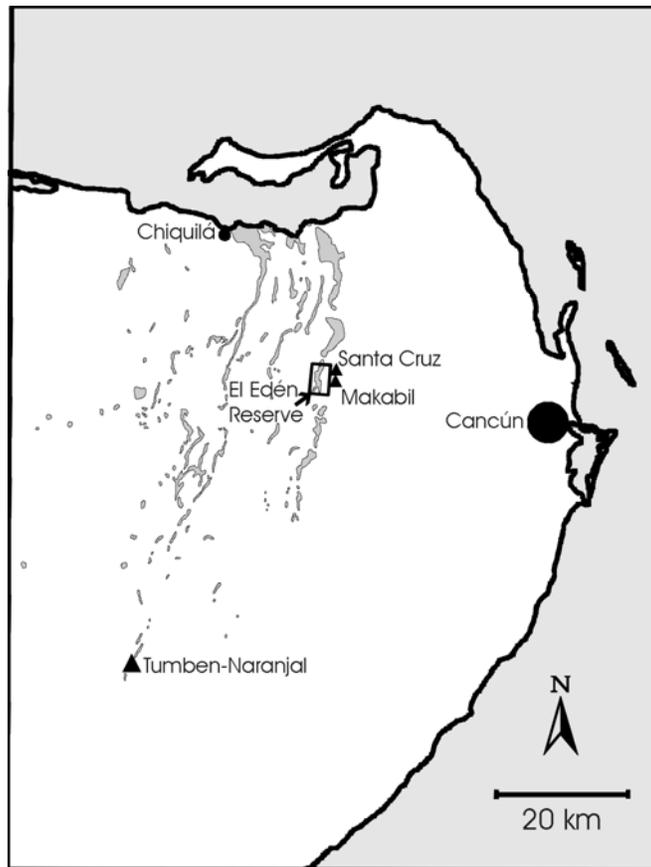


FIGURE 19.2. The Yalahau region with places mentioned in the text. Wetlands are shown as shaded areas.

high rainfall. Soils within the wetlands tend to be relatively thin, sandy silts, and silty clay, about 20 centimeters (cm) over bedrock. The lower areas within the wetlands contain soils up to about 50-cm deep with peaty deposits over silty to sandy clay.

The wetlands support a variety of distinct vegetation zones that differ depending on the duration of annual flooding. Zones that contain water throughout the year are dominated by cattail (*Typha dominguensis*), with water lily (*Nymphaea* sp.) found in open ponds. Zones subject to regular flooding, and that remain moist through the dry season, are dominated by dense stands of sawgrass (*Cladium jamaicense*). As terrain rises slightly and the duration of flooding consequently decreases, the stands of sawgrass thin and are mixed with tasiste palm (*Acoelorrhaphe wrightii*) and the calabash tree (*Crescentia cujete*). Relatively higher ground within the wetland is dominated by a swamp forest or tinal association characterized by the palo tinto (*Haematoxylon campechianum*), with an abundance of black chechem (*Metopium brownei*), ya'axnik (*Vitex gaumeri*), nance (*Byrsonima bucidaeifolia*) and a stunted variety of sapote (*Manilkara zapota*).

PREVIOUS STUDIES OF WETLAND USE IN THE NORTHERN MAYA LOWLANDS

The ancient Maya made use of the northern coastal wetlands for salt production (Andrews 1983; Kepecs and Boucher 1996:81–82; Sierra 1999:43), and numerous canals of both historic and ancient origin cross the coastal wetlands, apparently serving as access routes for watercraft traveling between the interior and the ocean (Matheny 1976, 1978; López 1983; Millet 1984). Prior to the survey (see next section) of the wetland at the El Edén Ecological Reserve, the only evidence for ancient agricultural use of the freshwater wetlands in the Yalahau region, or anywhere in the northern lowlands, was the spatial association of ancient settlements with wetlands in the Yalahau region, and a single rock-alignment feature constructed within the margin of a wetland adjacent to the ancient civic-ceremonial of Tumben-Narnanj, in the southern end of the Yalahau region (Figure 19.2; see Fedick and Hovey 1995). In 1994, Gómez-Pompa (personal communication) reported that a rock-alignment feature had been found well within a wetland at El Edén, on the east-central side of the Yalahau region (Figure 19.2). Visits to El Edén by the author in 1994 and 1995 indicated that a system of rock alignments was present throughout the wetland, and plans were made for a full-scale survey.

SURVEY METHODS

The El Edén wetland is approximately 5.5 kilometers (km) long (N–S) by 0.8 km wide (E–W) and covers 3.5 km². The margin of the wetland is marked along most of the perimeter by a narrow band of exposed bedrock that contains virtually no soil. Outside of the wetland the terrain raises very gradually, leaving a broad transitional zone at least 2 km in width, which is subject to occasional flooding associated with severe hurricanes (see Morrison and Cozatl-Manzano, this book).

Prior to the initiation of the survey, a 1:75,000-scale aerial photograph of the wetland (INEGI 1985) was enlarged, and the Universal Transverse Mercator (UTM) grid, based on the published topographic map (INEGI 1988), was superimposed on the enlarged photograph. The archaeological survey covered the entire wetland and a narrow band of land extending approximately 25 meters (m) beyond the wetland margin.

The survey was conducted by a crew of four to six archaeologists who walked parallel transects that were separated by about 10 to 20 m, depending on the density of vegetation cover. The crew member walking one of the outside transects along a compass bearing marked the trail with biodegradable paper flagging. When a transect across the wetland was completed,

the crew pivoted at the end of the flagged transect and started back in the opposite direction with one outside surveyor keeping the previously marked transect in sight, while the crew member on the other end of the line of surveyors flagged the new transect. A satellite-based Global Positioning System (GPS) was used by the field crew to keep track of their location during the survey.

When a feature was encountered, it was marked with orange plastic flagging tape and assigned a provisional field number until the crew completed the transect. Once several features were identified in an area, the crew returned to map them. Mapping was accomplished with a Brunton pocket transit and tape measure. A written description of each feature was recorded, and most were photographed with still or video cameras. Each feature was marked with a permanent aluminum tag inscribed with a sequential number, and a GPS reading was taken to aid in marking the location of the feature on the aerial photograph.

RESULTS

A total of 78 rock-alignment features were recorded as a result of the survey (Figure 19.3). In addition, an historic rail line was found to cross the El Edén wetland on an east-west (E-W) orientation (Figure 19.3), extending for at least several kilometers from the wetland to the west, and running to the east for several kilometers toward an abandoned historic settlement known as Santa Cruz.

Rock alignment features

The 78 rock-alignment features recorded within the El Edén wetland varied in length from a few meters to about 700 m in length (Figure 19.3). The alignments consist of limestone cobbles, boulders, and slabs that range in size from about 15 cm to over 1 m in diameter (Figure 19.4). The alignments are arranged in single to double rows and are rarely more than two courses high. The rock alignments vary quite a bit in shape and length in relation to the physiographic setting in which they were constructed. Five different types of alignments have been defined (following Fedick et al. 2000).

- *Type 1*: Two long alignments (Alignments 41 and 48) spanned the northern end of the wetland, dividing higher, broken, limestone terrain to the north from a broad saw grass-dominated depression to the south. These are the longest alignments recorded during the survey, with

Alignment 41 measuring about 700 m in length, and Alignment 48 measuring about 390 m.

- *Type 2*: To the north of Alignment 41, and in the southern end of the wetland, is a series of natural depressions about 10 to 25 m in diameter. Rock alignments were constructed so as to block the lowest margin of each depression (e.g., Alignments 36, 38–40, 42–47, and 51). These alignments generally follow the curvature of the depressions, forming fairly regular circular to ovoid basins.
- *Type 3*: Within higher terrain of the wetland, in areas dominated by thinly scattered sawgrass and swamp forest with relatively deep soil, are alignments that run perpendicular to very slight slopes (Alignments 35, 53, 54, 57, and 77). Three of these alignments—35, 57, and 77—have distinctive zigzag shapes.
- *Type 4*: Numerous alignments are scattered along the margins of the larger depressions within the wetland. These features run perpendicular to slight slope gradients and generally mark the boundary between higher land dominated by swamp forest, and the lower depressions dominated by sawgrass (e.g., Alignments 1–11).
- *Type 5*: Within the wetland, numerous shallow channels can be discerned, running into the larger depressions, particularly along the western and southern sides of the wetland. These channels represent low, wet areas that are dominated by cattail. Numerous rock alignments cross these channels at perpendicular angles, forming check dams at fairly regular intervals (e.g., Alignments 32, 52, and 63–68). The rock alignments, and the channels they span, range from 10 m to 60 m across.

Historic features, artifacts, and sites

The narrow-gauge rail line that runs across the El Edén wetland is laid on top of a cobble and gravel bed about 1.5 m in width (Figure 19.5). The height of the road bed varies from about 10 cm on level ground to about 1 m in areas where the natural ground surface dips. Within the wetland, there are two places where the rail line was apparently once supported by bridges that crossed channels, the largest of which is about 20 m wide. Wooden ties slightly over 1 m long are still present along some parts of the road bed, spaced at intervals of about 1–1.5 m. Within the wetland, these ties are of un-hewn lengths of palo tinto (*Haematoxylon campechianum*) logs that range from about 5–10 cm in diameter.

Three broken bottles found along the side of the track about 1.5 km east of the wetland have embossing that provides dates, or datable marks. One embossed bottle reads “PATENTATA OCTUBRE 5 oe 1910 No 4338,”

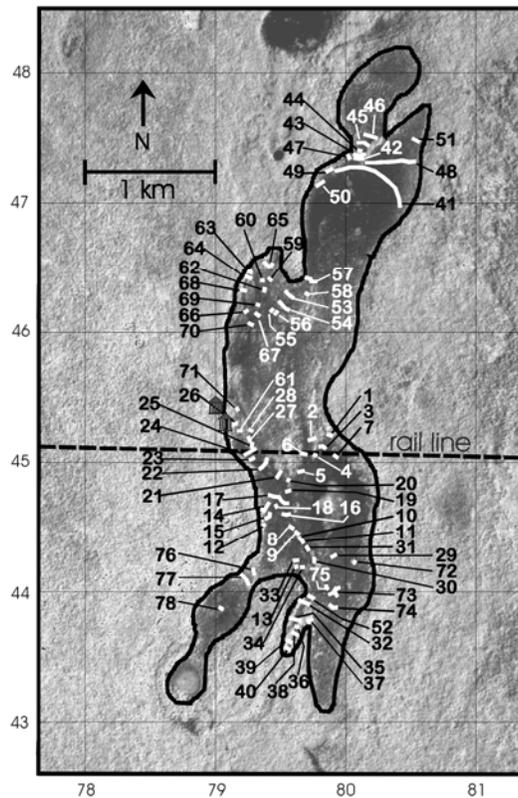


FIGURE 19.3. Air photo of the El Edén wetland with 1 km UTM grid superimposed, and corresponding kilometer designations along the south and west sides. A solid line encloses the area of the wetland survey. Rock-alignment features are numbered 1 through 78.

indicating a manufacture date that probably post-dates 1910. The second bottle is embossed “WF and S / 37 / MIL,” and was manufactured by William Franzen and Son, of Milwaukee, Wisconsin between 1900 and 1929 (Toulouse 1971:536–538). The third bottle reads “GIFFORD and CO. / H.H.H. LINAMENT / CHICAGO” on the front, with “THE CELEBRATED” embossed on one side, and “D.D.T. 1868 . . .” on the other side. This bottle contained “Indian Vegetable Pain Extractor for Horses,” which was developed and introduced in 1868 by Daniel D. Tomlinson (D.D.T.) of Stockton, California (Fike 1987:147). The formula was sold to L. L. Gifford in 1880, and the medicine was bottled in Chicago and sold under the names of both the H.H.H. Medicine Company and Gifford and Company at least through 1907, and as Tomlinson’s H.H.H. Liniment as late as 1948 (Fike 1987:147). Contemporary advertisements noted that the liniment contained 65 percent alcohol and could be taken orally as a “reliable remedy for those ailments, both of mankind and of all domestic animals, for which it is recommended,” such as coughs, colds, stomach-cramps, and diarrhea (Fike 1987:147).



FIGURE 19.4. A section of rock Alignment 41 near the north end of the El Edén wetland.

Near where these bottles were found, the rail line turns slightly north of east, in the direction of an abandoned settlement indicated on the 1:50,000 topographic map (INEGI 1988) as Santa Cruz (see Figure 19.2). Local residents identify Santa Cruz as a former logging or chicle camp. Chicle, the sap of the chicozapote tree (*Manilkara zapota*), was the main ingredient used in the production of chewing gum before being replaced by artificial ingredients after World War II (Urrutia de Bulajich and Bezaury 1993). A reconnaissance visit to the location of Santa Cruz identified a large area that had been cleared of trees and is currently dominated by a dense stand of tall, probably non-native grass. A cenote, or natural well, was present and measuring about 40 m in diameter, it was largely choked with rubble and vegetation, but contains some standing water along the margins. On the west side of the cenote is a large ancient platform, about 30 m on each side and about 1 m high.

In addition to prehistoric ceramics, a dense accumulation of historic trash is present on and around the platform. An embossed bottle found on the platform reads “SBand C Co,” and was manufactured by the Streator Bottle and Glass Company, of Streator, Illinois, between 1881 and 1905 (Toulouse 1971:461–463). Loose sections of rail and a Decauville cart were present at Santa Cruz, and have been moved to the El Edén research station for preservation and display (Figure 19.6). Embossed metal work on the cart reads “DECAUVILLE / AINE / PETIT-BOURG / B. 107.”



FIGURE 19.5. A section of rail line within the El Edén wetland.

INTERPRETATION

Chronology of activities associated with the El Edén wetland

Assigning dates for the construction and use of the rock-alignment features remains somewhat problematic, while the historic materials can be placed in time and socio-economic context. The only known historic activities in the immediate area of the El Edén wetland are associated with a corporation known as the *Compania Colonizadora de la Costa de Yucatán* (Colonizer Company of the Coast of Yucatan), which operated throughout northern Quintana Roo between 1896 and 1936, as discussed by Andrews (1985:140–141). The company, owned by the *Banco de Londres y México* (Bank of London and Mexico), was involved in the extraction of lumber and chicle, cattle ranching, and the development of plantations for corn, tobacco, and vanilla (Andrews 1985:141). The company is known to have installed a number of Decauville rail lines to facilitate the transport of raw materials and supplies (Andrews 1985:140–141). Although Andrews makes no specific mention of a rail line or company activities that could definitely be associated with the El Edén area, he does state that Decauville lines were laid out from Yalikin, which he tentatively identifies as Chiquilá (see Figure 19.2), into the interior (Andrews 1985:140–141). Such a route could account for the historic rail line and activities at El Edén and Santa Cruz. The embossed bottles found in association with the rail line at El Edén and the trash deposit at Santa Cruz



FIGURE 19.6. The Decauville cart in front of the El Edén research station.

are consistent with the dates of operation for the *Compania Colonizadora de la Costa de Yucatán*, as is the presence of the Decauville cart from Santa Cruz.

Dating of the rock-alignment features is more problematic. It is highly unlikely that they are associated with any activity of the Historic period. No historic artifacts were found anywhere in the El Edén wetland, except in direct association with the rail line. Unfortunately, prehistoric artifacts are also lacking in the wetland, or at least have not been recovered as yet. Therefore, dating of the rock alignments is assumed to be associated with the numerous ancient sites that have been identified in the area. The closest site to the El Edén wetland identified to date is the small ancient community of Makabil, discussed by Morrison and Cozatl- in a separate chapter of this volume (see also Morrison 2000; Fedick et al. 2000). Ceramics recovered from Makabil are assigned to the Late Preclassic period (ca. 100 B.C.–A.D. 350). This chronological placement is consistent with other sites in the region, although there is evidence for continuing occupation into the early part of the Early Classic period (until about A.D. 450), and a later reoccupation of some sites during the Late Postclassic period (ca. A.D. 1250–1520) (see Fedick et al. 2000; Lorenzen 1999). While recognizing that the chronological placement of the rock-alignment features is in need of further investigations, they are considered most likely to have been constructed and used during the Late Preclassic period and transition to the Early Classic (ca. 100 B.C.– A.D. 350/450).

Hydrologic and Edaphic Function of the Rock-Alignment Features

The rock-alignment features most likely functioned to control the movement of water and soil within the wetland. It is difficult to imagine a cultivation system that would work under today's hydrological conditions, as much of the wetland lies under nearly 1 m of water during much of the wet season. It is significant to note, however, that current hydrological conditions are probably different from prehistoric times when the alignments are likely to have been built. Recent studies of a sediment core taken from Punta Laguna, about 80 km southwest of El Edén, indicate a decrease in precipitation that began at about A.D. 250 and returned to levels comparable to today at about A.D. 1100 (Curtis, Hodell, and Brenner 1996). Numerous studies demonstrate that sea-level rise has been slow but progressive since the close of the Pleistocene epoch, which would, in turn, raise the water table in the interior of the Yucatán Peninsula (Folan, Fletcher, and Kintz 1983; Fairbanks 1989; Coke, Perry, and Long 1991; Dunn and Mazzullo 1993; Alcalá et al. 1994:43–48; McKillop 1995). It is likely that the water table was at least 0.75 to 1.0 m lower during the Late Preclassic, implying that the El Edén wetland did not flood to the extent it does currently. A lower water table in the past would mean the El Edén wetland was probably a wetland during Late Preclassic times, but was only saturated or partly flooded during the height of the rainy season.

Variation in the form and physiographic setting of the rock alignments suggests that the various types of features functioned in different ways. The deepest soils of the El Edén wetland are located within the large, sawgrass-dominated depressions in the north, north-central, and south-east areas of the wetland (Figure 19.3). The rock alignments are placed so as to block or slow water flow into these areas. Protecting crops from in-rushing water would have been an important function of the rock alignments if the large depressions had been cultivated. If the alignments had once been covered with soil (that has since eroded away), the features would have formed efficient dikes. The long alignments that close off the north end of the wetland (Alignment Type 1) may have served such a function, slowing the rush of rainwater into the northern depression from the channels and higher ground farther to the north. Staff members of the El Edén Ecological Reserve have reported strong flows of water in that area moving from the north and into the depression to the south. The smaller alignments along the margins of the large depressions (Alignment Type 4) may have served similar functions.

The rock alignments that close off the lower margins of small depressions (Alignment Type 2) appear to have a distinctly different function, in that they seem intended to retain water. Several of these features still function in this manner, where soil build-up behind the alignments retain

water in the depression well into, or throughout, the dry season. Alignments that form check dams (Alignment Type 5) are similar in form to the ones that help retain ponds, but are situated in channels and would seem to function more like traditional check dams, slowing the flow of water and building up a terrace of soil behind them that could potentially be cultivated.

The long, and often sinuous alignments (Alignment Type 3) found on higher ground supporting swamp forest/tintal vegetation appear intended to function in slowing sheet wash and encouraging moisture retention, as similar features do in other part of the world (e.g., Masse 1991; Van West and Altschul 1997). Today, these parts of the wetland are inundated only during periods of heavy rain; given a lower water table in the past, it is likely that these settings were not formerly part of the wetland.

Potential cultivars/products of the wetland

Recovery of pollen and other plant remains from wetland contexts in the southern Maya lowlands document the cultivation of maize, cotton, and other domesticates (Miksicek 1983; Wiseman 1983; for a recent summary of plant remains recovered from Maya sites, see Lentz 1999). Future pollen studies may identify cultivation of these traditional crops within the El Edén wetland, but it is also productive to consider other species that are native to the wetland that could potentially have been cultivated. While not an exhaustive treatment, some of the more common plants and animals of the El Edén wetland are discussed as follows.

Cattail (*Typha dominguensis*) is an amazingly useful plant that has been used by cultures in many parts of the world, providing nutritious food from its rhizomes, shoots, and pollen (Harrington 1967; Morton 1975). Cattail pollen has been recovered from ancient Maya sites; interestingly, however, it has not been discussed as a potential food source (Lentz 1999:9). Cattail grows today in abundance behind the check-dam alignments in the El Edén wetland and in some of the ponds retained by alignments in natural depressions. If these features were maintained, and soil was not allowed to build up too deeply behind them, a result could have been an increase in cattail production. Sawgrass (*Cladium jamaicense*), found in slightly better drained settings than cattail, also have edible shoots, but in general are not as productive a food source as cattail. Sawgrass remains have been identified from ancient Maya sites, but the possible use of the plant has not been specified (Lentz 1999:7).

The annona tree (*Annona* sp.) is another plant that thrives in seasonally inundated areas of the El Edén wetland that contain deeper soils. Several wild and domesticated species produce edible fruit (e.g., *Annona cherimola*, see Andrés Agustín and Regollar Alviter 1996; Flores Guido and Flores Serrano 2000), and have been recovered from ancient Maya sites (Lentz

1999:6). Manipulation of the wetland hydrology could promote annona growth.

The nance tree (or shrub) (*Byrsonima bucidaefolia*) is a delicacy of Maya cuisine that thrives in the swamp forest habitat of the El Edén wetland. Although found today throughout the drier parts of the wetland, its distribution at El Edén could have been more widespread in the past because of a lower water table.

A variety of palms have recently been suggested as significant subsistence resources of the ancient Maya (Lentz 1990, 1999; McKillop 1994, 1996). The tasiste palm (*Acoelorrhaphe wrightii*) grows in abundance within the El Edén wetland, and is a consistent producer of numerous edible berries; the palm can also be used as construction and thatching material. The nutritional value and productivity of the tasiste palm is currently under investigation by the author, but is another species that could be encouraged by manipulation of the wetland hydrology.

One of the more common animals of the El Edén wetland is the apple snail (*Pomacea flagellata*) that thrives in areas of the wetland that contain water throughout the year. Apple snails are known to have been exploited by the ancient Maya as a food resource (see Andrews 1969; Moholy-Nagy 1978) and they could have been collected or even cultivated as food at El Edén. The ponds that form within the small natural depressions hold water that is deeper or present for a longer period of time, when built up along their lower margins by artificial retaining walls formed by the rock alignments. These habitats may encourage the growth and reproduction of the apple snail.

The final wetland resource to be considered is perhaps the most intriguing, consisting of the algae mat (periphyton) that grows in profusion across most of the El Edén wetland (fig. 7). Periphyton is a complex community of microbiota—primarily algae—that attaches to larger plants or inorganic materials, forming a nearly continuous mat of growth across the wetland. There are many varieties of periphyton communities present in the El Edén wetland, and these are currently under investigation by a group of colleagues working at the El Edén Ecological Reserve (see chapters in this volume by Novelo and Tavera, and by Palacios et al.). Edible species of freshwater algae are known to have been components of ancient Aztec and Inca diets, particularly the blue-green algae of the genera *Spirulina* and *Nostoc* (Coe 1994:100–104, 186). While both of these genera are represented in the periphyton communities of the El Edén wetland (see chapter in this volume by Novelo and Tavera), they are part of a mixture that includes many non-edible varieties. The economic value of the periphyton is likely to have been its potential use as an agricultural fertilizer rather than as an edible food resource. Some varieties of the El Edén periphyton have very high levels of phosphorus and nitrogen, both essential plant nutrients that are generally low



FIGURE 19.7. Periphyton growth in the El Edén wetland.

or easily depleted in agricultural systems of the Yucatán Peninsula (see chapters in this volume by Novelo and Tavera, and by Palacios et al.). It is possible that the ancient Maya harvested periphyton, or the nutrient-enriched muck soil from the wetlands, to incorporate into gardens and fields (Fedick 1998; Morrison 2000). Archaeological evidence for this practice is presented in a chapter in this volume by Morrison and Cózatl-Manzano.

CONCLUSIONS

The El Edén wetland was subjected to fairly intensive management in the past, most likely by the ancient Maya of the Late Preclassic to Early Classic period (ca. 100 B.C.–A.D. 350/450). While direct evidence is currently lacking on the function of rock-alignment features recorded within the El Edén wetland, they probably served as water- and soil-control devices in a cultivation system for either domesticated crops such as maize and cotton, or to promote the growth of economically valuable wetland resources. Reconnaissance has identified rock-alignment features similar to those at El Edén in other wetlands of the Yalahau region. For unknown reasons ancient communities associated with the El Edén wetland, and other wetlands of the

Yalahau region, were for the most part abandoned by the beginning of the Early Classic period. Changes in climatic conditions, particularly a rising water table, made cultivation of the wetlands impractical.

After many centuries of abandonment, there is limited evidence for reoccupation of some areas within the Yalahau region during the Late Postclassic (i.e., after A.D. 1250). There is little documentary or archaeological evidence for occupation in the Yalahau region after European contact until the *Compania Colonizadora de la Costa de Yucatán* began operations in the area about 1900. In the El Edén area, the Decauville rail line indicates extractive activities were conducted, most likely of timber and chicle. Although the palo tinto tree (*Haematoxylon campechianum*) that grows in abundance in the El Edén wetland was once a highly valued source of fabric dye, by the early 1900s the widespread availability of synthetic dyes had negated the economic value of palo tinto; these formerly valuable trees were instead cut for use as railroad ties. For the Historic period forestry industry, the wetland was an obstacle to be crossed during the exploitation of upland forest resources.

The Yalahau region has recently entered a new cycle of human activity. With the development of the Cancún resort community in the late 1970s, the rich groundwater resources of the Yalahau region were tapped as the primary source of water for the resort development. Access roads for the wells, pumping stations, and water lines began attracting agricultural immigrants to the area, who were actively encouraged by government agricultural-development programs. The immigrants who settled in the area—many unfamiliar with the practice of slash-and-burn cultivation—have often been blamed for the numerous wildfires that have swept through the region in recent years. A number of large cattle ranches were also established in the 1980s. The ranches cleared vast tracts of land, many of which have been abandoned and taken over by fire-resistant bracken fern. In recent years, both ranchers and farmers have found the Yalahau region to be a difficult environment in which to survive, let alone prosper. Even the ancient Maya, who apparently occupied the region in great numbers during the Preclassic, did not stay very long. Why is the Yalahau region such a challenging environment? Perhaps the region represents one of the most interesting and productive natural laboratories in the Maya lowlands for the study of the human-wildland interface.

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Chapter 20

Three Millennia in the Southern Yucatán Peninsula: Implications for Occupancy, Use, and Carrying Capacity

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Laura C. Schneider

INTRODUCTION

The southern Yucatán peninsular region lies within the upland terrain of southern Campeche and Quintana Roo, Mexico, and abuts northern Petén, Guatemala, and northwestern Belize (Figure 20.1). In regard to ancient Maya occupancy, it corresponds to the “central Maya lowlands,” defined by Turner (1983, 7–9; 1990a), and to the central hills and Petén karst plateau of the lowland Maya “adaptive” regions, defined by Dunning and Beach (2000: 182).

The lands demarcated are similar environmentally and share a common human-environment history. They constitute the uplifted, karstic spine of the southern part of the peninsular shelf, rising as high as 300 m amsl (meters above mean sea level) between the Caribbean and Gulf Coast littorals. Well-drained slopelands, dominated by shallow rendzinas (mollisols) and seasonal tropical forests, cover about 20 percent of the region (Figure 20.2).¹

Parts of this paper draw upon information generated by the Land-Cover and Land-Use Change-Southern Yucatán Peninsular Region (SYPR) project, a cooperative research venture among the George Perkins Marsh Institute, Clark University, Harvard Forest-Harvard University, and El Colegio de la Frontera Sur—Unidad Chetumal, with major support from NASA’s LCLUC program and the Center for the Integrated Studies of the Human Dimensions of Global Change (Carnegie Mellon University, NSF) and additional support from a number of other agencies and institutions. We thank the members of the project for their assistance.

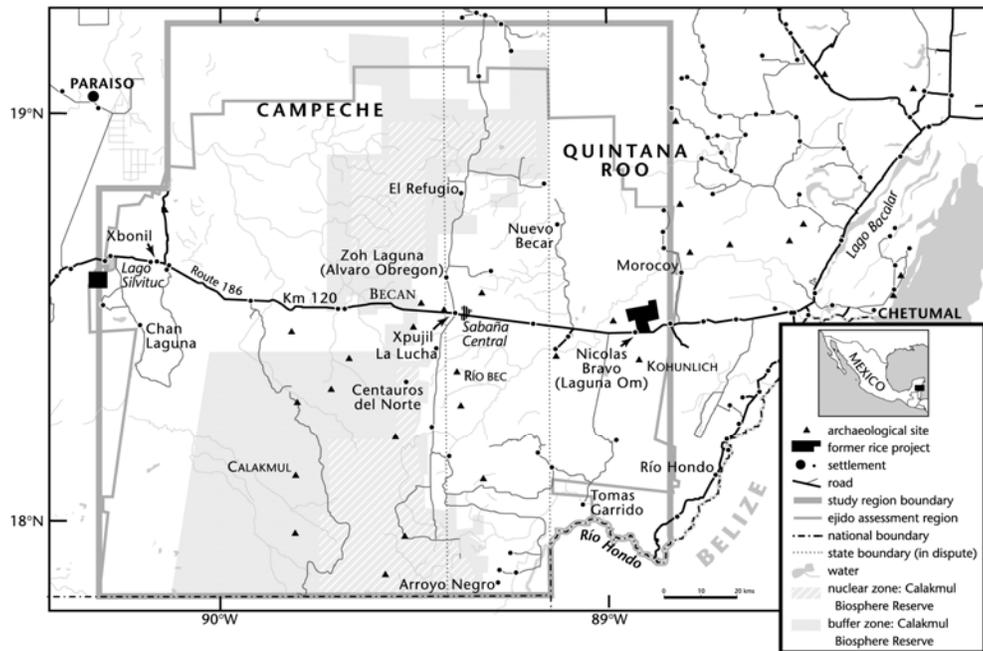


FIGURE 20.1. Location of the southern Yucatán peninsular region. The solid gray line represents the boundaries of the region established by an ongoing project of the same name as the region (see footnote on chapter title page). Note the location of the Calakmul Biosphere Reserve. (*Source*: Reprinted from *Land Use Policy*, 18, P. Klepeis and B.L. Turner, Integrated land history and global change science: The example of the southern Yucatan peninsular region project, pp. 27-39, 2001, with permission of Elsevier Science.)

Interspersed among them are seasonally inundated poljes or bajos (karstic sinks), characterized by clay-rich vertisols and less-deciduous forests of similar but smaller-sized species that occur on the slopelands (Turner et al. 2001).

The ancient Maya entered these lands sometime before 3000 B.P. (ca. 1000 B.C.) and subsequently transformed them into the “heartland” of the Classic Period lowland civilization, as measured by the sheer volume of architecture, population, and land change, especially deforestation (Adams 1981; Dunning and Beach 2000; Turner 1990a), that is known to have occurred there. By 1000 B.P. (A.D. 950), however, the Maya civilization collapsed and the region depopulated by 90 percent or more (Turner 1990a; 1990b).² The forest returned, albeit altered in species composition, and the region remained a refuge until recently. By the middle of the twentieth century, the region witnessed significant logging of its hardwoods (Spanish cedar and mahogany), followed by extensive colonization from various parts in Mexico. Today, the southern Yucatán peninsular region finds itself struggling to strike a balance between the agricultural needs of re-emerging

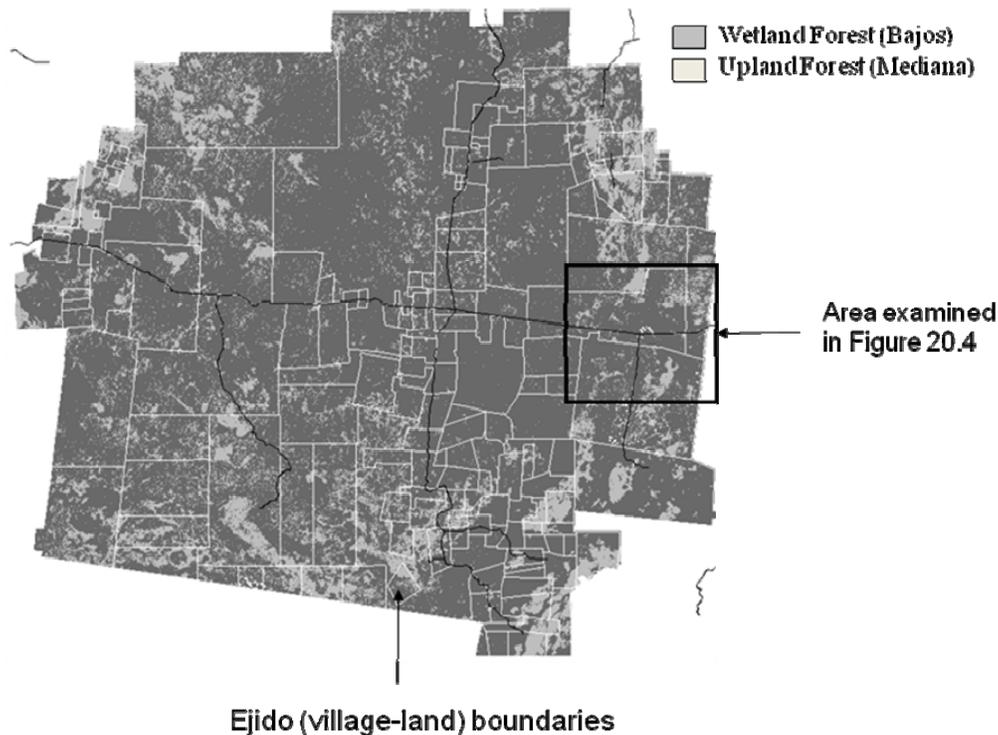


FIGURE 20.2. Forest cover in the southern Yucatán peninsular region. The area covered represents all ejidos situated fully within the southern Yucatan peninsular region as defined here. Forest type and coverage based on Landsat TM imagery analysis and ground studies.

settlements (Figure 20.1) and the broader aims of preserving and conserving the region as biotic reserves and corridors, as well as part of El Mundo Maya, perhaps the largest archaeo-eco-tourist scheme in the world. The Calakmul Biosphere Reserve is anchored in the middle of the region (Figure 20.1) which is also fully covered by *ejidos* (“communal” peasant or smallholder lands; Figure 20.2), although some of the *ejidos* in the western part are designated only for forest extraction uses.

The population history of the southern Yucatán peninsular region is somewhat unique because it involves only one long wave of growth and decline (Whitmore et al. 1990); despite reasonably good soils for nonriverine tropical environments, the region remains today sparsely occupied. At its apex in the Late Classic Period (about 1500–1000 B.P. [A.D. 450–950]), the region held millions of people with subregional population densities ascending well above 100 people/km² (Culbert and Rice 1990). The subsequent collapse and depopulation was rapid and dramatic; by 500 B.P. (A.D. 1450) if not before, the region was, for all practical purposes, vacated, save for outposts along its edges.³ Even the rapid population growth throughout much of the region over the past 30 years, leading to its designation as a “hot spot” of tropical

deforestation (Achard et al. 1988), has generated regional population densities far below those present in ancient times (Dunning and Beach 2000, 198; Turner et al. 2001).

Given its tropical location and history, the southern Yucatán peninsular region succumbs to various interpretations concerning occupational or use limits that have been subsumed—explicitly and implicitly—under the concept of “carrying capacity.” Thus, the arguments go that most tropical environments are not suited for intensive occupation and use, that the Maya exceeded their technological capacity to sustain their civilization in this environment, or that they reached a critical human-environment threshold that was tipped owing to climate or some other major change, and that low environmental capacity has been registered in various failed modern-day agricultural projects (e.g., Lowe 1985; Tainter 1988; Turner 1990b). In the remainder of this chapter, the logic of the carrying capacity concept, its use in regard to the southern Yucatán peninsular region, and its implications for understanding human-environment relationships there, focusing on four environmental issues will be explored. From this exercise, several lessons of which two are paramount will be examined: (1) carrying capacity is determined as much, if not more so, by the technologies and strategies of use than by the base environmental conditions; and (2) the critical thresholds or tipping points that exist in all environmental use systems are largely underexplored for the region in question.

THE CONCEPT OF CARRYING CAPACITY

Carrying capacity refers to the maximum population (or production) that can be sustained indefinitely within a specified environment without major degradation to that environment. This concept held major currency in the human-environment sciences in 1960s and 1970s when systems and ecosystems permeated environmental issues. Given this association, it is not surprising that carrying capacity is commonly thought to have its origins in the ecological sciences and that it was borrowed and modified by human-environment subfields to address their own concerns. In reality, the roots of this concept can not only be traced back to the works of Thomas Malthus (eighteenth-century British political economist-demographer who addressed food ceiling-population dynamics), but can also be found in various guises thereafter, including John Wesley Powell’s (nineteenth-century America geologist-explorer) critique of the United States Homestead Act of 1862 for lands west of the 100th meridian (Darrah 1951).

Full development and labeling of the concept for human-environment systems, however, lay in British colonial planning administrations, which sought to orchestrate systematic strategies for optimal land uses, especially in

Africa (Allan 1967; Brush 1975; Street 1969). In this use, carrying capacity identified different land capacities to sustain different levels of occupation under a given use strategy, and/or land responses to different techno-managerial strategies employed on them. The higher the land capacity, the more people that could be supported on it, and the greater the response to added inputs.

The appeal of carrying capacity, in retrospect, is understandable. It offered a simple measure for planning, and its robustness seemed to be confirmed by the long-term adjustments of indigenous farmers to follow different techno-managerial strategies and the concomitant intensities of cultivation on different lands. The more intensively used and highly productive lands invariably coincided with attributes that made them superior for this purpose than their counterparts elsewhere. Uncritical or careless use of carrying capacity, therefore, de-emphasized techno-managerial considerations that transformed “unfriendly” environments to prime cultivation lands (e.g., tidal land to polders in the Netherlands, steep slopes to terraces along the Andes, and desert to irrigation in the Middle East), and implicitly granted “cause” to the environment. High-quality physical conditions for cultivation were not made so by human ingenuity, they simply existed. The reality, of course, is that environmental opportunities for land use vary widely, as do environmental responses to different land uses, but techno-managerial strategies change these capacities and shift consideration to the socioeconomic need and capacity to improve environmental conditions and maintain them through techno-managerial inputs.

Given this reality, carrying capacity involves at least two critical elements in its measure: (1) E, the physical attributes of the environment used (e.g., soil, climate, vegetation), and (2) S, the techno-managerial strategies applied to use this environment, including their sensitivity and resilience to perturbations. In this sense, no “native” carrying capacity exists for any environment in terms of land use; rather, a number of potential capacities exist depending on the strategies employed. The synergisms between E and S hold the key to land use in general, and longitudinal and cross-sectional studies reveal several important lessons about them that transcend cultures and locations (Wagner 1961):

1. Environments favoring a given production strategy are developed for that activity before others, and improvements focus on those environments as long as marginal returns remain positive (Turner and Brush 1987). The “prime” agricultural lands of the world, therefore, rarely experience a loss in production intensification over the long term, while more marginal lands made highly productive (e.g., colonial New England, high Andean terracing) are taken in

- and out of production in concert with economic conditions (Cronon 1983; Denevan 2001; Doolittle 2000).
2. Cultural preferences (e.g., foods) lead to the search for those environments that favor associated land uses, and commonly bypass highly productive environments that support alternative strategies. For example, the Spaniards' search for Mediterranean-like environments in the New World that would enable the cultivation of winter wheat, as well as the introduction of European livestock systems, illustrates this preference (Butzer 1991). In many cases, far-more productive Native American systems of production were passed over or destroyed in order to facilitate the conqueror's preference (Turner and Butzer 1992; Whitmore and Turner 1992; 2001).
 3. Techno-managerial strategies are linked to land pressures; as these pressures increase, so do the human inputs required to control the environment and substitute for its drawdown (e.g., soil nutrients, water shortfalls) as do the investments for new strategies and technologies to meet its raising demands (Boserup 1965; 1981; Hayami and Ruttan 1971; Turner and Ali 1996). Low land pressures, therefore, tend to be linked to extensive production systems, and the reverse to intensive ones (Turner and Brush 1987).
 4. Every land-use system ultimately approaches marginal returns and then stagnates, unless new techno-managerial strategies are used to overcome the critical factor in production (i.e., insufficient water, soil nitrogen) (Hayami and Ruttan 1971; Turner and Ali 1996).
 5. Should production pressures mount absent these new strategies (or adequate investment in known strategies), the environment may "bite back" in ways that make human adjustments difficult, or even insurmountable (Kasperson et al. 1995). The salinization of ancient irrigation systems in the Tigris-Euphrates region (Adams 1965) and the recent death of the Aral Sea (Micklin 1988) are illustrative of this problem. This last lesson—bite back—has received the least attention in regard to carrying capacity, save as environmentally improper or highly stressed production systems have encountered large-scale climatic perturbation, such as the dust bowl on the American Great Plains during the 1930s (Glantz 1994; Worster 1979) as well as "desertification" in the Sahel (Glantz 1994; Thomas and Middleton 1994).
 6. The kind and significance of "biteback" observed is strongly affected by the scale of analysis (temporal, spatial, and hierarchical); increasing the scale of analysis usually mutes the role of carrying capacity.

Given the dynamic nature of the E-S relationship, it is difficult and often inappropriate to apply an inflexible view of carrying capacity, or to assume that the extant production system represents the maximum sustainable over the longer term. Whatever that maximum may be is, in large part, determined by technological and social capacities to employ and maintain the use system in question. In this sense, carrying capacity serves primarily as a heuristic guide to a more inclusive E-S relationship (Brush 1975). The danger here is to allow the human component of the relationship to overshadow the environmental component to such an extent that the latter is relegated to insignificance.

CARRYING CAPACITY AND THE SOUTHERN YUCATÁN PENINSULAR REGION

Nondynamic interpretations of carrying capacity commonly arise for those E-S relationships that stagnate and/or (approach) collapse. In such cases, problems of land degradation and food shortages, among others, are visibly heightened, focusing attention on the environment's sensitivity to use and impacts (bite back) on production. Various interpretations of the Classic Maya collapse and modern land uses in the southern Yucatán peninsular region follow this logic.

The collapse of the Classic Lowland Maya civilization, especially within the heartland zone, remains an enigma; simple causes do not stand the scrutiny of the evidence, and complex explanations are too difficult to demonstrate with any authority (Culbert 1973; Lowe 1985). A long-standing theme or hypothesis points to Malthusian "overshoot"—that is, population demands exceeded the environmental carrying capacity and/or the technological capacities of the Maya to enlarge this capacity sufficiently (Turner 1990b).

More often than not, interpretations of this kind use carrying capacity as a heuristic, and do not employ measures and metrics regarding land and resource uses (e.g., Cook 1921). Cooke (1931), for example, proposed a "mass wasting" of the landscape by an overtaxing population, presumably pushing the limits of swidden ("slash-and-burn") cultivation. Sanders (1973) made a somewhat similar case, although he recognized subregional variations and practices other than swidden. This variation is recognized by Fedick (1995), although he does not make explicit statements about overshoot. Others have made statements, however, most recently in regard to one of the most productive and resilient environments in the lowlands, the Copán Valley of Honduras. Webster and Freter (1990) and Lentz (1991), for example, refer to an overshoot in this valley based on the "calculated carrying capacity" of swidden. Wingard (1996) subsequently provide the metrics (see Table 20.1).

Gyuk and Harrison (1975) raised the scope of such work by creating a pan-Maya, population-overshoot model in which land degradation and collapse are linked to swidden. Finally, an element of overshoot is found in the more complex “system-stress” arguments that combine environmental degradation and other forcing functions with the collapse of the lowland subsistence base and capacity to conduct trade (e.g., Culbert 1973; Haas 1982, 212). These arguments, however, do not reduce the overshoot to environmental constraints on swidden cultivation, but point to tipping points or thresholds in “stressed” systems that create cascading, system-wide negative impacts.

Swidden carrying capacity

Actual estimates of carrying capacity—of population “limits” related to specific land uses—for the Maya lowlands are less common and almost always related to swidden or milpa cultivation as *currently* practiced in various part of the region (Table 20.1). Swidden is not practiced because of environmental limitations per se, but for its energy and labor efficiency, relying as it does on nature to replenish most of the critical biophysical elements usurped or lost in crop production. It is the system of choice, where land pressures are relatively low in non-fossil fuel and non-market agriculture (Boserup 1965; Turner and Brush 1987).

In the southern Yucatán peninsular region and throughout the Maya lowlands, milpa (or maize field) refers to fallow-based cultivation employing slash-and-burn or swidden techniques. The early Spanish chroniclers described versions of it; subsequently, this kind of swidden practice dominated subsistence production throughout the entire lowlands (Whitmore and Turner 1992). Milpa is an extensive production system in that more land than is cultivated must be in various stages of fallow. Crop-fallow cycles vary by the time and location in question, but 2–3:7–15 systems (2–3 years of cultivation; 7–15 years of fallow) were historically typical and remain so today, resulting in the need for about two to seven times more land in fallow than in cultivation (Reina [1967] 1999; Reina and Hill 1980). Related carrying capacity estimates range from about 20 to 80 people/km²; the lower figure tends toward the high side globally (Turner 1983, 7–9) and the higher figure stresses credibility (but heed notes to Table 20.1). Estimates of the global average population density associated with swidden systems is less than 6 people/km² (e.g., Watters 1960); according to Harris (1972), exceptional swidden systems (read “optimal” environments not taken over by more intensive systems, for whatever reason) may support up to 60 people/km². These last cases invariably are short fallow (1:1) and require substantial techno-managerial investments that move the system in question away from

TABLE 20.1. Explicit Carrying Capacity Estimates for the Maya Lowlands

Location	Production System ^a	Density (people/km ²)	Source
Northern Yucatán	Swidden/milpa	19	Cook (1972, 31)
Northern Yucatán	Swidden/milpa	23	Hester (1954, 129)
Copán Valley	Swidden/milpa	25-32 ^b	Wingard (1996)
Southern Petén	Swidden/milpa	41 ^c	Carter (1969, 142)
Greater Yucatán	Intensive swidden	57	Wagner (1968, 185)
Central Petén	Swidden/milpa	77 ^d	Cowgill (1961)

Source: From Turner 1983.

- a. Swidden/milpa = maize-based systems in which fallow exceeds cultivation (1:4 plus); Intensive swidden = maize-based system in which length of fallow and cultivation are equal (1:1).
- b. The lower figure for longer fallow (10 yr.); the higher figure for shorter fallow.
- c. Figure of “available land” or cropped land, not total area of some bounded unit; non-cropped land eliminated from estimate.
- d. Figure assumes that virtually all land is high quality and suitable for maize cultivation. It is very high by world standards for swidden systems.

the public meaning of “swidden” (literally, to burn) of low-input, rotational practices.⁴

The swidden carrying capacity estimates for the Maya lowlands, therefore, are several orders of magnitude below the population estimates derived from settlement studies of the ancient Maya. These figures vary for the southern Yucatán peninsular region, of course, but exceed 1,000 people/km² for “urban” areas, 800–500 people/km² for some peri-urban areas, and range up to 150 people/km² for large “rural” areas replete with evidence of significant landscape transformation (Culbert and Rice 1990). Assuming that the settlement evidence is not grossly inaccurate, the ancient Maya surely incurred very high levels of land pressures that would have required the use of multiple techno-managerial strategies—many of which would have had to have been far more intensive in scope than swidden.

Research from the 1970s onwards reveals that the Maya had begun to employ techno-managerial strategies quite different from swidden perhaps as early as 3000 B.P. (ca. 1000 B.C.) (Pope, Phol, and Jacob 1996). Although debate has focuses on the specifics of each major strategy employed (i.e., date of origin, distribution, and production implications), the broader picture emerging for the Maya lowlands and the region examined here is the use of multiple systems of cultivation, some more common to specific subregions

than to others (Dunning 1992; Dunning and Beach 2000; Fedick 1996; Harrison 1990; Turner 1993). House and orchard-gardens appear to have been present almost everywhere (Turner and Miksicek 1984; Whitmore and Turner 2001), and in some cases may have taken the form of small-scale agroforestry (Gómez-Pompa 1987; Gómez-Pompa, Flores, and Sosa 1987; McKillop 1994). Presumably such systems were relatively sustainable, given their more-or-less benign impacts on soil, but were subject to damage from hurricanes, fires, and crop disease.

Despite their importance, orchard-gardens and agroforestry did not dominate the landscape during the peak population times as registered by the pollen record (see below). More “open” cultivation dominated, which included short-fallow or near-permanent cultivation of the uplands. The southern Yucatán peninsular region is replete with stone-walled landscapes littered with cutting and cultivation tools (Turner 1983). Some of the walls are clearly the remnants of ancient terraces (Turner 1974). Similarly, bajos or seasonally inundated wetlands on the edges (coastal littorals) of the region were taken to wetland cultivation (Dunning et al. 1999; Pohl et al. 1996; Turner and Harrison 1981).⁵ Their use in higher perched upland bajos (ca. +100-m amsl) remains in question (Adams, Brown, and Culbert 1981; Adams et al. 1990; Pope and Dahlin 1989; 1993).

Logically, the intensively used and settled uplands seem ripe for wetland use (bajos constituting about 19 percent of the region), and recent work indicates the complexity of water works on occupation sites that drained toward bajos (Dunning and Beach 2000; Scarborough et al. 1995). The only established patterns indicating ancient fields in upland bajos, however, are in the huge Nicolas Bravo–Morocoy wetlands situated at 70-m amsl (Turner 1974). Some of the patterns there held small stone structures on them with sherds apparently Late Classic in origin (Gliessman et al. 1985). Whether or not these systems were used year-round, or during the dry season only—akin to highly managed recessional cultivation (Siemens 1983; Siemens et al. 1988)—is unknown.

Multiple-system carrying capacity

Estimating carrying capacities for them practices is fraught with problems, given the unknowns involved. Current swidden yields can be pressed upon assumptions that the above systems were harvested annually (and only periodically fallowed), yielding extremely large carrying capacities (e.g., Turner 1976). How meaningful these exercises are, however, is not clear. The consensus, at least as evidenced in the literature, is that the mixes of systems used by the Maya were sufficient to meet the high levels of demands and land pressures present during the Late Classic Period.⁶

Paleopathology research dealing with the region has indicate dietary stress in some locales as the Maya collapse approached, but the overall picture is varied and complex, and no evidence exists yet that dietary stress was any worse than those in comparable human-environmental conditions elsewhere in Mesoamerica (White 1999). Virtually no experts call for a lowering of the settlement-base population estimates to densities commensurate with known levels of swidden production. Thus, pan-regional densities approaching (or exceeding) 100 people/km²—and with many subregions, or large areas, far exceeding that figure—are believed to have been sustained hundreds of years or longer. This assumption is consistent with the settlement and landscape evidence, and is informed by analogues of other indigenous mixed-intensive systems.

To be sure, large labor investments and sophisticated techno-managerial strategies were required to sustain the requisite production level, especially for soil upkeep (e.g., mulch, night soil, muck, blue-green algae applications). In turn, the total system was undoubtedly under considerable stress and subject to repeated production shortfalls, especially in the face of nature's vagaries (e.g., hurricanes, drought, crop diseases). It is noteworthy, however, that pre-Hispanic populations in the Basin of Mexico also experienced these same stresses and shortfalls, but were able to sustain large populations and powerful states over the long haul (Whitmore and Turner 2001).⁷

ENVIRONMENTAL IMPACTS

The human imprint on the environment is ancient and large (Redman 1999; Thomas 1956; Turner et al. 1990), and paleoecological studies invariably register it commensurate with the size and duration of occupation and use of an area. The imprint of Maya land use and occupation on their tropical lowland environment was no exception. Binford and colleagues (1987) capture the broad stroke of these impacts in two powerful figures (combined here in Figure 20.3, following Rice 1993) that illustrates distinctly the significant deforestation, soil erosion, rates of sedimentation, and phosphorus (P) loading (phosphorus mobilized by Maya Activities and removed by erosion), in the central Petén lakes region during ancient Maya settlement. There is every reason to suspect that these broad trajectories of change were present throughout the southern Yucatán peninsular region, and thus constitute problems for modern redevelopment of the region.

It must be remembered, however, that the Maya confronted environmental problems for several thousand years, albeit with temporally localized failures. For this reason alone, interpretations must heed not only those techno-managerial strategies that worked, but also the socioeconomic

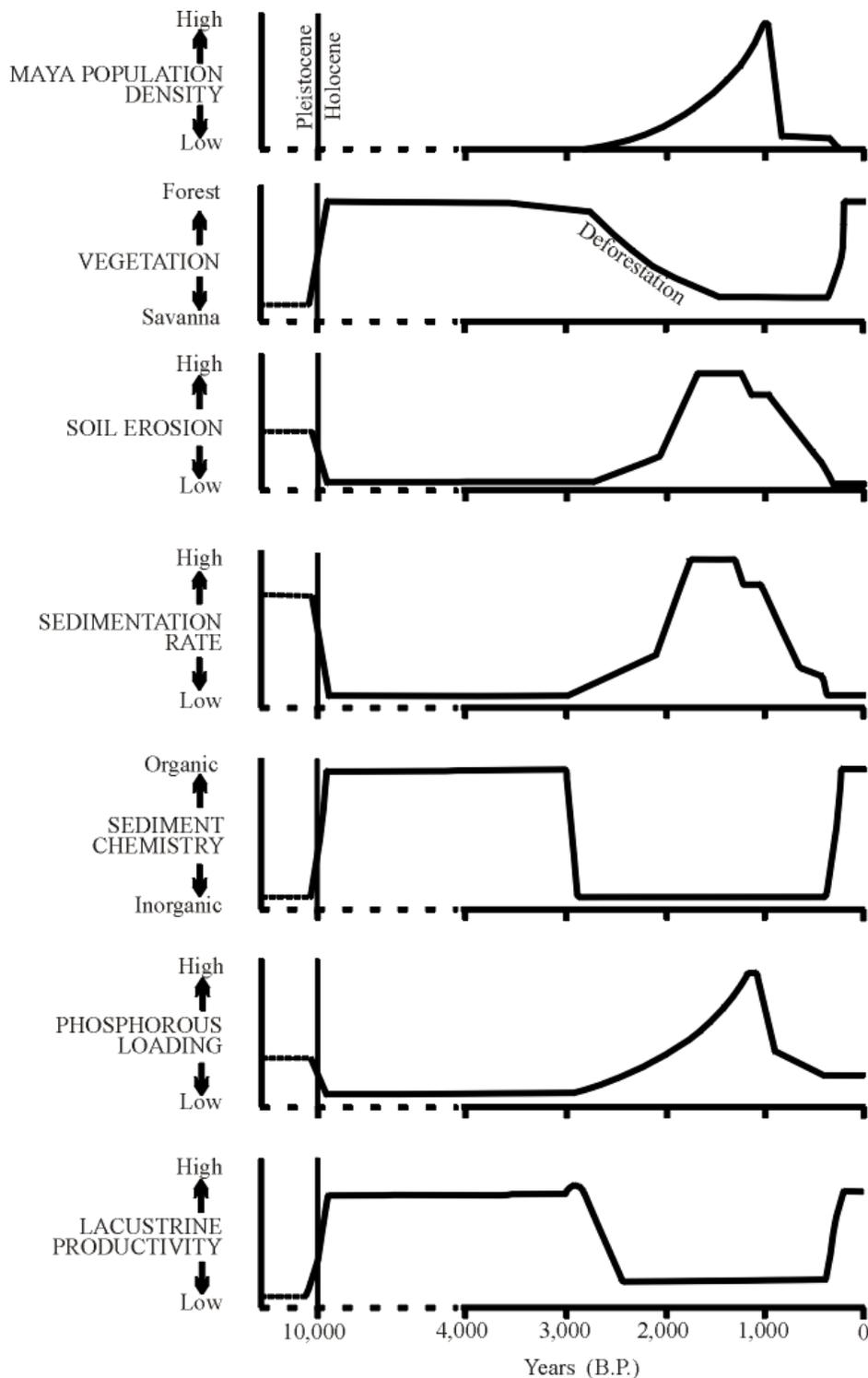


FIGURE 20.3. Summary of the long-term environmental impacts of Maya settlement in the central Petén lakes region. (Source: Reprinted from *Quaternary Science Reviews*, 6, M.W. Binford, M. Brenner, T.J. Whitmore, A. Higuera-Gundy, E.S. Deevey, and B. Leyden, *Ecosystems, paleoecology and human disturbance in subtropical and tropical America*, pp. 115-128. 1987, with permission of Elsevier Science).

conditions that supported them over the long run. The inherent danger of the use of carrying capacity, illustrated in its application to African development (Turner, Hyden, and Kates 1993), is to privilege the environment (E), or environmental problems or consequences, as the “determinant” of land-use failures and relegate the role of socioeconomic determinants (S) that affect the capacity and incentive to employ and sustain appropriate strategies of use. The E-S relationship, of course, may reach some critical threshold in which a perturbation (environmental or human) reduces carrying capacity, or makes the costs of sustaining carrying capacity unrewarding and unacceptable (Lee 1986; Lowe 1985). Unfortunately, to demonstrate this kind of synergism for the southern Yucatán peninsular region is well beyond our capacities at this time because of limitations in data.

Consideration of various kinds of environmental bite back that are central to the E-S relationship, however, is possible. Such bite backs do not specifically involve global climate change or rises in sea level because they are not endogenous to the use-occupation system. Rather, it includes those local-to-regional environmental impacts following from Maya land and resource uses.

Several bitebacks are apparent in the discussion above; others involve subset and other problems not so apparent or common in the literature. They involve (1) upland soil and soil nutrient loss; (2) weed and pest invasion, including “detrimental invasive species”; (3) wetland sedimentation; and (4) regional climate change and water stress. These possible sources of environmental feedbacks are registered in the paleoenvironmental evidence and suggested in studies of contemporary human-environmental relationships in the region. For example, various studies of swidden or milpa in Maya lowlands demonstrate declining second and third year yields (for maize) owing to soil nutrient losses, weed invasion, and pest infestation (Reina 1967; Wingard 1996). The assumption used here is that these base problems were magnified with the more-or-less permanent cropping that characterized the peak periods of occupation in the region.

Soil and soil nutrient loss

The southern Yucatán peninsular region was significantly deforested (see Figure 20.3), despite substantial use of house and orchard-gardens (Turner and Miksicek 1984; Rue, Jones, and Dunning 1995), the apparent need for wood-fuel lots, and possibly that some patches of forests were managed (Dunning and Beach 2000; Gómez-Pompa, Flores, and Sosa 1987). Although the regionwide pattern of deforestation follows that outlined in Figure 20.3, subregional or local variations undoubtedly existed. Certain large sites were

abandoned, presumably contributing to reforestation, and subsequently reoccupied in some way.⁸

Deforestation everywhere in the region (and the Maya lowlands) has been associated with accelerated soil erosion (Dunning and Beach 2000; Rice 1993; Rue 1987; Wingard 1996), as it is today under swidden systems on slope (Beach 1998). With this physical erosion, soil nutrients were lost as well, perhaps signified in the phosphorus loadings in the central Petén lakes region (Rice 1996).⁹ As slopelands were increasingly cleared, soil erosion and loss of soil nutrients increased until measures were taken to impede the rates of loss. The evidence suggests that by the Classic Period, terraces of various kinds were employed across the southern Yucatán peninsular region (Dunning and Beach 2000; Turner 1983); where intact, these features hold 2.7 to 3.6 times more soil than adjacent cultivated slopes (Dunning and Beach 2000). Deeper soils on slopelands tend to retain more moisture and maintain a superior capacity to respond to cropping inputs (e.g., mulch, manure) than do thinner, nonterraced slope soils.

The cropping impacts of these losses are not clear. Dunning and Beach (2000) suggest that Preclassic slope clearing was followed by substantial erosion, land degradation, and perhaps abandonment of certain locales (see the section on Wetland Sedimentation that follows). By the Classic Period, however, slope management increased significantly, reducing per-unit land degradation and contributing to more sustainable slope uses. Beach (1998), in fact, argues that there were surprisingly low losses of soil in Late Classic times where terraces were used. Terracing involved significant labor and management costs, however, especially in regard to various constructional and surface drainage measures required to combat hydrostatic pressure on the terraced walls, which resulted from the thickened soils that developed there. Loss of this management, for whatever reason, would have degraded the terrace system.

Weed and pest invasion

Pest damage to crops is large in the tropics, and at least one thesis speculates that the Maya collapsed owing to the spread of the maize mosaic virus by *Peregrinus maidis*, an insect that could have been carried by hurricanes from the Caribbean Islands to Yucatán (Brewbaker 1979). Swidden addresses pest disease problems by moving the plot and escaping the point source of the problem. Presumably the intensively used landscape of the Maya could not afford this luxury. Intercropping and use of species that repel certain crop predators were undoubtedly employed. Similarly, the use of many species varieties and intercropping were the principal combatants against crop

diseases as well (Thurston et al. 1994). Unfortunately, little is known about the strategies used to combat pest diseases and rely on analogues.

In contrast, one of the few methods to combat weeds (absent herbicides) is to remove them manually, and the paleo-record is replete with indications that increased occupancy and use of the lowlands tracks with significant losses in arboreal pollen as well as increases in maize, grass, and weed pollen (see review, Rice 1996). Milpa cultivation practiced with steel machetes largely involves cutting weeds at the surface, and is not an appropriate analogue for intensive cultivation. Frequent cropping would have required hoeing (digging up weeds) or preparing earthen hillocks (montones) or ridges for planting (pulverizing soil and reworking its shape).

These labor costly strategies, if not employed thoroughly and in conjunction with soil nutrient upkeep, may have triggered another environmental biteback that has been little considered for the region. Work on contemporary land-use/cover practices in southern Campeche and Quintana Roo reveals that three invasive species pose considerable problems to “overcropped” plots: (1) bracken fern or helecho (*Pteridium aquilinum* L.), (2) tajon (*Viguiera dentata* [Cav.] Spreng), and (3) *Cecropia peltata* L. (Turner et al. 2001). Of these, bracken fern poses almost insurmountable problems because it impedes (and even arrests) successional growth; it fails to produce quality biomass necessary for agriculture (biomass is produced, but it has low nutrient composition); and it regenerates rapidly after burning (for Amazonia see Uhl et al. 1982; Suazo 1998).

If bracken invades sufficiently large areas (continuous plots), farmers today virtually give up attempts to control or defeat it. If the species invades small, isolated plots, farmers attempt to control it by regular cutting—presumably permitting surrounding regrowth to increasingly shade the plot and reduce the bracken. There is no evidence that regular cutting will completely remove plots of bracken, although it may be effective in minimizing its spread.

Unfortunately, virtually no work has been undertaken to date on the causes of bracken invasion; thus, possible causes are subject to various interpretation. One view suggests that bracken invasion is related to long-term swidden cultivation and/or reduced crop-fallow cycles. Another view suggests that “out-of-control” fires burning through large areas give rise to large areas of bracken that farmers are unable or unwilling to control. Regardless of the cause, the problem is a growing one. For example, of the nearly 18,000 km² area examined in southern Campeche and Quintana Roo during 1987, about 1 percent of the land that had been disturbed for cultivation (mostly to medium fallow milpa) during a period of 20 to 30 years was covered by bracken fern; ten years later (and under mounting land pressures), almost 5 percent of the disturbed land cover was in bracken (Figure 20.4; Turner et al. 1990).

As noted, the role of bracken fern and other such invasive species on ancient Maya cultivation is not known. The paleo-record indicates fern spores and maize pollen are inversely related for the lowlands at large. Rue (1987) demonstrates, however, the increased presence of fern in the Late Classic based on cores taken from Agauda Petapilla (Copán Valley peat) and Lago Yojoa, Honduras. It is unlikely that bracken is a recent arrival to the region, which suggesting that the Maya found some means to deal with the species or that it proliferates when crop fallows are shortened, without requisite inputs to account for nutrient and other soil losses. Nevertheless, bracken deserve far more attention than it has received in terms of its bite back impacts.

Wetland sedimentation

Commensurate with Preclassic soil erosion, the evidence indicates substantial sedimentation in wetlands, especially those on the Caribbean littoral (Dunning and Beach 2000; Dunning et. al. 1999; Jacob 1995; Pope, Pohl, and Jacob 1996). These sediments covered peaty wetlands, some of which were apparently in use by the Maya (Pohl et al. 1996). The duration and pace of this process remain debated, but its impact on Maya cultivation would have been substantial, especially on the littoral. The suggestion that

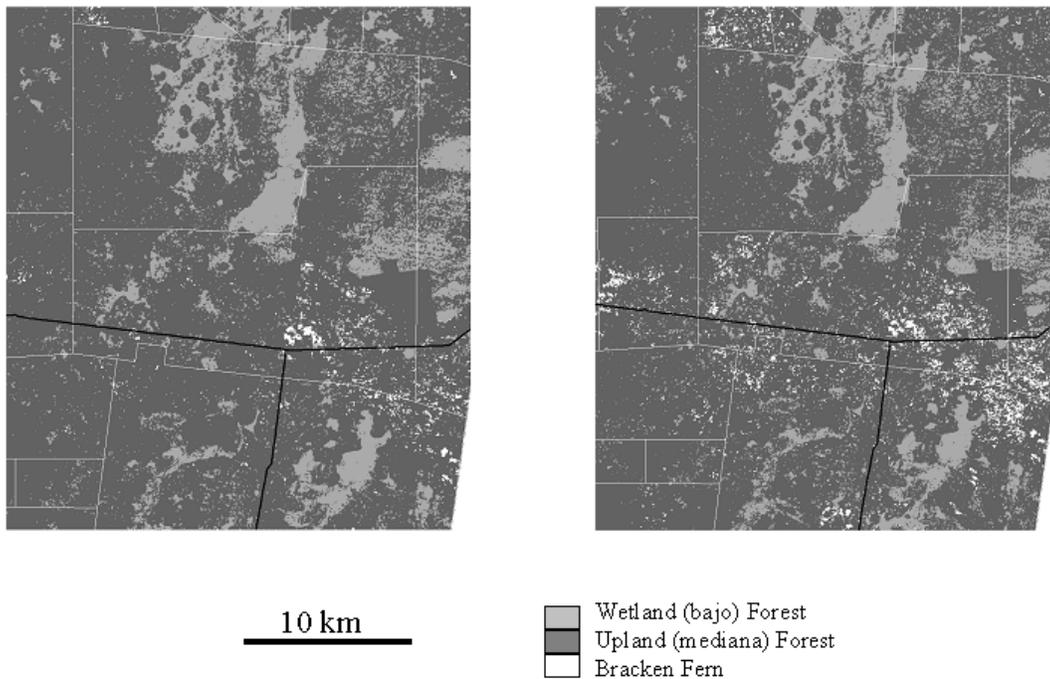


FIGURE. 20.4. Area increase and location of bracken fern from 1987 to 1997: 19 km² to 92 km². (See Figure 20.2 for location of this area within the region.)

sedimentation arrested Maya use of wetlands on the littoral appears doubtful, given settlement gravitation toward wetlands in some places during the Classic Period, as well as the apparent Late Classic ceramic evidence from the Nicolas Bravo–Morocoy wetland (above). It would appear that by the Middle to Late Classic, the Maya had recovered wetland cultivation.

The implications for the southern Yucatán peninsular region are problematic. With the exception of the Bajo Nicolas Bravo–Morocoy, no other wetland patterning associated with possible cultivation has been reported with confidence, or even confirmed. Human manipulation of small wetlands is reported in the northeastern Petén (Culbert, Levi, and Cruz 1990), and the adjacent area indicates upland hydraulic works engineered to move surface water from settlement areas to reservoirs and, ultimately, to wetlands (Scarborough et al. 1995). Although this engineering has numerous implications, it raises issues about the possible role of bajos in the maintenance of the southern Yucatán peninsular region—if not for food production, perhaps for some other purpose.

Regional climate change and water stress

The southern Yucatán peninsular region experiences a pronounced dry season. Its karst geology is not favorable for surface water, and elevations ranging between 100 to 300 m amsl promotes deep water tables, commonly 200 m or more below the surface. The paucity of dry season surface water hampers cattle projects in the region today, as well as various tourist-based development schemes (e.g., as *El Mundo Maya*). Given demands in the Late Classic, the provisioning of water during the late dry season must have posed a significant problem and required substantial attention.

Interestingly, the very landscape changes triggered by large-scale Maya occupation in the past may have aggravated water stresses. One of the more intriguing findings from earth system science research is the profound affect that region land-cover change may have on local climate, especially on rainfall (IGBP 1999). If the southern Yucatán peninsular region was long denuded at sufficient spatial scale, as the pollen records hints, significant decreases in average annual precipitation or increase in the length and severity of the dry season may have followed. It is not surprising, therefore, that Maya-made reservoirs of various sizes abound throughout the region, especially large ones concentrated at major sites. Scarborough (et al. 1995) has demonstrated the engineering feats expended by the Maya to control water flow from settlements to reservoirs (clay lined) and, ultimately, wetlands (clay lens). Either feature retained surface water, although the area and volume of *bajos* far exceeds that of reservoirs.¹⁰

Critical questions remained unresolved, such as why runoff was directed to bajos, as well as to what purpose bajo water was put. Bajos were, of course,

the natural drainage features; engineering feats related to them may have served only to alleviate excessive upland water during the height of the rainy season. Alternatively, bajos may have provided critical water resources and biomass (wood fuel); the hydraulic works would thus have ensured that more water would be delivered to them than percolated through the upland limestone to the deep aquifers below (see Scarborough et al. 1995; Scarborough 1996). Of course, if these wetlands were used for cultivation the runoff features would help to supply water for dry season cultivation (Siemens 1983; Siemens et al. 1988).

Some, if not many, wetlands may have resembled shallow lakes more than seasonal wetlands when the Maya entered the region (e.g., Dunning and Beach 2000)—an idea offered previously by Ricketson and Ricketson (1937) and Harrison (1977). The subsequent infill by Maya-made sediments dispersed surface water and made them more shallow and subject to evaporation. Engineering works, therefore, may have served to deliver more water to bajos over a longer period of the year, for whatever purposes bajos were put. Unlike former hypotheses, however, sedimentation of wetlands did not coincide with the Maya collapse; rather, the carrying capacity of the southern Yucatán peninsular region increased subsequently, as indicated by the huge rise in regional populations.

THREE MILLENNIA CLUES

Three thousand years of human-environment relationships in the southern Yucatán peninsular region, as exhaustively studied as they have been, provide support for only the most general lessons regarding occupancy, carrying capacity, and use. The evidence strongly supports the well-known understanding (if often understated) that the capacity of the lowlands to support large populations over long periods has been intimately tied to techno-managerial strategies used to manipulate the environments there; thus, carrying capacity is a dynamic outcome of the human-environment condition. Use of contemporary analogues to explain the region's past are largely valid only if they are applicable to the human-environment conditions of the past. In this case, current swidden cultivation and landscape configurations are a far cry from those present at the apex of Maya occupancy.

The same evidence also supports the case that the Maya, as with all other peoples, could not sustain themselves without a large human impress on the "native" conditions they encountered upon entering the region. They changed these conditions considerably—transforming a tropical forestland into an open, managed complex of integrated landscapes. This conclusion appears

little disputed, although the specifics of the individual practices and landscapes are still in contention.

Transformation, however, does not come without costs; for most environmental changes, sustaining the substitutes for nature's losses dominates these costs. If these costs become impractical, for whatever reason, the transformations degrade as part of nature's biteback. Recent attention refocuses on the bitebacks to Maya land and resource systems, with several individual problems elevated in attention—especially upland soil loss and wetland sedimentation—to which water stress and critical invasive species also can be added. Comparative studies of environmental degradation reveal, however, that few, if any, individual bitebacks create collapses akin to that experienced in the southern Yucatán peninsular region (Kasperson, Kasperson, and Turner 1995). Rather, multiple synergistic “stressors” must be active and sufficient in their damage to make social choices to combat them difficult.

It is precisely such human-environment conditions that are especially vulnerable to exogenous perturbations (e.g., invasion, climate change) that can tip the production systems. The role of climate change as a perturbation of this kind has long been proposed; Huntington (1917), based on observations in the Copán Valley, Honduras, proposed that the collapse was associated with *increased* precipitation. Recently, new evidence indicates that, in fact, the north-central lowlands experienced a shift to drier climatic conditions (Hodell 2000). If this shift was pan-lowland geographically (an assumption questioned by Dunning and Beach [2000]), coupled with the extant water stresses as well as possible land-change induced rainfall reductions, the biteback on the southern Yucatán peninsular region would have been significant.

Unlike the northern Maya lowlands and the coastal littorals, subterranean water was not accessible in the uplands, and captured surface water would have been in short supply. This scenario is dangerously simplistic, however. Although it may serve to explain a reduced carrying capacity and the collapse of the Maya heartland, it fails to account for the resulting catastrophic depopulation—the virtual abandonment of the southern Yucatán peninsular region and the resulting forest regrowth that almost swallowed the Cortés expedition.

Finally, the human-environment history of the region demonstrates the resilience of terrestrial systems, at least in regard to land cover over the long term. The tropical forests did return, if altered in species abundance owing to past land uses or the subsequent impacts of these uses (Gómez-Pompa, Flores, and Sosa 1987; Miksicek et al. 1981; Lambert and Arnason 1981). Interestingly, species abundance in the region is one of the few modern impacts matching those of the Maya. Selective logging in the middle of the twentieth century reduced significantly the presence of mahogany and Spanish cedar on the uplands proper. Ironically, the “humanized” forests of the

southern Yucatán peninsular region are those now central to various biological preservation and carbon sequestering programs.

NOTES

1. The percentage of Maya lowlands covered by slopelands or uplands and bajos (depressions or poljes) varies by location and size of area examined. The figures provided here are based on TM (Landsat 7) image analysis for a 22,000 km² portion of southern Quintana Roo and Campeche, Mexico (Figures 20.1 and 20.2; Turner et al. 2001). Absent of agriculture, uplands are dominated by mediana (uplands forest) and bajos by bajo forest in areas covered by the imagery (Figure 20.2).

2. In 1524, Hernando Cortés led an ill-fated expedition across the region that struggled through dense forest—largely absent trails and settlements of any kind—until they reached the Maya settlements on the central lakes of Petén (Whitmore and Turner 2001, Chapter 8). From colonial times until the early twentieth century, the “forest frontier” of the study region served as a refuge for Maya and others who sought to escape state control, for whatever reasons (Jones 1989).

3. Sidrys and Berger (1979) speculated that the Classic Maya collapse may not have involved a massive depopulation. Although it is true that some lowland areas, especially in northern Yucatán and on the coastal littorals, retained substantial populations, research on the southern Yucatán peninsular region strongly supports substantial depopulation there after about 1000 B.P. (ca. A.D. 950).

4. Sanders noted (during the question and answer session of the symposium in which this chapter was delivered) a definitional issue that may create confusion among those using the term *swidden* or its various counterparts in the study of the Maya. Some researchers use the term (or that of “super-milpa”) to refer to near-permanent cropping (1:1–2 crop-fallow cycle), especially if major landesque capital is not employed. Others, including the authors, do not employ the term in this way because of the public meaning that *swidden* has taken in a large, interdisciplinary literature. This public meaning is not consistent with near-permanent or predominately permanent cultivation that requires substantial labor and techno-managerial investments to overcome the limitations and vagaries of nature. Although we refer to techno-labeled systems of cultivation (e.g., *swidden*, terracing), the critical analytical issue is the level of inputs or costs of production. We infer a loose connection between these labels and the input issue. Those using the term *super-swidden*, or others with similar implications, are, in fact, consistent in meaning, if not labels, with our use here. Insufficiently explained labels, however, can lead to confusion.

5. Although remnants of wetland fields occur in these low-lying coastal zones is not disputed, their age and principal period of use are in contention. Condensing the various arguments, one viewpoint sees the fields as Preclassic in origin—largely peat-based systems that subsequently were abandoned, or only ephemerally used once major sediments from Maya land uses elsewhere began to cover them (Pohl et al. 1996; Pope and Dahlin 1989). Alternative views suggest that early experiments in wetland cultivation culminated in major wetland systems in the Late Classic Period, apparently in concert with, or after, major sedimentation (Harrison 1990; Turner 1993).

6. Our reading of the literature indicates that the expert community does not take seriously statements akin to the following: “One doubts that intensive methods were ever responsible for more than 10 percent of the subsistence base [of the Maya]” (Gyuk and Harrison 1975).

7. The evidence also mounts in regard to large-scale, pre-Hispanic soil erosion and sedimentation in the “altiplano” of Mexico mounts, as well (O’Hara, Street-Perrott, and Timothy 1993; Whitmore and Turner 2001). The evidence suggests that graphics akin to those in Figure 20.3 are applicable for the highlands, although massive abandonment of large regions did not follow.

8. Deep within the Río de la Passi6n region of Guatemala, bi-model deforestation evidence is found corresponding to the Late Preclassic and Classic periods. The second deforestation period, however, appears to have been less extensive and suggests agroforestry, given the apparent loss of certain species as well as the increase in fruit-bearing species (Dunning and Beach 2000:190).

9. Turner has long suspected that the phosphorus loadings found in the lake cores in question reflects increased human waste and night soils used within the lake drainages.

10. Bajos typically release water through surface drainage during high-water periods. They connect to one another by way of ephemeral waterways that remain dry and/or nonrunning for most of the year. At high water, and especially during hurricanes, these waterways not only flow, but they also flood adjacent, lower-elevated lands.

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Chapter 21

Periphyton As a Potential Biofertilizer in Intensive Agriculture of the Ancient Maya

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INTRODUCTION

The Yucatecan Maya developed an advanced civilization based on a set of poorly-known systems of intensive agriculture, in a dry tropical region climate and in shallow lithosols and rendzinas, with a low content of organic matter, fast leaching of nutrients, and high phosphorus fixation, that constrain agriculture. In contrast, some Maya communities still practice intensive agriculture using some organic materials as fertilizers. It is assumed that ancient Maya used them too.

The soils of the Yucatán Peninsula are shallow lithosols and rendzinas that are susceptible to biological degradation. In many areas, the soils are very poor in organic matter and have a very high level of phosphorus retention due to their calcimagnesian origin. One interesting problem is how the ancient Maya, over centuries, could provide enough food to sustain a population density in rural areas and urban centers significantly higher than in existence today. Another has been the replenishment of nutrients after several years of milpa cultivation. It has been accepted that the main source of nutrient replenishment came from the natural process of succession known as the

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milpa fallow period. There is no evidence of organic fertilizers in pre-Hispanic times; however, it is assumed that they used them in their intensive agricultural fields (Gómez-Pompa 1978; Wilken 1971). Some present-day Maya communities still practice intensive traditional agriculture and follow agroforestry systems in which they use a number of organic materials as fertilizer (Flores 1983; Gómez-Pompa 1996).

An ancient early Maya settlement has recently been discovered and studied (Fedick 1998) at the El Edén Ecological Reserve (northeast of the Yucatán Peninsula in the state of Quintana Roo, México). Archaeological research has shown a densely populated area that was sustained by agricultural production for several centuries (Morrison 2001). One intriguing discovery has been the presence of a series of rock alignments (some kind of dykes) in the wetlands. It seems that people living in the area were managing the flooding of the wetlands for unknown purposes. One hypothesis that the wetlands were used for agricultural purposes. Unfortunately, up to now, no plant has been found that was worth the effort of these major artificial works in the wetlands, or any proof that plants were grown (or animals raised) in the wetlands.

Agricultural production came from the use of two main groups of soils: (1) those that are seasonally flooded (lowlands and wetlands), and (2) those that are never inundated (uplands). Soils from the upland areas are covered by different kinds of secondary and mature forests on very poor and shallow soils. These soils are the ones used in traditional shifting (*milpa*) agriculture.

The lowland soils are covered by several wetland vegetation types, from seasonally inundated forests and savannas to permanently inundated swamps. One outstanding component of all wetland vegetation is the presence of impressive algal growth (known as periphyton) that covers all submerged substrata. It is composed of an algal mat and an assemblage of microscopic and very small macroscopic organisms that live by attached themselves to a great diversity of submerged substrata, are enmeshed by the attached species, or are feeding among them.

Periphyton is an extremely important component of the wetlands and serve as an important producer in the food web of these ecosystems and also as a nutrient concentrator and producer (Novelo-Maldonado and Tavera 1997). Initial studies by Anaya-Lang (cited by Fedick 1998) on the nutrient content of periphyton showed an outstanding concentration of nutrients, thereby underscoring their potential use as a biofertilizer. The hypothesis that ancient Maya settlers of the El Edén region may have used periphyton as fertilizer is tested, and this paper presents some results on the importance of periphyton as fertilizer. Two methods were used to evaluate its use as a fertilizer: (1) periphyton's chemical properties were analyzed by standard techniques, as well as an elemental analysis by particle-induced X-ray

emission (PIXE), and (2) a greenhouse experiment to compare the effect of periphyton on plant growth and arbuscular mycorrhizal fungi colonization with the effect of a chemical fertilizer was conducted.

MATERIALS AND METHODS

Periphyton samples were collected in three different dry seasons: 1997, 1999, and 2000. Triplicate samples of both materials were collected. For chemical analysis, samples were dried at 50°C, then milled and sieved with 2 mm mesh for edaphological analysis. For PIXE analysis, materials were milled in an agate mortar, sieved with a 100 mm mesh, and tableted (3 x 5-mm) using a hydraulic press.

Chemical analysis

Soil and periphyton pH (in H₂O, 1:2.5) were determined according to Soil Conservation Service (1984); organic matter (O.M.) by the dichromate method (Walkley 1947); total nitrogen (T.N.) by the Kjeldahl method (Black et al. 1965); total phosphorus (T.P.) by acid digestion (Black et al. 1965); available phosphorus (A.P.) by the Olsen method (Black et al. 1965); potassium (K) by flame photometry, and soluble calcium (Ca) and magnesium (Mg) by atomic absorption spectroscopy (Richards 1985; APHA-AWWA-WPCF 1992).

PIXE elemental analysis

Tablets of periphyton were bombarded with a beam of particle-induced X-ray emission (PIXE) under air conditions (Johansson and Campbell 1988). The bombardment was at 3 MeV using a proton beam pelletron accelerator at Instituto de Física, Universidad Nacional Autónoma de México (IF-UNAM). Two radiation detectors were used: (1) a hyperpure-Ge detector (GL0055P) with a resolution of 150 eV Full-Width-Half-Maximum (FWHM) to 5.9 KeV of the X-ray line of manganese (Mn), and (2) a Si(Li) detector (XR-100CR) made with 250 eV FWHM to 5.9 eV. The detectors were placed 5 cm from the sample. To calibrate the PIXE measurements, a lake sediment was used as a reference material (Corte, Parr, and Clements 1994). The multielemental analysis was obtained by using the Guelph PIXE software package II (Maxwell, Teesdale, and Campbell 1995). The PIXE technique was applied using the Van de Graaff accelerator 5.5 MeV of the IF-UNAM under vacuum conditions. The Si(Li) detector was used, but not under vacuum conditions, from 180 eV resolution to the X-ray line of Mn.

Greenhouse experiments

Soil, classified as Calcaric Phaeozem, was characterized as follows: medium-alkaline pH (7.70); clay loam texture; high-cation exchange capacity (33.0); low content of organic matter (1.16 percent); low total nitrogen of 0.13 percent; and available phosphorus of 2.30 ppm (parts per million). The experiments were carried out using sets of black plastic trays with pots of 50 g capacity. To avoid compaction, we mixed 30 percent silica sand with the soil.

A preliminary test was carried out to evaluate the efficiency of the indigenous arbuscular mycorrhizal fungi (IAMF); in this case, sterilized soil (IAMF eliminated, but native soil bacteria added) was compared with natural soil (nonautoclaved). The light period was eight hours; humidity was about 70 percent of soil-holding capacity; temperature ranged from about 25°C during the day to 10 to 15°C during the night. The experimental plants were tomato (*Lycopersicon esculentum* Mill., variety: "salades") and maize (*Zea mays* L., variety: "criollo blanco").

Experimental design

In our final experiment, only natural soil (non-autoclaved) was used. Seven treatments were applied: (1) control, natural soil alone; (2) low dose of periphyton (1.3 g/kg of soil); (3) medium dose of periphyton (1.65 g/kg of soil); (4) high dose of periphyton (2.3 g/kg of soil); (5) low dose of ammonium sulfate (0.26 g/kg of soil); (6) medium dose of ammonium sulfate (0.325 g/kg of soil); and (7) high dose of ammonium sulfate (0.455 g/kg of soil). Variables evaluated included the dry weight of foliage (dried at 45°C until constant weight); root volume (by measuring the displaced volume in a graduated cylinder); and indigenous AMF root-colonization level (staining the roots by the method of Phillips and Hayman 1970, and measuring by the method of Giovannetti and Mosse 1980). Statistical analysis included ANOVA and Tukey tests (Statistica for Windows[®] Release 4.3 D 1993).

RESULTS AND DISCUSSION

Chemical soil properties

The analysis revealed that all soils, which correspond to lowlands and low and medium high forest near to them, were very rich in organic matter (O.M.), so they have to be considered as organic soils. Values ranged from 17.9 to 26.9 percent (Table 21.1); the lowest value corresponded to Rancho Santa María, and the highest values to two samples of acahual low forest (burned areas \pm 25 and \pm 10 years old, respectively) in El Edén. Similar values were

found by Anaya-Lang, Palacios-Mayorga, and González-Velázquez (1997). These authors also found the highest O.M. contents in soils from burned areas.

In our sites, the exchangeable Ca and Mg were lower than the levels detected by Anaya-Lang, Palacios-Mayorga, and González-Velázquez (1997), but K values were higher; lower pH values were also found. The higher values of total phosphorus (TP) corresponded to burned areas because of the effect of ash (Boyer and Dell 1980), but the highest value (6.29 percent) corresponded to Rancho Santa María, an archaeological area. The highest values of K corresponded to low forest from burned area. The total nitrogen (TN) levels varied from 0.26 to 1.42 percent, which are very high and relate to the richness of OM. These values were also similar to those mentioned by Anaya, Palacios-Mayorga, and González-Velázquez (1997). TP was high and available phosphorus (AP) was very low (Table 21.1) as occurs in calcareic soils (Duchaufour 1984).

Chemical periphyton properties

The chemical analysis (Table 21.2) shows a very rich organomineral complex with a neutral pH in which the exchangeable Ca and Mg were very

TABLE 21.1. Chemical properties of El Edén soils.

Locality	Site	pH	%				mg kg ⁻¹		
			O.M.	T.N.	T.P.	A.P.	K	Ca	Mg
El Edén Medium high forest	Well Preserved	6.8	22.8	1.42	3.34	0.45	16	61.89	3.23
Acahual Low forest	Burned area (±25 years old)	7	25.5	1.28	3.59	0.35	5	48.90	1.40
Acahual Low forest	Burned area (±10 years old)	7.2	26.9	0.95	4.11	0.20	27.2	58.39	2.32
Rancho Santa María Low forest	Archaeological Area	7	17.9	0.26	6.29	0.35	9.8	37.39	2.39

OM = organic matter; TN = total nitrogen; TP = total phosphorus; AP = available phosphorus

high and the K was high; the percent of O.M. was high, similar to an organic horizon of a tropical forest soil. T.N. and T.P. were very high.

According to these results, periphyton are richer in total nitrogen than any other manure or compost used at present time, and similar (and sometimes richer) in total phosphorus than chicken manure (Monroy-Hernández and Viniestra-González 1990). Periphyton analysis by PIXE indicates a similar pattern of total macronutrients concentration: Ca > P > S > K (Table 21.3). For micronutrients, only Mn and Fe presented a similar pattern concentration (Fe > Mn). Cu and Zn were present (Zn > Cu) in most sites where both were present (Table 21.3 and Figure 21.1); it was also found that most trace elements show a different pattern across the spectrum (Figure 21.1).

Effect of periphyton on foliage dry weight

With this variable, the best response of both crop plants (tomato and maize) was obtained with dose 3 (D3) (Figure 21.2a and 21.2d); foliage dry weight was significantly higher when compared with control (C) and dose 3 (D3) of ammonium sulfate.

Effect of periphyton on root volume

The most significant increase was obtained in tomato with dose 3 (D3) of periphyton, while a smaller effect was observed with the same dose of ammonium sulfate (Figure 21.2b). Nevertheless, a response was observed in maize root volume only with dose 3 (D3) of periphyton, compared with the control (C) (Figure 21.2e).

TABLE 21.2. Chemical properties of periphyton from El Edén.

Periphyton Type	pH	O.M.	%			K	mg kg ⁻¹	
			T.N.	T.P.	A.P.		Ca	Mg
Ordinary	7	21.8	1.22	1.43	0.35	60.0	59.77	3.10
Rich in Chara	6.6	33.8	1.10	4.89	0.10	35.4	67.01	2.68

OM = organic matter; TN = total nitrogen; TP = total phosphorus; AP = available phosphorus

TABLE 21.3. Elemental analysis of periphyton samples by PIXE [mg kg⁻¹].

Element	Periphyton 1997							Periphyton 1999			Periphyton 2000	
	1	2	3	4	5	6	7	1	2	1	2	
P	83.5	63.5	35.9	84.6	84.3	84.9	72.9	87.4	82.3	54.5	59	
S	23.6	22.6	20.3	22	22.5	23.1	17.4	24.4	27.9	5.8	9.5	
Cl	3.1	6.6	5.3	5.7	4.5	12.2	4.5	6.8	1.9	2	5.6	
K	1.2	127	4	9.1	7	7.5	41.3	4.2	3.3	10	15.1	
Ca	498.8	402.6	212.5	433.5	426.1	453.8	425.2	497.2	503.2	598.3	580.1	
Ti	281	66	3.3	⊗	⊗	37	⊗	32	36	⊗	⊗	
V	66	61	93	47	31	⊗	⊗	⊗	52	⊗	428	
Cr	56	61	177	58	⊗	⊗	⊗	⊗	42	533	278	
Mn	258	488	2.1	570	472	275	602	516	616	1.4	635	
Fe	4.9	1.4	41.3	1.3	1	809	1.5	1.5	2.4	2.8	2.1	
Co	⊗	⊗	256	⊗	⊗	⊗	⊗	⊗	⊗	2	4	
Ni	203	⊗	45	557	372	220	149	93	83	⊗	⊗	
Cu	⊗	16	49	19	⊗	⊗	⊗	⊗	⊗	3	2	
Zn	64	36	84	71	21	44	⊗	⊗	⊗	2	1	
Ga	⊗	56	64	43	55	⊗	⊗	⊗	⊗	⊗	⊗	
As	⊗	⊗	20	⊗	42	⊗	⊗	⊗	⊗	⊗	⊗	
Br	100	⊗	176	⊗	56	⊗	⊗	⊗	⊗	6	9	
Rb	243	⊗	211	83	⊗	⊗	⊗	⊗	⊗	2	3	
Sr	⊗	⊗	605	⊗	⊗	⊗	200	⊗	⊗	49	50	
Y	⊗	⊗	⊗	⊗	⊗	1.2	⊗	697	⊗	⊗	⊗	

TABLE 21.3. (continued)

Element	<u>Periphyton 1997</u>							<u>Periphyton 1999</u>			<u>Periphyton 2000</u>	
	1	2	3	4	5	6	7	1	2	1	2	
Zr	⊗	⊗	465	⊗	290	100	⊗	⊗	⊗	⊗	⊗	
Ba	327	⊗	⊗	⊗	43	⊗	⊗	⊗	200	7	18	
Pb	⊗	⊗	⊗	166	⊗	⊗	181	⊗	⊗	⊗	⊗	

⊗ = out of minimum detectable level (MDL).

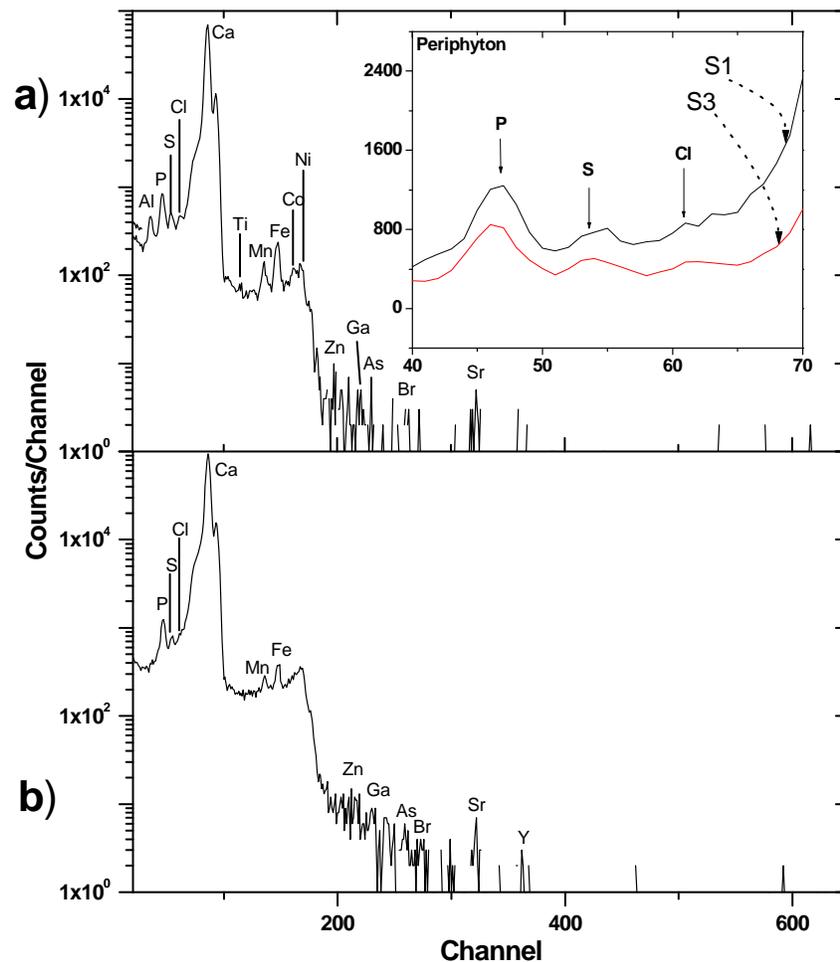


FIGURE 21.1. Comparison of the PIXE spectra of two samples of periphyton: S3 (site 3, 1997) and S1 (site 1, 1999). S3 has a higher phosphorus (P) content (amplification square, Figure 1a); nevertheless, a fingerprint of P, S, Cl, and Ca is observed among sites (Figures 1a and 1b).

Effect of periphyton on indigenous AMF root-colonization level

A significant positive effect was observed in tomato with all doses of both periphyton and ammonium sulfate (Figure 21.2c); in the case of maize, a similar effect was detected with dose 1 (D1) and dose 3 (D3) of periphyton, and only with dose 2 (D2) of ammonium sulfate (Figure 21.2f). The negative effect of ammonium sulfate on indigenous AMF reported by some authors (Hayman 1987; Chambers, Smith, and Smith 1980) is still not clear; in this context, our results could be controversial, due to the fact that we detected a positive effect with ammonium sulfate as well as with periphyton. However, the effects can vary from one soil site to another and may depend on the availability of phosphorus (Sieverding 1991).

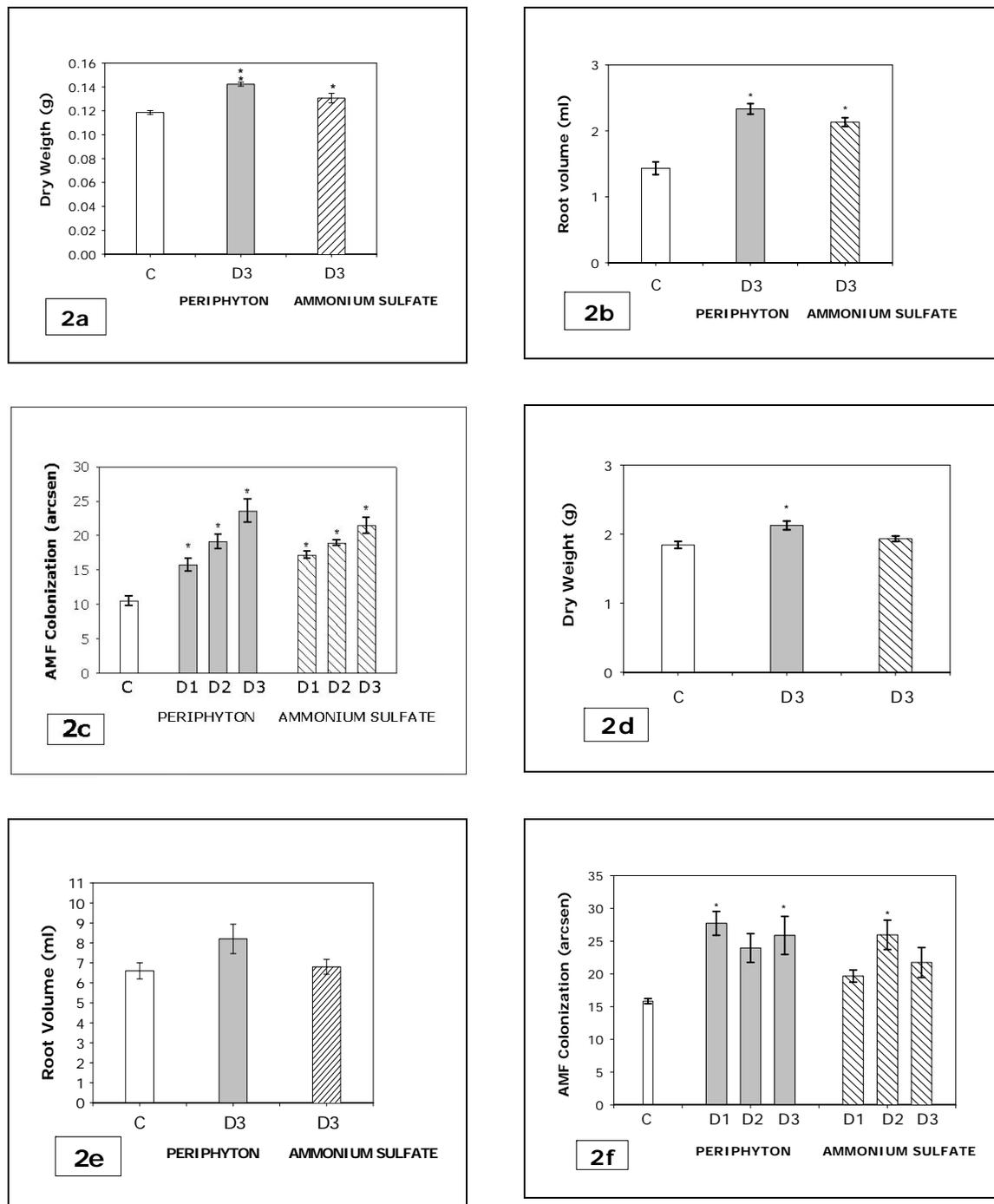


Figure 21.2. Greenhouse experiments. Effect of periphyton and ammonium sulfate on tomato foliage dry weight (2a); on tomato root volume (2b); on indigenous AMF colonization of tomato (2c); on maize foliage dry weight (2d); on maize root volume (2e); on indigenous AMF colonization of maize (2f). C = control, D1 = (low), D2 = (medium), D3 = (high). * = Significant differences with respect to control, $p < 0.05$. ** = Significant differences with respect to homologous dose, $p < 0.01$.

CONCLUSIONS

A number of important conclusions can be drawn from our research. First, the chemical analysis of periphyton indicated that this biological complex could be used as a natural source of two of most important macronutrients—nitrogen and phosphorus. Thus, periphyton are as good as (or better than) modern organic fertilizers. Second, PIXE analysis detected that periphyton have a complex chemical composition. Therefore, periphyton play a very important role in biogeochemical cycling because they act as a natural source of micronutrients in the ecosystem.

Third, periphyton are a biological complex that absorb and concentrate macronutrients and micronutrients; therefore, they could also be useful to detect the natural distribution of some trace elements in wetland ecosystems. According to these properties, PIXE analysis could be a useful technique to obtain an elemental “fingerprint” of different types of periphyton, plants, soils, and sediments.

Fourth, our greenhouse experiments showed that most of the periphyton doses applied to plants produced a positive effect on plant growth, which was equivalent (and sometimes superior) to the effect of ammonium sulfate. Finally, periphyton improved indigenous arbuscular mycorrhizal symbiosis.

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Chapter 22

Initial Evidence for Use of Periphyton As an Agricultural Fertilizer by the Ancient Maya associated with the El Edén Wetland, Northern Quintana Roo, Mexico

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Roberto Cózatl-Manzano

INTRODUCTION

In-depth studies of periphyton at the El Edén Ecological Reserve in Quintana Roo, Mexico, have revealing the diverse nature of this complex community of algae and other organisms, as well as its integral role in the chemical ecology of its local environment. As reported in this book in this book in the chapters by Novelo and Tavera, and Palacios-Mayorga et al., the presence of periphyton dramatically affects the amount of phosphorus and nitrogen available in wetland soils, creating a substrate markedly more fertile than other soils available in the area. Periphyton applied to greenhouse specimens improved growth even better than the application of commonly used commercial fertilizers (see Palacios-Mayorga et al., this book). This chapter addresses the following question: Might the ancient Maya inhabitants of the El Edén area also have recognized the powers of periphyton and put them to use? One line of evidence suggests that this may have been the case.

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THE YALAHAU WETLANDS

The area of wetlands referred to as the Yalahau region (Figure 22.1) in the northeastern corner of the Yucatán Peninsula has historically been inaccessible and sparsely populated (see Fedick, this book). The extremely thin soils above karstic limestone bedrock make modern agriculture difficult and keep yields low. The wetlands themselves, however, are an unusual source of fresh water in the northern peninsula, and recent discoveries of a complex array of prehistoric Maya sites surrounding these wetlands (Figure 22.2) suggest that the area was once much more productive and able to support a substantial population (Fedick and Taube 1995; Morrison 2000).

The wetlands, altered by the ancient Maya to increase or sustain their usefulness, were central to the ancient Yalahau economy (Fedick, this book; Fedick et al. 2000). Many potential uses have been suggested for these wetlands (see Fedick, this book; Fedick 1998; Fedick et al. 2000; Morrison 2000), one of which is the production of fertilizer, either in the form of pure periphyton or periphyton-enriched wetland soils. The study reported in this chapter examines soil samples collected from an ancient Maya settlement associated with the wetland at El Edén. The study's goal was to uncover

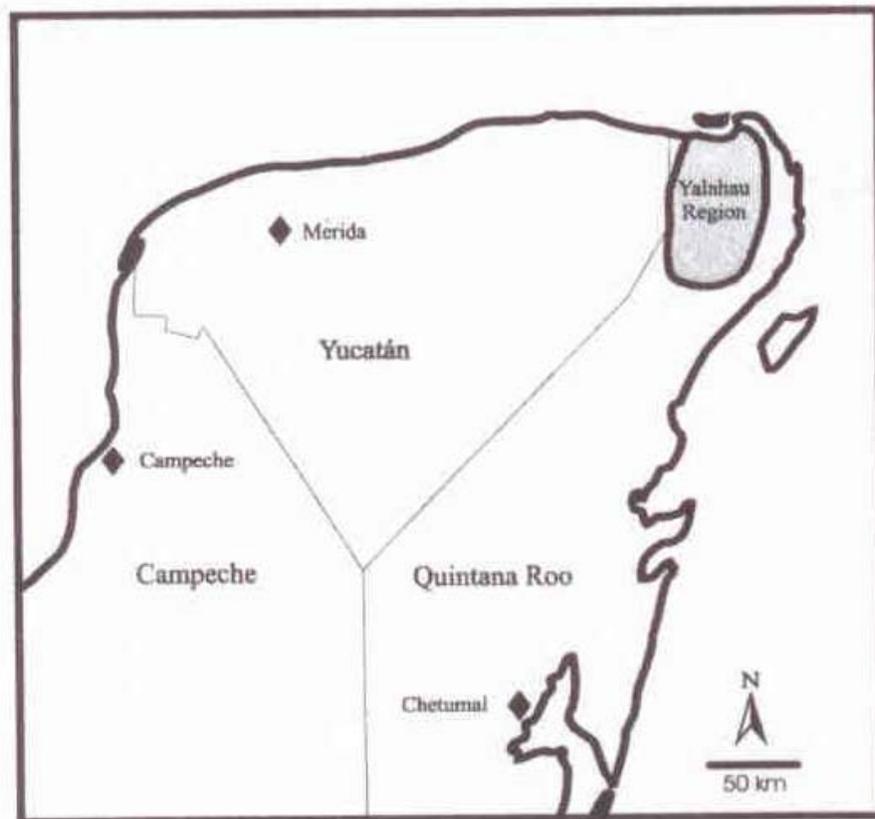


FIGURE 22.1. The Yalahau region of the Yucatán Peninsula.

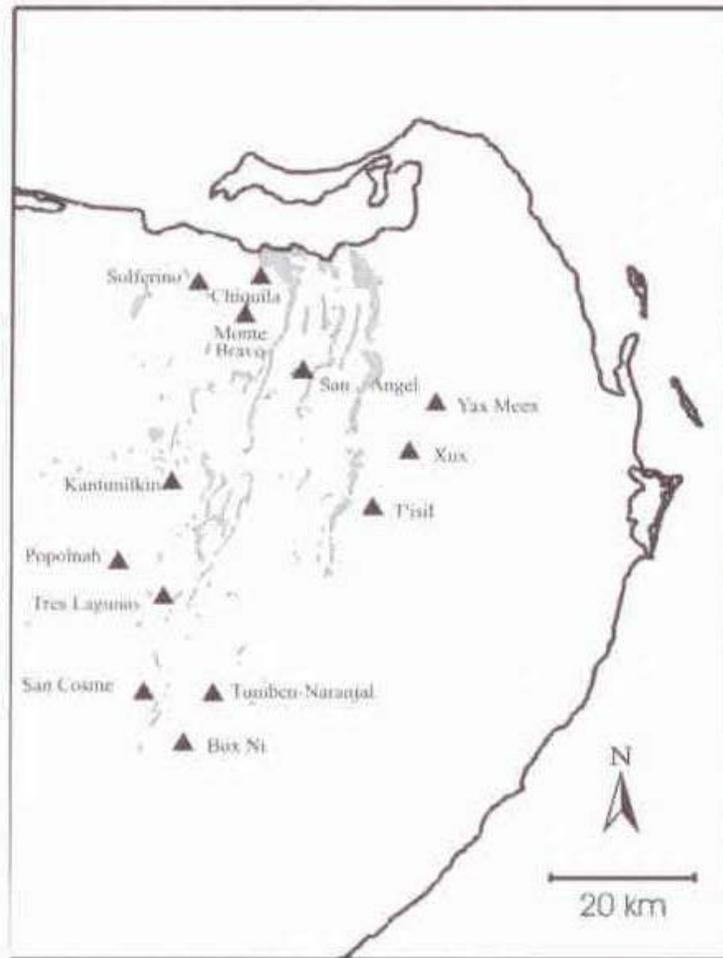


FIGURE 22.2. Wetlands of the Yalahau region and associated ancient Maya sites.

evidence for the transport of periphyton or wetland soils out of the wetland and into areas of either milpa or home-garden cultivation.

MAKABIL

Makabil (Figure 22.3) is a small Maya site located approximately three kilometers (km) east of the El Edén wetland. Ceramics recovered from the site date it to the Late Preclassic period (ca. 100 B.C.–A.D. 350), a date consistent with the occupation of other sites in the Yalahau region (Morrison 2000). Makabil consists of 55 structures, each measuring from 3 to 25 meters (m) across. The vast majority of these structures are broad platforms of limestone rubble and roughly shaped blocks that each probably supported one or more perishable structures. Most of the platforms are less than 100 cubic meters (m^3) in volume and probably served as outbuildings such as kitchens and

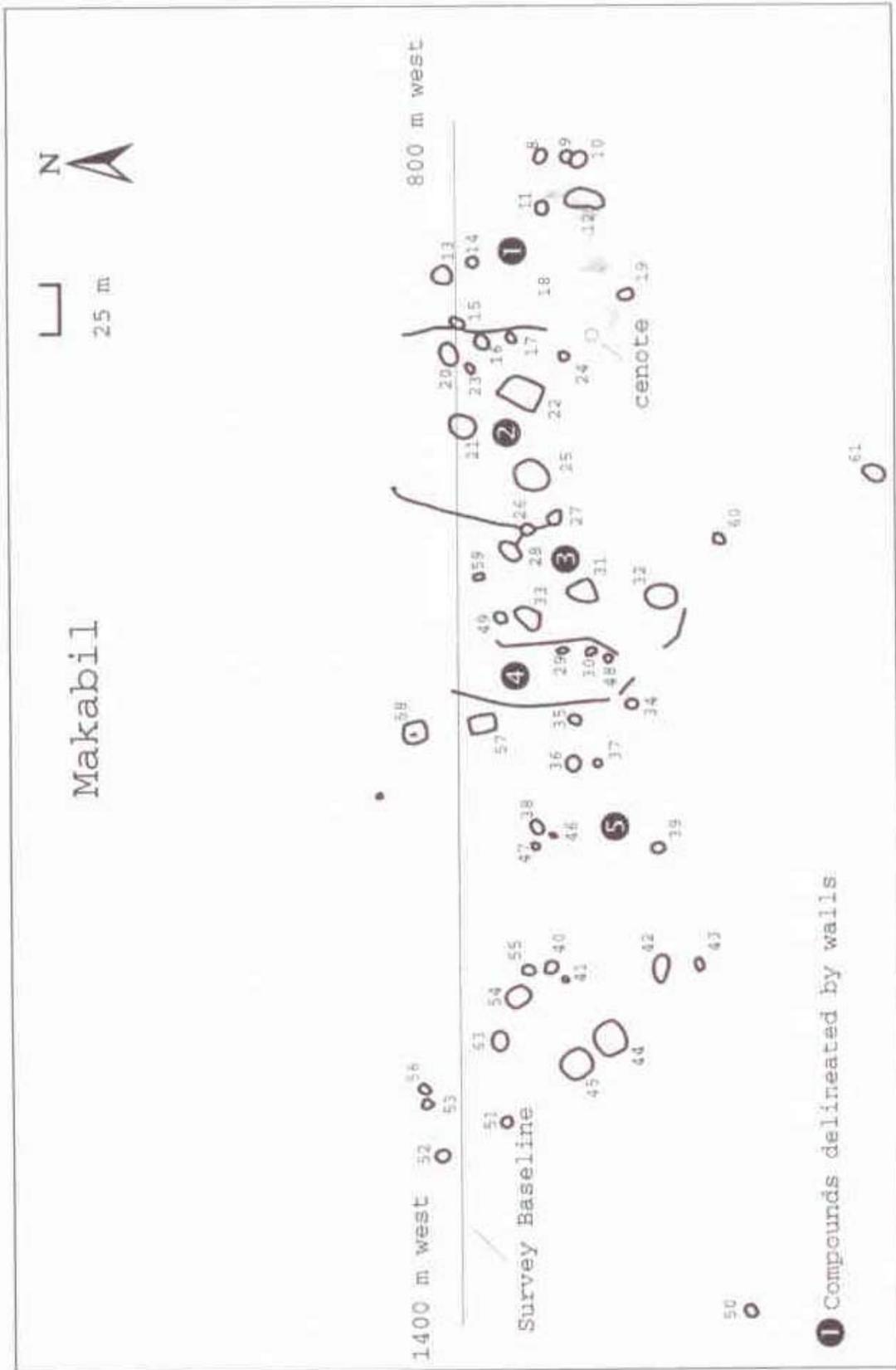


FIGURE 22.3. Map of the Late Preclassic Maya site, Makabil, located 3 km east of the El Edén wetland.

storage facilities. There are 14 platforms at Makabil that clearly seem large enough to have supported residences.

The Makabil settlement is divided into five sections, or compounds, by a series of low stone walls that tend to run parallel to each other in a north-south alignment, breaking up the settlement, which is distributed along an east-west axis. Walls surrounding and separating residential units at sites such as Cozumel (Sierra 1994), Cobá (Folan, Kintz, and Fletcher 1983), Mayapán (Bullard 1962), and Playa del Carmen (Silva and María del Carmen 1991) have been likened to modern-day solares, or houselots (Herrera et al. 1993; Herrera 1994), and interpreted as household boundary markers and evidence of ancient home gardens (see Goñi 1993).

TOPOGRAPHY OF EL EDÉN

The terrain of the Yalahau region, especially around El Edén, is remarkably flat. Due to the shallow relief, many of the area's wetlands have no clear margins, and inundation during the rainy season can cause them to increase greatly in size, flooding surrounding areas. In order to determine the extent of the flood zone associated with the wetland at El Edén, a detailed topographic study was conducted by Morrison along a transect leading from the dry-season margin of the wetland, through Makabil, and on to another ancient Maya site located at Cenote Azul, 4 km from the wetland (Figure 22.4). As the topography of the Yalahau region consists of subtle ridges and depressions that run north-south, measurements taken along the east-west baseline would reflect a cross section of the local terrain (for a detailed discussion of the archaeological survey of this transect, see Morrison 2000).

At the time of the project, there was no point on or near the El Edén Ecological Reserve with a known elevation. As the project was concerned with elevations relative to flood levels, it was decided that measurements would be taken relative to the high-water mark from the 1995 rainy season, a point that is permanently recorded on a support piling of the El Edén research station structure. The hurricane season of 1995 was recorded by the American Meteorological Society (AMS) as the second most active season in 125 years—falling short only of 1933 for number of storms, while breaking the record for days of storm activity (AMS 1995). In view of this, the flood levels from 1995 are considered to be a good approximation of high-water levels for the area over time. Elevations were measured to the nearest centimeter (cm) with a transit and a stadia rod.

Elevations along the baseline only vary by 4.3 m. About 300 m east of the dry-season margin of the wetland, the bedrock rises to 2.2 m above the dry-season water level and 3.0 m below the 1995 flood level. Here, the

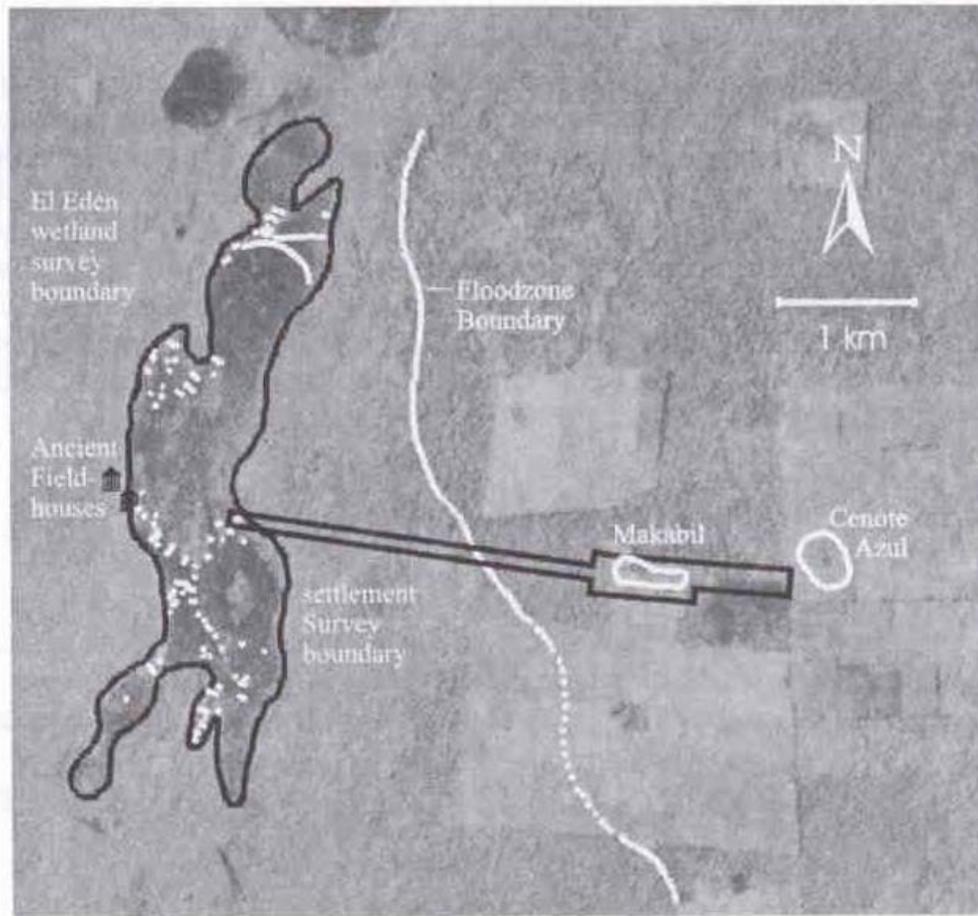


FIGURE 22.4. The survey transect between the El Edén wetland and Cenote Azul, encompassing Makabil. Areas east of the flood zone boundary would not provide the aqueous environment required by the fresh water mollusks associated with periphyton.

vegetation changes from open savanna and palo tinto trees (*Haematoxylon campechianum*) to denser, higher forest. During most years, this point probably marks the wet-season extent of the wetland. However, waters as high as those in 1995 could spread as much as another kilometer east where a ridge was recorded 0.75 m above the 1995 flood levels. This estimation of the extent of the El Edén flood zone is supported by evidence visible in the modern terrain. Depressions west of this ridge are marked by a lack of vegetation and high densities of snail shells, indicating prolonged periods of high moisture or of inundation. Additionally, aerial photos of the reserve and surrounding areas indicate a change in vegetation types associated with this ridge, also suggesting a difference in soil quality and/or moisture levels. The boundary of the flood zone indicated in Figure 22.4 follows this change in vegetation, crossing the transect at the ridge.

Makabil, therefore, is located 1.5 km outside of the extreme flood zone of the El Edén wetland, secure from inundation, and also well outside the natural habitat of periphyton and the aquatic species of mollusks that are part of this biotic community.

SEARCHING FOR PERIPHYTON AT MAKABIL

The samples

Among the community of organisms that makes up periphyton are several species of small freshwater mollusks (Figure 22.5). These creatures are significant to this study for two reasons: (1) their shells, unlike other parts of the periphyton, will preserve archaeologically, and (2) they cannot survive naturally outside of the wetland environment. If periphyton, or the substrate immediately beneath them, had been transported to the settlement or other areas outside of the wetland for the purpose of soil augmentation, some of these shells should have been transported along with them. These shells, then, should be recoverable from soil samples collected in the treated areas.

Ten-liter (L) soil samples were collected by Morrison (2000) at intervals along the baseline between the El Edén wetland and Cenote Azul at maximum intervals of 200 m. The soil samples were water-screened with 1-millimeter (mm) mesh, and all material retained in the screen was then dried and prepared for analysis. Mollusk shells were sorted out from the processed soil samples and then sent to Cózatl for identification and verification of either a terrestrial or freshwater niche.



FIGURE 22.5. Examples of mollusks that live among periphyton.

Identifying freshwater vs. terrestrial mollusks

The mollusks recovered during the study were members of two subclasses of gastropods: Prosobranchia and Pulmonata. Species of these groups live in aqueous as well as terrestrial environments, so it was critical to determine the native habitat of each specimen collected.

Some characteristics are helpful in differentiating shells at the initial stage of identification. Characteristics common in the shells of terrestrial species include thicker shells and aperture lips, the presence of fine striations in the periostrac (outer shell), and visible teeth at the aperture. These distinctions, however, may be less helpful among putative ecological assemblages—for example, from a habitat including the freshwater genus *Lymnaea* and the land snail *Succinea*, both of which are dextrally coiled, with similar mouth shapes and columellar folds.

To avoid possible confusion, a careful analysis and measurement of pre-established ratios and lengths was taken from informative parts of each shell. This information was matched with that available in taxonomic keys (see Ellis 1969; Cameron and Redfern 1976; Burch 1989; Burch and Cruz-Reyes 1987). Many of these informative features (e.g., length/width ratios, columellar folding, number of whorls, shape of the umbilicus, and spire height) remain unaltered by physical agents such as erosion or partial material replacement, and endure harsh events such as partial shell breakage. In other cases it is possible to infer the original shapes and dimensions.

Finally, a comparison of shells sampled was made with shells from other current ecological surveys. Species identified were similar to those reported by ecological surveys made in similar sites (Cózatl-Manzano 1999; Gómez Espinosa 1999).

RESULTS

In all, six freshwater and seven terrestrial species of mollusk were identified to at least the family level. These are listed in Table 22.1. The distribution of terrestrial snails collected from the water-screened soil samples is shown in Table 22.2, and the distribution of freshwater snails is shown in Table 22.3. As expected, frequencies of freshwater mollusks decline dramatically beyond the edge of the permanent section of the wetland and drop off completely around 2500 m west (of Cenote Azul), in the area of the protective ridge. Then, a few specimens occur again between 800 m and 1,400 m west, precisely within the settlement of Makabil. Although the actual number of freshwater mollusks found outside of their natural environment is

TABLE 22.1 Mollusk species identified in soil samples from the Cenote Azul transect.

Family	Genus	Species
Terrestrial:		
Achatinidae	<i>Lamellaxis</i>	<i>martensi</i>
Bulimulidae	<i>Bulimulus</i>	-----
Bulimulidae	<i>Leptinaria</i>	<i>interstriata</i>
Cydothoridae	<i>Neocyclotus</i>	<i>dysoni</i>
Oleacinidae	<i>Streptostyla</i>	<i>meridana</i>
Pupillidae	<i>Gastrocopta</i>	<i>pellucida</i>
Subulinidae	<i>Leptinaria</i>	-----
Freshwater:		
Ampullariidae	<i>Pomacea</i>	<i>flagellata</i>
Ancylidae	<i>Hebetancylus</i>	<i>excentricus</i>
Hydrobiidae	<i>Pyrgophorus</i>	<i>coronatus</i>
Physidae	<i>Physella</i>	-----
Pisidiidae	<i>Sphaerium</i>	<i>transversum</i>
Planorbidae	<i>Biomphalaria</i>	-----

small (only 11), they clearly show the presence of transported wetland species.

The possibility remains, however, that the freshwater mollusks were transported by some natural means, perhaps by unusually high floodwaters. In such a situation, mollusks outside of their natural habitat ought to reflect a random distribution. A chi-square test was performed, indicating a 99.5 percent assurance of a non-random distribution of freshwater snails outside of the flood zone (between 0 and 2,500 m west of Cenote Azul).

DISCUSSION

Freshwater mollusks recovered from soil deposits at Makabil are exciting evidence for the prehistoric use of periphyton or wetland soil as a fertilizer. The support of periphyton communities was likely one purpose of the hydro-management system constructed within the El Edén wetland (see Fedick, this book). By augmenting upland soils with nutrients harvested from the wetland,

Table 22.2 Terrestrial snail distributions at El Edén by taxonomic family

meters	Achatinidae	Bulimulidae	Cyclophoridae	Oleacinidae	Pupillidae	Subulinidae
200						2
400						
600						
800	7			2		
902						
1000						
1125						
1200				7		
1400				2		
1600				15		
1800						
2000						
2200	1			1		
2600				5		
2700				3		
2750				1		
2800			1	6		
2850				8		
2900				1		
3000						
3090						
3200				8		
3600		5		10		
3800						
4000						
4200	31				6	

Note: * 0 to 2,200 meters west is the area securely outside the wetland flood zone. Shaded cells indicate area of Makabil settlement.

Table 3 Freshwater snail distributions at El Edén by taxonomic family.

meters w ^a	Ampul- lariidae	Ancylidae	Hydrobiidae	Physidae	Pisidiidae	Planor- bidae
200						
400						
600						
800				1		
902						
1000						
1125						2
1200						
1400		1	7			
1600						
1800						
2000						
2200						
2600						
2700						2
2750						3
2800						
2850						
2900						
3000					11	
3090						
3200						
3600			4			
3800	25			10	24	100s ^b
4000	4					1
4200	50	10	100s ^b	100s ^b	20	100s ^b

Note: Shaded cells indicate area of Makabil settlement.

^a0 to 2,200 meters west is the area securely outside the wetland flood zone.

^bHundreds of specimens (100s) counted; exact number not provided.

the ancient inhabitants of Makabil could have better provided for their families in an environment otherwise quite inhospitable.

The limited number of mollusks recovered during this study makes detailed analysis of their distribution within and adjacent to the site difficult. Further sampling is planned to help discern whether periphyton were used within the area of settlement (i.e., in home gardens) and/or in neighboring fields. The next phase of the periphyton project began during the 2000 and 2001 field seasons at the ancient community of T'isil, located 3 km from a wetland and approximately 12 km south of El Edén. T'isil has several distinct areas thought to have been used for agriculture. Soil samples taken there will be analyzed for the presence of transported periphyton at an additional site, as well as their distribution within the settlement.

The discovery of periphyton remains at Makabil is a significant contribution to our understanding of ancient subsistence practices in the Yalahau region and of ancient Maya agricultural intensification and regional variability. Equally important, it is a testimony to the insight of the ancient Maya and their ability to successfully interface with a unique "wildland" environment.

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Chapter 23

Domestication and Distribution of the Chocolate Tree (*Theobroma cacao* L.) in Mesoamerica

Nisao Ogata

INTRODUCTION

The history of *Theobroma cacao* L. in Mesoamerica is especially important as historical and archaeological evidence place this area as the center of domestication for the species since at least 2,000 years ago. Mesoamerica represents the extreme northern distribution where *T. cacao* ssp. *cacao* occurs naturally and is also the place where a unique segment of genetic diversity has been recently documented (De la Cruz et al. 1995; Whitkus et al. 1998).

T. cacao represents one of the best examples to examine the idea of domestication with respect to plants, as well as forests. From this perspective, domestication may not only be used to refer to the process of changing wild plant species to cultivated species, but also to the process of converting “wild” forests into managed forests. This process is characterized as the

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transformation of a natural forest into a forest in which the original structure and composition has been changed to better suit specific human purposes (Wiersum 1998). These managed forests systems have been recently proposed as one of the best alternatives for long-term production, biodiversity conservation, and environmental protection (Rice and Greenberg 2000).

T. cacao is also a very well-known species because its seeds have had immense importance either socially, religiously, medically, economically, or gastronomically across several different cultures over the last 2,000 years. In the last three decades, *T. cacao* production has shown a rapid expansion from 1.5 million tons produced in 1970 to 3 million tons in 1995 with more than 2.5 million hectares (ha.) cultivated (Rice and Greenberg 2000).

T. cacao reached its zenith of domestication in Mesoamerica; it is also the place where, supposedly, the Spanish took the stock genetic material that they then distributed around the world after 1519. It is precisely in Mesoamerica where historical reconstruction and studies on the diversity of cacao are important to understanding domestication processes in tropical rain forests, as well as the diversity and origin of the plant.

The objective of this paper is to describe the diversity and distribution of cacao in ancient Mesoamerica and compare it with present times. Based on historical accounts and fieldwork, I describe the occurrence and distribution of putative wild and pre-Hispanic abandoned populations in present times in Mesoamerica. At the end, new evidence is presented to propose that the domestication and use of cacao as chocolate in pre-Hispanic times was not exclusive to Mesoamerica, but to several indigenous groups from South America as well.

TAXONOMIC BACKGROUND

Theobroma is a Neotropical genus that originated in South America with 22 described species (Cuatrecasas 1964). Recently the genus was reclassified in the family Malvaceae, subfamily Byttnerioideae, tribe Theobromeae (Bayer et al. 1999).

In 1964, Cuatrecasas divided *T. cacao* into two subspecies: *T. cacao* ssp. *cacao* and *T. cacao* ssp. *sphaerocarpum*. Their characteristics are discussed below.

T. cacao ssp. *cacao*, commonly known as “Criollo” (native) is distributed from Mexico to South America. It is characterized by having elongate, fusiform, claviform, or ovoid-oblong fruits that are tapering and pointed, more or less strongly five to ten costate, sometimes verrucose; ovoid or ellipsoid seeds, usually rounded in cross section; white or yellowish-white cotyledons. Three forms have been described for this subspecies, based mainly on the shape of the fruit:

1. *T. cacao cacao* f. *pentagonum* is characterized by claviform fruits, strongly 5-costate; prominent and smooth ridges, with sides strongly verrucose; thinner pericarp; and lacking a woody mesocarp and endocarp. This form, commonly known as “cacao lagarto,” is originally from Central America and is known only in cultivation. Although this variety is susceptible to diseases, it is one of the best quality of cacao known (Cuatrecasas 1964; López-Mendoza 1987).
2. *T. cacao cacao* f. *leiocarpum* is defined by having ovoid fruits that are shallowly 5-furrowed (almost smooth) and obtusely attenuate at apex. This form, known in Guatemala as “Cumacaco,” is considered high-quality cacao. It is distributed along the Atlantic coast of Guatemala, and occasionally in other parts of Central America and southern Mexico. The cultivar porcelaine Java Criollo probably represents this form (Cuatrecasas 1964).
3. *T. cacao cacao* f. *lacandonense* is characterized by having ovoid-oblong fruits that are acute and 10-furrowed. It is known only from the Lacandon forest in the northeast section of Chiapas. According to Cuatrecasas (1964, pg. 514), the stem is half vine, about 7 meters (m) tall, with very long branches; its trunk is 15 centimeters (cm) in diameter.

T. cacao ssp. *sphaerocarpum* corresponds to well-known “Forasteros” (nonnative), ‘Calabacillos’, ‘Amelonados’, ‘Amazonian Forasteros’, etc. from South America. It is characterized by having ellipsoid, rounded, rather smooth fruits; violet cotyledons; fast growth with high yields; and by being resistant to disease (Cuatrecasas 1964).

As mentioned before, in general terms Criollo (meaning native) cultivars correspond to *T. cacao* ssp. *cacao* and “Forastero” (meaning nonnative) to *T. cacao* ssp. *sphaerocarpum*. However, a more complex diversity exists along the distribution range of the species because hybridization between subspecies is not an uncommon event (Young 1994). Because Mesoamerica was the main area of cacao domestication in pre-Hispanic times, an important question to be explored is the diversity of cacao in ancient Mesoamerica.

DIVERSITY OF CACAO IN ANCIENT MESOAMERICA

Cacao production in Mesoamerica was based mainly on the domestication of *T. cacao* ssp. *cacao*, especially the ‘Criollo’ cultivars (Cuatrecasas 1964; Coe and Coe 1996; Young 1994). However, some sources suggest that several cultivars, and possibly more than one subspecies, were cultivated in ancient Mesoamerica.

In this regard, the work of Francisco Hernández ([1790] 1942) is perhaps the first western attempt to document Mesoamerican cacao diversity. He presents prints and descriptions of the cacao tree, including its Nahuatl name *cacahoquahuitl*, along with four varieties called *quauhcacahoatl*, *mecacahoatl*, *xochicacahoatl*, and *tlalcacahoatl*; these varieties are distinguished by fruits that diminish in size from first to last, which presumably represent cultivars. Hernández also mentions *quauhpatachtli*, which undoubtedly refers to *T. bicolor* Humb. & Bonpl., a relative of cacao used as a shade tree, and sometimes by Indians to counterfeit cacao seeds (Coe and Coe 1996). Hernández describes cacao pods as “large and similar to a great cucumber but grooved and red” (Hernández [1790] 1942:146). One of his illustrations of *T. cacao* is undoubtedly Criollo cacao.

The diversity of cacao in Mesoamerica has also been mentioned in other old sources (Torquemada [1723] 1983; Sahagún [1590] 1946; Codex Mendoza 1938; Alvarado-Tezozomoc [1598] 1944; Relación de Yucatán, cited in Millon 1955; Ciudad Real [1872] 1993). For example, Torquemada ([1723] 1983) describes cacao trees as beginning to produce in the third year, which is interesting to note because this is a well-known characteristic exclusive to Forastero cultivars and not for Criollo, which is described elsewhere as not producing before the fifth year. Sahagún ([1590] 1946) described the inside of the beans as red or bright red; he also states that either the outer covering of the bean or the pod itself was violet (is this a reference to Forastero cultivars?). Alvarado-Tezozomoc ([1598] 1944) describes the beans as black and brown. The Codex Mendoza (1938) and The Relación of Mérida (Millon 1955) both describe the beans as red, while Ciudad Real ([1872] 1993) writes that they are red and black in color.

In regard to the presence of cacao Forastero in Mesoamerica in pre-Hispanic times, Wolters (1999) suggests the importance of the Amerindian sea navigation for the dissemination of tropical crop plants in the Americas along the Pacific coast, which he believes has been underestimated. Wolters (1999) suggests that the Valdivia culture (3500–1600 B.C.), and all successive cultures in west Ecuador, conducted coastal shipping to Peru, Middle America, and southern Mexico from 2200 to 1450 B.C. Presumably, crop plant export occurred from western Ecuador to Peru and Middle America (sweet manioc, *Annona cherimola*, *Carica papaya*, early great-grained corn) and Mexico (tobacco and cacao). On the other hand, Wolters (1999) suggests that the Valdivias are also responsible for the dispersion of *Persea americana* and *Capsicum annuum* from Mexico to Ecuador and Peru. If this hypothesis is true, then we would expect the presence of Forasteros in Mesoamerica around 1,500 years ago would be expected.

López-Mendoza (1987) describes Mexican Criollo cultivars in Tabasco and mention the existence of eight varieties of Mexican Criollos cultivated since pre-Hispanic times in Michoacán, Oaxaca, and Guerrero (see Figure

23.1). The characteristics of these varieties are based mainly on the whiteness of the cotyledons, as well as on the color and texture of the pods. According to López-Mendoza (1987), a major introduction from South America occurred at the beginning of 1930. From that introduction arose a variety called “Ceylan,” which was planted in Chiapas and reached Tabasco by 1936. From this introduction, local selections gave rise to two new varieties called ‘Calabacillo’ and ‘Guayaquil’, respectively. These selected cultivars were planted only in Chiapas and Tabasco during the 1930s and the 1950s.

Two recent papers regarding the diversity of cacao in Mesoamerica documented the genetic diversity of putative old ancient abandoned populations in the Yucatán Peninsula and putative wild populations as unique segments of genetic diversity (De la Cruz et al. 1995; Whitkus et al. 1998). They also pointed out that commercial Criollo cultivars were genetically more similar to the wild South American populations than to wild and old abandoned Mexican populations; this supports a South American origin for present-day cultivated cacao. De la Cruz et al. (1995) and Whitkus et al. (1998) concluded that the cacao cultivated by the Maya do not exist in modern germ-plasm collections because managed groves were probably abandoned after the arrival of the Spanish in 1519, with a few remaining in isolation, protected by Maya descendants. In this sense, are there ancient abandoned populations more widespread in Mesoamerica that represent unique segments of genetic diversity?

THE DISTRIBUTION OF T. CACAO

Pre-Hispanic Times

The distribution of cacao in pre-Hispanic times has been reconstructed from Spanish sources as early as 10 years after the arrival of Cortés in 1519 (Millon 1955; Bergmann 1969; Young 1994; Coe and Coe 1996). From these sources, it has been suggested that cacao was cultivated practically everywhere where environmental conditions allowed it, from Michoacán to Nicaragua in the west, and from north Veracruz to Honduras in the east. Even in places such as the Yucatán Peninsula, where suitable places for cacao cultivation are very limited, the Maya managed to cultivate cacao in underground sinkholes (Gómez-Pompa, Flores, and Aliphath-Fernández 1990). Some important pre-Hispanic areas of cacao production were Tabasco, northern Oaxaca, central and southern Veracruz, southern Chiapas, northern Guerrero, southwestern Guatemala, and Honduras (Millon 1955). Elsewhere in Mesoamerica, production was on a considerably smaller scale (Figure 23.1).

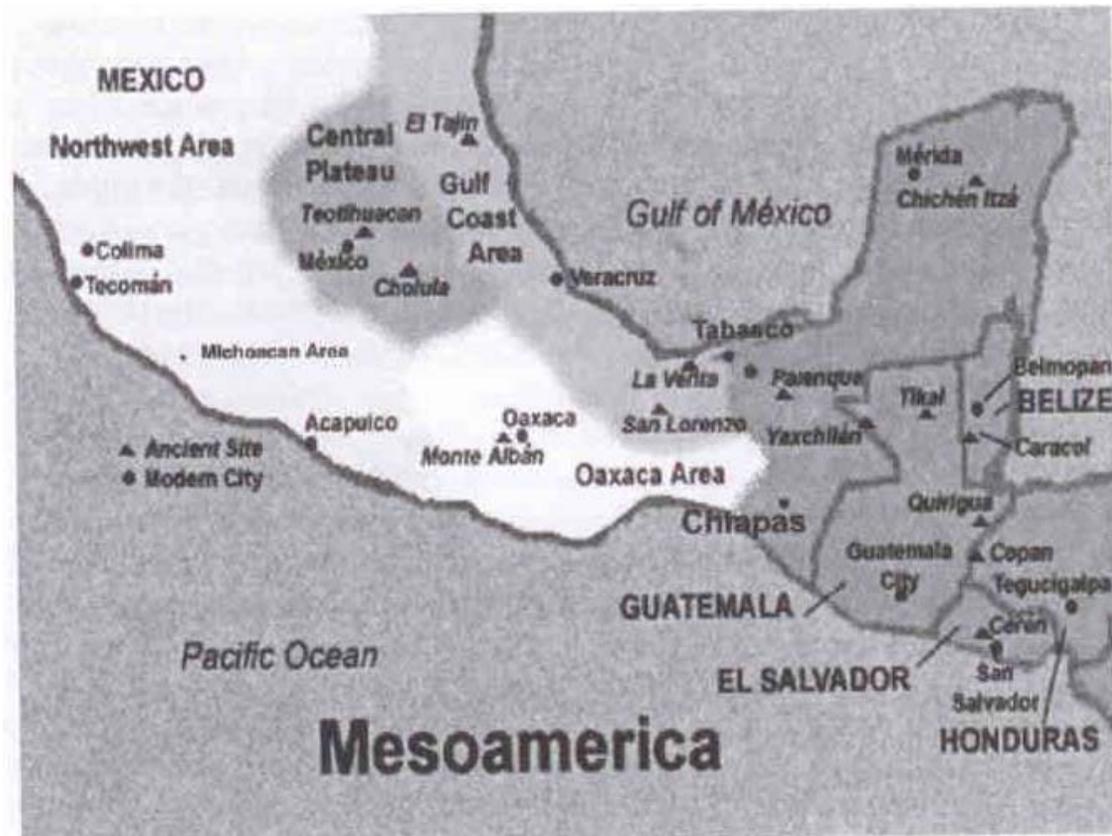


FIGURE 23.1. Main areas of Mesoamerica in ancient and modern times.

An outstanding characteristic of cacao cultivation is the degree of development reached by Mesoamericans, especially the Maya. They developed a complex and sophisticated agroforestry system using shade trees, irrigation systems, nurseries, and transplantation techniques (Ciudad Real [1872] 1993; Torquemada ([1723] 1983); Alvarado-Tezozomoc [1598] 1944). One of these transplantation techniques involved wrapping the roots of seedlings in mats during the transplantation process, which involved significant hand labor (Alvarado-Tezozomoc [1598] 1944). This evidence suggests not only that cacao was a crop of great importance in Mesoamerica, but also that it must have had a long history of cultivation.

The production of cacao in pre-Hispanic times was low, in comparison to the present, and would mostly have been consumed locally. The one exception is the case of Tabasco, where the beginnings of specialization showed that the cultivation of cotton had been abandoned because of the demands of cacao. Cotton was imported from Yucatán in exchange for cacao. By the time of the Spanish arrival, Millon (1955) estimated cacao production in Mesoamerica to have been no more than 1,350 tons a year.

Modern Times

One part of the work on the diversity and origin of cacao in Mesoamerica has been to focus on the study of old documents trying to locate ancient abandoned populations, as well as searching for wild populations. In a preliminary search for cacao populations, we based our research on the *Suma de visitas de pueblos* (Paso y Troncoso 1905). This document consists of a series of accounts from 907 towns in Central Mexico, collected between 1531 and 1544. From these towns, we chose those known in the *Suma* as cacao producers in pre-Hispanic times, were chosen where currently there are no traces of cacao cultivation. In the case of the Yucatán Peninsula, the search was based on Millon (1955) as well as Gómez-Pompa, Flores, and Aliphath-Fernández (1990). Places such as Tabasco were excluded because it is known that an introduction of South American cultivars occurred at the beginning of the 1930s.

Based on these sources, 23 cacao populations were found in places referred to as ancient cacao-producer areas where there are no traces of recent cacao cultivation. Up to now, the populations found represented Criollo types. Populations have been located in backyard gardens and/or mixed in plantations of coffee, banana, and orange in the north of Veracruz, Southern Veracruz, northern Oaxaca, northern Guerrero, and Yucatán.

***DO WILD POPULATIONS OF T. CACAO
EXIST IN MEXICO?***

The possible natural distribution of wild cacao populations in Mesoamerica has generated some controversy because this could help to explain the natural distribution and origin of domestication of the species (Schultes 1984; Cuatrecasas 1964). One hypothesis proposes that wild populations of *T. cacao* existed exclusively in South America. If humans introduced *T. cacao* (Criollo) to Mesoamerica from the upper Amazon basin, then no wild cacaos could exist in Mesoamerica (Cheesman 1944; Schultes 1984). Evidence supporting this hypothesis includes the high diversity of cacao found in the Amazon basin.

An alternative hypothesis proposes a wide natural geographic distribution of the species from the Amazon basin to southern Mexico, with the two recognized subspecies produced by differentiation in the wild. From this perspective, independent domestication from these subspecies took place to produce the two main cultivars, Criollo and Forastero (Cuatrecasas 1964). Evidence supporting this hypothesis includes the description of Miranda (Cuatrecasas 1964 page 514) of presumptively wild cacao from *T. cacao* ssp.

cacao f. *lacandonense* in the Lacandon forest of Chiapas. Specimens were described as having a stem that is half vine, about 7 m tall, with very long branches and ovoid-oblong fruits that were acute and ten-furrowed.

This hypothesis is also supported by Whitkus et al. (1998), who point out that the significant genetic differentiation between Chiapas populations and commercial 'Criollo' cultivars, coupled with Chiapas occurrence in the native rain forest without evidence of cultivation or management, suggests that Chiapas populations may represent wild cacao. In our recent research, four populations of *T. cacao* were found that need some attention in this regard. Two populations were sampled in the state of Chiapas in the Lacandon forest; the other two were on the border of Mexico (Campeche–Quintana Roo) and Guatemala, within the limits of the Reserva de la Biosfera Calakmul.

In the Lacandon forest, 11 individuals were found in the forest or along water streams. Most of them were scattered and solitary, with the exception of two groups of two individuals in an area of approximately 4 ha. In another locality in the same area, a cluster of five individuals was found in an area of approximately 1 ha. In this locality, individuals were found around 50 m away from one another.

In the Reserva de la Biosfera Calakmul, two populations were sampled from two separated ravines about 50 kilometers (km) apart. One population consisted of four individuals; the other population contained twelve individuals. Isolated clusters of individuals were found with no other individuals within 5 ha. In general, individuals collected were tall (e.g., 7–13 m in height), with few or no fruits.

It was not concluded whether these populations are wild. They show a very similar pattern with those described by Allen (1988) as wild from Ecuador, similar in terms of distribution and density of individuals, and similar in the small number of fruits produced per tree per year. In Ecuador, for example, although the density of individuals varies widely, it is always low. In some areas, a day's exploration of the forest yields only one or two trees, while other sites are found with 5 to 10 individuals/ha. In an area of approximately 12 ha., 56 trees were located. In summary, the observed density by Allen (1988) of 4.7 trees/ha is similar to that at other sites in Ecuador where wild cocoa has been found. The number of fruits reported by Allen (1988) is between one and three pods a year. In study samples, individuals usually had one or no pods during two consecutive years. These findings agree with the hypothesis of Cuatrecasas (1964), who supported a wide natural distribution of the species.

**THE CULTIVATION OF T. CACAO
IN SOUTH AMERICA**

The history of cacao in South America has been surrounded by a series of statements and interpretations leading to the idea that South American Indians did not cultivate cacao, or use it as in Mesoamerica, and that the Spanish were the responsible for bringing cacao cultivation to this part of the continent.

One of the main sources for this interpretation comes from an absence of evidence, as well as a biased narrative in the accounts from Mesoamerica. For example, historical accounts on the occurrence, distribution, cultivation, and use of cacao during the early arrival of the Spanish are characterized by a disproportionate interest in this plant. As cacao was an entirely new product for the Spanish, the first accounts were very detailed and included greatly exaggerated properties. However, after some time, cacao occupied a less important place in the chronicles; travelers' accounts and related information became meager and dispersed, especially as travelers reached places in Central and South America (Erneholm 1948).

Perhaps one of the most influential statements based on an absence of evidence comes from Humboldt, who wrote:

No hemos hallado tribu alguna del Orinoco que prepare la bebida con la semilla del cacao. Los salvajes chupan la pulpa de la mazorca, y desechan la semilla, las cuales se encuentran amontonadas allí donde han vivaqueado. Aunque hacia la costa miran el Chorote, que es un infusión de cacao en extremo delgada, como muy antigua bebida, ningún hecho histórico prueba que los indígeneas de Venezuela hayan conocido el chocolate, o una preparación cualquiera de cacao, antes de la llegada de los españoles. Más probable me parece que las plantaciones de cacao de Caracas se fundaron a imitación de las de México y Guatemala, y que los españoles que habitaban tierra firme aprendieron el cultivo del cacao, abrigandolo cuando tierno con la sombra de la Erythrina y el bananero, tanto como la fabricación de tabletas de chocolate y el uso del brevaje del mismo nombre, debido a sus comunicaciones con México, Guatemala y Nicaragua, tres países cuyos habitantes eran de origen tolteca y azteca. (Humbolt [1800] 1941, III:XVI: 170-171).

[We haven't found any tribe in the Orinoco preparing any drink out of cacao seeds. The savages suck the flesh of the pod and throw away the seeds, which remain in clusters where they were eating. Although towards the coast they have the Chorote, which is a very weak cacao infusion, as well as old drink, there is no historical evidence that Venezuelan Indians knew the Chocolate or any other drink prepared

with cacao before the Spanish arrival. It is more probable that cacao plantations in Caracas were founded as an imitation from Mexico and Guatemala, where mainland Spanish learn how to cultivate cacao, nursed in the shade of Erythrina and Banana, as well as the confection of Chocolate tablets and used as a drink due to their communications with Mexico, Guatemala and Nicaragua, three countries of Toltec and Aztec origin.]

This statement, along with the fact that most accounts for South America did not say specifically that cacao was cultivated, led recent historians to conclude that cacao was not cultivated before the Spanish arrival (see Bergmann 1969). These conclusions were also reinforced by erroneous information on cacao cultivation in South America. For example, Prescott (1843) stated that the men of Pizarro's 1526–1527 expedition along the Ecuadorian coast encountered plantations of cacao. However, when Bergmann (1969) revised Prescott's sources, he did not find any information on cacao from where Prescott apparently based his statements.

Further writings took for granted that cacao was not cultivated in South America in pre-Hispanic times. For example, Stone (1984:124) states that "cacao was never cultivated in its native habitat before the arrival of the Spaniards" without providing any evidence for her statement. Other sources not only take for granted that cacao was not cultivated in South America, but also even propose routes and possible actors (such as Spanish missionaries or settlers) as responsible for bringing cacao and starting its cultivation in South America (Young 1994; Coe and Coe 1996).

However, to paraphrase the astronomer Carl Sagan (1977), sometimes the absence of evidence is not evidence for absence. In this sense, an analysis and interpretation of several different factors (anthropological, biology of cacao, cultivation methods, uses of cacao by South American Indians, and old accounts) not considered before can provide a different view about the cultivation of cacao in South America.

The first European contact with cacao dates from 1502 during Columbus' fourth voyage (Las Casas [1528] 1951). However, the main information in regard to the distribution, cultivation, and use of cacao comes from the letters of Cortés (1519) to Charles V, as well as from Díaz del Castillo in his *Historia Verdadera de la conquista de la Nueva España* ([1632] 1955). There is no reliable information as to when Europeans started to get acquainted with the use of chocolate, although there is a general agreement that chocolate became acclimatized in the Spanish court during the first half of the seventeenth century.

According to Coe and Coe (1996), the first formal arrival of cacao to Spain might have taken place either at the end of 1528 when Cortés presented himself at the court of Charles V, or in 1544 when Dominican friars took a

delegation of Maya nobles to visit Prince Philip in Spain. Nevertheless, Coe and Coe (1996) also point out that, by the mid-sixteenth century, there was already a constant exchange of goods between Spain and America. In any case, the first official shipment of cacao reached Sevilla in 1585 from Veracruz (Coe and Coe 1996). It is also by this time that the demand for cacao doubled—due to the exigencies of the Mexican (Creole Spaniards) and European market, and despite near extinction of hand labor in the major areas of production in Mesoamerica.

It has been calculated that the Indian population in 1519 was about 4.5 million people (Aguirre-Beltrán 1989). However, epidemic diseases such as smallpox in 1520, measles in 1529, typhus in 1545 and 1576, along with bad treatment from Spanish conquistadors, reduced the Indian population to 1,336,860 living Indians in Mesoamerica at the end of the sixteenth century (Aguirre-Beltrán 1989). In areas of cacao production, Millon (1955) states that in the 50 years following the arrival of the Spanish, the population in the Soconusco had been reduced by 85%. In this regard, according to Coe and Coe (1996), Díaz del Castillo pointed out: “the whole province (Soconusco) was a garden of Cacao trees and was very pleasant, and now in 1578 it is so desolate and abandoned that there are no more than twelve hundred inhabitants in it.”

Another important issue is that by the last quarter of the sixteenth century, cacao production in Mesoamerica was not geared to large-scale production for the market. Instead, most of the cacao produced seems to have been locally consumed. Mesoamerican annual production in pre-Hispanic times has been estimated to be no more than 1,350 tons (Millon 1955). This suggests that nowhere in ancient Mesoamerica did cacao form the basis of a one-crop economy.

Even in modern times, it has been shown that small-scale cacao production forms the backbone of the worldwide industry. In general, small-to medium-sized farms (1–5 ha.) are both more productive in pods per ha and more efficient in pods per dollar input than larger corporate holdings (Ruf, Yoddang, and Ardhy 1995). An important aspect frequently overlooked is that cacao requires special care in order to achieve good production. In the words of Rice and Greenberg (2000:170), “Smaller farmers are positioned to have an intimate knowledge of their plots. This knowledge and careful tending is ideal for a crop like cacao, a crop often characterized by small plots of 1,000 to 3,000 trees”.

Taking into consideration the background knowledge necessary to cultivate cacao, this means that by 1585 (the time of the first official shipment to Spain), the few Indian survivors either were trying to take care of extensive areas of cacao, or training the Spanish how to cultivate it! Some evidence supporting the first assumption comes from Coe and Coe (1996), who cite a report from 1549 where it was claimed that because there were no

encomenderos [former conquistadores] left in the Soconusco, the Indians had Negro servants and pieces of silver plat, and rode horseback to cope with the cacao production. There is no evidence, however, for the second assumption because the main attraction for the Spanish was not crop cultivation, but precious metals such as gold and silver.

The possible influence that African slaves could have had on the production of cacao at that time does not seem to be very important, especially in main cacao areas such as Tabasco or Soconusco (see fig. 1). According to Aguirre-Beltrán (1989), from a total of 20,569 Africans in 1570, most of them (10,569 individuals) were located in Mexico City. Slightly more than 2,000 people escaped slavery. The rest were slaves located in Tlaxcala (2,958 individuals), Oaxaca (481 individuals), Michoacán (1,765 individuals), Nueva Galicia (2,375 individuals), Yucatán (265 individuals), and Chiapas (130 individuals). How, then, did the Spanish manage to supply the growing cacao market in Mexico and Europe during the last 25 years of the sixteenth century and the beginning of the seventeenth century?

Coe and Coe (1996) state that as Mesoamerican production fell and prices rose in the market, producers rushed to supply the growing demand. They also state that the supply came from plantation owners from Ecuador and Venezuela, where extensive forests of wild cacao came under cultivation merely by clearing the forest around the cacao trees. This hypothesis is untenable, however, because wild cacao grows in very small numbers within the forest. As mentioned before, Allen's (1988) census on wild cacao trees from Ecuador gave a density of about 4.7 trees/ha., and our experience on wild cacao in southern Mexico produced similar results. This information suggests that it was improbable to find natural "forests of cacao" unless cacao was already cultivated before the arrival of the Spanish.

In the case of Ecuador, evidence for cacao cultivation in pre-Hispanic times fails because, according to Bergmann (1969), Prescott's sources do not demonstrate that Pizarro's 1526–1527 expedition found cacao plantations in Bahia de Mateus (in the present-day province of Esmeraldas). It is unknown if Prescott invented this story, or misplaced his source references to support his accounts; however, it is interesting to note that by the mid-eighteenth century, Ulloa ([1748] 1978) makes a full description of cacao plantations from the same area.

The idea for cacao cultivation in pre-Hispanic times in Venezuela is better supported. According to Ernehalm (1948), Venezuela—more specifically, the Maracaibo basin—was the area that first appeared as an exporter of cacao and the first leading cacao export district of the whole continent, a position it retained until the end of the seventeenth century. Ernehalm (1948) also states that export on a small scale seems to have begun in this area by the end of the sixteenth century—that is, more or less by the

same time that Mesoamerican production fell, and the demand for cacao increased.

In the earlier period of colonization, Spain paid little attention to Venezuela because of its lack of precious metals. By the middle of the sixteenth century, the Spanish in South America were still colonizing new areas, fighting against Indians, and even among themselves (Zamora [1701] 1930). In 1558, a settlement close to the Maracaibo basin was founded by Juan Rodríguez Suarez and named Mérida. A year later, his rival, Juan Maldonado, relocated the Spanish settlement to the modern-day city of Mérida, keeping the same name. It is from this settlement, in 1570, that Juan López de Velasco mentions an abundance of cacao, probably cultivated. In his accounts of the city of Mérida, López de Velasco states:

Pobló esta ciudad Juan Rodríguez Suárez, vecino de Pamplona por el año 60, que habiendo salido á descubrir minas llegó á esta provincia, por haber hallado en ella gente vestida como en el Nuevo Reyno; muy abundante de todo género de comida y cacao como en la Nueva España y muchas minas de oro. (López de Velasco [1894] 1971: 187)

[Juan Rodríguez Suárez founded this city, he lived in the Pamplona's neighborhoods around the 60's, and reached this province looking for mines where he found people dressed in the same way as in the New Kingdom, very abundant in every kind of food and cacao the same way as in the New Spain and many gold mines.]

An important point, besides mentioning cacao, is that the area was already populated. In this regard, according to Febres-Cordero (1920), many different Indian groups populated the area before the arrival of the Spanish. The main groups around Mérida were Mucuñoes, Mucubaches, Mirripuyes, Miguríes, Aricaguas, Judigues, Mucutuyes, Timotes, and Canaguaes, among others.

How did the Spanish manage to cultivate cacao in this region in order to supply the cacao market? There are three hypotheses: (1) The Spanish brought Mesoamerican Indians to train South American Indians in cultivate cacao; (2) the Spanish knew how to cultivate cacao, and then trained South Americans how to do it; and (3) the Spanish found the area already cultivated with cacao, and they started to exploit it as if cacao plantations were metal mines. The first and second hypotheses are untenable because there were not enough Mesoamerican Indians to take care of the existing plantations, and the Spanish were looking for an easy way to get rich. The third hypothesis, however, can be supported with López de Velasco's account. For example, when he states that Mérida was abundant in every kind of food and cacao as in Nueva España, the most probable explanation is that cacao was also cultivated as in

Nueva España. In this sense, it is possible that once the Spanish realized there were not enough metals in the area, they started to exploit the Indian's cacao plantations as they did in Mesoamerica.

Additional strong evidence can be found in *Noticias historiales de las conquistas de Tierra Firme en las Indias Occidentales* (Simon [1627] 1882). The work as known consists of three parts, each containing seven noticias; Acosta (1848) mentions a fourth part as lost. Only the first part was printed in 1627; the second and third parts were published almost two centuries later. The first part relates to Venezuela and the "El Dorado" expedition of Ursua and Aguirre. The second part describes the discoveries on the Magdalena River, starting from Santa Marta and the Maracaibo basin; the third part gives an account of the conquests of Carthagena, Popayán, Antioquia, and Chocó.

In the fifth noticia of the first part, Fr. Simón describes the Cuica Indians (originally from Trujillo and neighbors of the Timotes of Mérida):

Hay muchos jeques y hechiceros que hablan con el diablo, á quienes les manda le ofrezcan quemado en braserillos de tierra las brasas del cacao; para lo cual lo muelen y cuecen (que los españoles llaman chorote) y dejandole enfriar se cuaja encima la manteca, muy blanca, la cual cogen y le ofrecen como se lo mandan, por ser la cosa mejor que tienen los indios . . . (Simón [1627] 1882, Chapter XXIV:406)

[There are many sorcerers who talk with the devil, who request from them cacao burned in clay pots. To do this they grind and boil cacao (the Spanish call it Chorote) and once cooled a whitish butter on the top is collected and offered because this is the best thing the Indians have.]

In the fourth noticia of the second part, Fr. Simón writes about the Antioquia Indians. In this next extract, he compares their drinks with those of the Indians from Mérida and Trujillo:

La bebida destas gentes y de las demás provincias sola es la que hacen del maíz que llaman chicha o mazato, porque la del cacao o chocolate que se hace desta fruta no la han alcanzado como los indios de la Gobernación de Mérida y Trujillo, que la bebían y beben mejor que la chicha, por ser sus tierras tan fértiles desta fruta del cacao, de quien han tomado el beberlo los españoles con tanta frecuencia como en Nueva España, que es la que el mundo sabe, aunque con diferencia porque en la ciudad de Trujillo y casi entrada la Gobernación de Caracas y Mérida hasta la ciudad de Pamplona, lo beben hecho chorote que lo es los granos del cacao molidos y hechos masa, sin ningunas especias, de la cual echan la que quieren en un vaso pequeño

de barro y a fuego manso, con poca agua, va cociendo y subiendo el graso arriba, (que es como manteca), de la cual sacan si es mucha, y después de cocido le echan el agua caliente que basta y las especias y azúcar o miel y así lo beben, nadando la manteca encima, en lo que se diferencia del chocolate a quien antes que se cueza en masa echan las especias y al cocer el azúcar y no echa aquel graso encima. Otros le mezclan harina de maíz y otra frutilla que llaman achiote y otros que hay que llaman pinole y atole. Dicen algunos que bebido en día de ayuno no lo quebranta si es raro y no espeso, como lo siente en su Suma el Padre Luis López, aunque yo tendría por más seguro no beberlo en tales días si no es a la comida, para salir de escrúpulos, pues se bebe más por vicio que necesidad y es cierto que hace mayores daños que provechos hablando por lo general. (Simón [1891] 1953, Chapter VI: 304).

[The drink of this people as well as the rest of this province is made with corn and is called Chicha or Mazato. The drink made out of cacao or chocolate fruit has not reached here as with those Indians from the Gobernación of Mérida and Trujillo, which was drunk and still drink better than Chicha, because these lands are very fertile of cacao fruits, from where Spanish started to drink as in the Nueva España which is the one known around the world with the difference that in the city of Trujillo and the entrance to the Gobernación of Caracas, Mérida and the city of Pamplona is drunk as Chorote, which is made out of ground cacao converted into a paste with no spices, from which they put an amount into a small clay vase and heat slowly with little water and when is getting cook the butter goes up, which they take out some if it is too much, and once is cooked they put hot water some species, sugar or honey and they drink it as it is, with butter swimming or the top, which is different from chocolate because you put spices before the paste is cooked and then doesn't produce butter on the top. Other people mixed it with flour and a small fruit called achiote and some others called pinole and atole. Some people say that it is ok to be drunk during fast if it is not frequent and weak, as pointed out by father Luis López, although I would rather not drink it during such days unless it is at lunch, since it is drunk as a vice other than for necessity and it is true that is more harmful than healthy in general terms.]

The next piece of evidence comes from Alonso de Zamora (1635–1717), in his *Historia de la provincia de San Antonino del Nuevo Reino de Granada* (Zamora [1701] 1930). In chapter XVIII (“Fundaciones de los conventos de la Villa de Tolú, y ciudades de Mérida, y Muso; y de la muerte del Obispo D.

Fray Juan de los Barrios”), he refers two times to cacao. The first mention is in relation to the rivalry between Juan Rodríguez Suarez and Juan Maldonado, and the consequent division of the settlement into two antagonistic groups, which impeded the development of Mérida in spite of its abundance of cacao, tobacco, and cotton. Zamora states:

. . . Pero como se fundó con vandos, y parcialidades uno con nombre de Serradas, en favor del Capitan Maldonado; otra en el del Capitan Suarez con nombre de Gavirias, tan obstinadas que con malos sucessos, y muertes lastimosas de ambas partes, y consumidas sus haziendas en pleytos, se atrassó el crecimiento, á que pudiera aver llegado la Ciudad, y nuestro Convento por la abundancia que ay en aquella Governación de cacao, tabaco, y algodon. (Zamora [1701] 1930, Chapter XVIII, 250–251)

[. . . Since the city was founded with two antagonistic factions, one named Serradas, favoring Capitan Maldonado and the other named Gavirias in favor of Capital Suarez, there were bad events, pitiful deaths in both sides, and Haciendas were consumed in endless fights delaying the growth the city and our convent could have had because this Gobernación is abundant in cacao, tobacco, and cotton.]

In the second reference, Zamora describes with more detail the pre-Hispanic use of cacao among Indians of this area. He states:

Lo mas memorable de esta Governación es aver participado de ella este Reyno el uso del chocolate, bebida, que usaban los Indios desde su antigüedad, como tambien los Mexicanos. Tostaban los granos del cacao, y molido, le sacaban al fuego la grassa, que llaman oy manteca de cacao, de qualidad frigidissima: era de tanta estimación, que con ella daban sahumero á sus Idolos. Bolvian á moler lo que restaba en la vasija, y era su regalada bebida con nombre de chorote. Quando entraron los Españoles, lo empezaron á componer con algun dulce. Despues lo fueron sublimando, hasta llegar al punto tan sazonado, que tiene oy en todo el mundo le celebrada bebida del chocolate. Su estimación aumenta los caudales de aquella Governación, por ser toda ella fertilissima, y llena de plantaciones de cacao, como tambien del tabaco celebrado de Varinas; y de ambos generos ay continuos tratos con las embarcaciones de Europa, y Nueva España, que vienen todos los años á la laguna de Maracaybo, termino de esta Governación. (Zamora [1701] 1930, Chapter XVIII, 252–253)

[The most memorable of this gobernación is being participant in the use of chocolate, a drink, Indians used since ancient times, as well as

Mexicans. They roasted the cacao seeds, and once ground, they extracted the butter under the fire, today called *Manteca de cacao*, frigid in quality; It was such the estimation that Indians burned to their idols. They used to grind the leftovers in a vase and became the drink called *Chorote*. When Spanish arrived, they sweetened. Later on they sublimated to reach the chocolate taste known all over the world. Its estimation increases the income in that *Gobernación*, because it is so fertile and full of cacao plantations as well as the celebrated tobacco from *Varinas*; There are continuous treats for both products with ships from Europe and *Nueva España*, and every year they come to the *Maracaibo lagoon*, the limit of this *Gobernación*.]

More recently, *Febres-Cordero* (1927) mentions that cacao was known in the area with the names of *Chiré* (*Mirrupú* dialect) and *Spiti* (*Mucuhí* dialect).

Based on the previous historical accounts, we can conclude that (1) the *Maracaibo basin* was already populated by the time of the Spanish arrival; and 2) by that same time, cacao was very abundant in this area. The way Indians prepared cacao to extract butter (used in their rituals), as well as the way they used it as a drink, suggest they already knew this plant very well before the Spanish arrival.

The biology of cacao makes it improbable that, at the time of the Spanish arrival, there were forests of cacao unless there was a previous human intervention because, as mentioned before, cacao grows at low densities in the wild (*Allen* 1988; this work). It is improbable that, only after the mid–sixteenth century, Indians from the *Maracaibo basin* learned from the Spanish how to cultivate a plant surrounding them since ancestral times, while at the same time they already knew how to cultivate other plants in the area. It is also unlikely that the ethnobotanical knowledge around this plant—involving naming, rituals, and use as drink—was developed by the Indians of the *Maracaibo basin* only after the arrival of the Spanish.

As the previous accounts make clear, the cacao drink was known along the *Maracaibo basin* as *chorote*. *Febres-Cordero* (1927) proposed that the Spanish coined this word to name the cacao drink in this area. Apparently the word was taken from a kind of vase used by the Indians to boil the cacao seeds (previously ground) that they used to extract cacao butter. In these vases, Indians offered cacao butter to their idols. To support this idea, *Febres-Cordero* makes reference to a publication written by *Zerda* (1882, 253–257) in which he describes seven gold statuettes, 17 cm tall, found in a cavern where Indians used to perform their rituals. Each statuette represented a different god (war, drinking, fishing, dance, music, agriculture and arts). One of them, the goddess of drinking, is represented by a seated woman, holding in each hand a vase similar to those vases made out of clay (*chorotes*) in which Indians drank *chicha*, a fermented drink of maize (*Figure 23.2*).

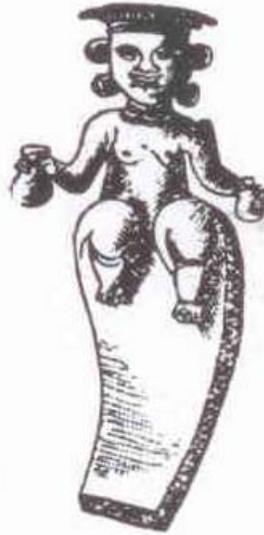


FIGURE 23.2. One of the seven gold statuettes found by Liborio Zerda (1882) in a cavern where Indians used to perform rituals. This statuette is 17 cm tall and shows the goddess of drinking, holding in each hand a *chorote* (vase)-a word coined by the Spanish to name the cacao drink in South America. (Source: Zerda 1882:256.)

Finally, it is interesting to point out the remarkable similarity in the way the different inhabitants of Mérida, Trujillo, and the Maracaibo basin prepared the *chorote* with the way the Indians of Nicaragua made chocolate. For a comparison, compare the previous accounts of Simón and Zamora with the following extract from Fernández de Oviedo, who refers to the way in which chocolate was made in Nicaragua.

...Tostadas las almendras, móndanlas de aquella cáscara delgada, é muéleelas dos ó tres veces sin gota de agua alguna: antes de su propia humedad está asaz líquida la pasta, é en tanto que se muele, ponen a un fuego dulce y lento una ollica que quepa una acumbre de agua, poco mas o menos, é hinchén de buena agua limpia la olla hasta las dos partes: é despueés que ha hervido un poco despacio, echan el cacao en ella (questá molido como es dicho), é con una caña delgada ó un palito muy limpio menéanlo al rededor, hasta tanto que levantando el palillo o caña, una é dos é más veces, se vé questá cocido después que ha hervido bien; é vésse que está cocido en que en el palillo o caña no queda nada pegado del cacao, que sale limpio, é todo está líquido é cocido é corre, como agua. Fecho aquesto, dan con la caña en medio de la masa ú olla, para abaxo, golpes pasico, como para que se abra: é por allí sale arriba luego el acyte, é con una cuchareta sotilmente cójese poco a poco, guardando que no coja el cacao con el

aceyte, poque el aceyte es la flor é virtud principal, é lo que ya queda del cacao es accessorio, é de menos valor. E assí aquello que se coje con la cuchara, se pone aparte. Después que desta forma que he dicho se ha sacado lo mas que ha seydo possible, lançcan en una higüera, que está aparte fuera del fuego con agua limpia, el dicho cacao, despues de sacado dél aceyte, la mitad ó el tercio ó quarta parte del cacao, é en otra é otras higüeras lo demás; é revuélvenlo, e luego se sube sobre el agua el aceyte que quedó, que no se pudo sacar con la cuchara, é aquello bebido, assí fecho aquel caldo, es excelente é saníssimo. (Fernández de Oviedo [1851] 1959, Book 8th, Chapter XXX, 272)

[. . . the roasted seeds are peel out and ground without water to get a paste, in the meantime a vase with two parts of water is heated slowly. Once the water is hot the paste is added and stirred with a thin stick until no cacao butter is stuck to it. Afterwards hit the bottom of the vase to release the drink the oil towards the top and collect it carefully with a spoon to avoid mixing the oil with cacao, because the oil is the flower and principal virtue and the remains are of less value. Then the oil collected with the spoon is putted apart. Once the oil was collected a half or a third or a fourth part of cacao is served in another vase and stirred until more oil goes up and then this soup is drunk which is excellent and healthy.]

CONCLUSION

Mesoamerica holds three different species of *Theobroma* out of 22 species described for the Neotropics: *T. cacao* L.; *T. angustifolium* Mociño & Sessé; and *T. bicolor* Humb. & Bonpl. The use of *T. cacao* and *T. bicolor* has been described in this paper. *T. angustifolium* Mociño and Sessé has been reported as an alternative source of chocolate (Standley 1923), and has also been reported as used for medicinal purposes (Emmart 1940). Cuatrecasas (1964) mentions that this species is cultivated in Central America and Southern Mexico; however, at least in the southern part of Mexico, a specimen of this species has not been collected or observed.

Although the diversity of *T. cacao* seems high in Mesoamerica, this has not yet been thoroughly evaluated (De la Cruz et al. 1995; Whitkus et al. 1998; this work). This diversity should be found in places documented as pre-Hispanic areas. Although an introduction of Forasteros from South America at the beginning of the 1930s has been documented, it is probable that the presence of Forasteros dates from 1,500 years ago, when they were introduced from Ecuador by the Valdivia culture. This possibility, however, still needs to be documented.

The historical accounts found for South America question the common and widespread idea that the Spanish were responsible for bringing the cultivation of cacao to South America. In this sense, the common idea that *T. cacao* ssp. *cacao* was originally domesticated in Mesoamerica, brought to South America, and later hybridized with *T. cacao* ssp. *sphaerocarpum* needs to be retold. That is, Trinitarios are the result of the hybridization of *T. cacao* ssp. *cacao* from Venezuela and not from Mesoamerica as has been demonstrated several times (Young 1994). Molecular evidence provided by De la Cruz et al. (see also Whitkus et al. 1998) support this idea.

Our evidence suggests that as the Spanish were invading new areas, they kept exploiting Indians' labor, as well as valuable crops such as cacao, until the depletion of either the Indians or their crops. If Venezuela became the first leading area of cacao export by the end of sixteenth century, as pointed out by Ernehlm (1948), it was because cacao was already planted. Taking into account that cacao plantations are more successful on a smaller scale (Rice and Greenberg 2000), following the patterns described by Millon (1955) for Mesoamerica, the accounts of Simón ([1891] 1953), and Zamora ([1701] 1930), it seems probable that cacao was cultivated on a small scale all along the Orinoco basin. As cacao in the wild grows in small densities, it is improbable that the "cacao mountains" (Coe and Coe 1996) found by the Spanish when they reached South America were wild, but rather cultivated populations.

The use of cacao butter in rituals, as a drink, as names given by several cultures (Febres-Cordero 1920, 1927), and the beginning of exportation after the Spanish arrival are strong evidence to sustain a pre-Hispanic cultivation and ancient knowledge of cacao by cultures of the Maracaibo basin. This evidence, coupled with similarities in the way chorote and chocolate are prepared between people from the Orinoco basin and Nicaragua, suggests a South American origin of cacao domestication, with later development and transformation in Mesoamerica.

When the Mesoamerican Indian population was depleted, only some areas such as Tabasco and Soconusco continued producing cacao. Other important cacao-producing areas, such as Valle Nacional in Oaxaca (Millon 1955) or Cihuatlan in Guerrero (King 1971), were left aside. According to our research, pre-Hispanic cacao remnants still can be found in these areas—spread either in backyards, or among recent crops such as coffee, banana, or orange. In many of these areas there is no evidence for a recent introduction of these plants, nor are there programs to promote the cultivation of cacao; this suggests that the chocolate once drunk by the Maya, Mexicas, and Charles V has hardly been tasted since the sixteenth century.

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Chapter 24

The Domestication of Henequen (*Agave fourcroydes* Lem.)

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INTRODUCTION

Henequen (*Agave fourcroydes* Lem.) is a cultivar of the Agavaceae family that has been cultivated for its fiber in the Maya area since pre-Hispanic times. Henequen is a different species from sisal (*A. sisalana* Perrine), even though the fiber of both plants is named “sisal hemp” in English. Sisal is also a Mexican cultivar, probably originating in the state of Chiapas (Gentry 1982). Sisal is presently cultivated in Africa and Brazil, while henequen originated in the Yucatán Peninsula and, at present, is cultivated only in Mexico and Cuba. The main morphological difference between both species is that sisal lacks lateral spines in its leaves (teeth), while henequen has a coarser fiber than sisal.

The evolutionary history and diversity of this crop before the arrival of the Spanish is not known, but several illustrations in the Dresden and Tro-Cortesian codices (presumably made in the thirteenth and fifteenth centuries, respectively) indicate the social importance that fiber production had for the lowland ancient Maya. Irigoyen (1950) reproduced some of these illustrations from the codices, which show several human figures hunting, fishing, or carrying bags for trade, while using cordage or nets that the author asserts were made from Agave fibers. In addition, Irigoyen (1950) included an illustration of the “God F” where the God is holding what is probably a bundle of Agave fibers.

What we do know for certain is that at the moment of the Maya-Spanish contact, henequen was already a domesticated plant. In his work *Relación de las Cosas de Yucatán*, Fray Diego de Landa said that “henequen was cultivated in house-gardens, and it was of much better quality than the wild” (de Landa [1566] 1978:128).

But what is the wild ancestor of henequen? According to Gentry's (1982) classification of the *Agaves* of North America, all the wild *Agave* populations in the Yucatán Peninsula belong to *A. angustifolia* Haworth. This is the species most widely distributed of the genus. It is found from Costa Rica, on both Atlantic and Pacific coasts, to Tamaulipas and northwestern Sonora in Mexico. The major vegetation formations in which it occurs are tropical savannah, thorn forest, and deciduous tropical forest, at heights from sea level to 1,500 meters (or sometimes higher). *Agave angustifolia* is an extensive variable species. Gentry (1982) could not separate subspecies populations consistently with any combination of characters; in this species he included 21 synonyms. Gentry considered that variation of this species illustrate that it is a freely-seeding outbreeding complex, which has been widely assorted by circumstances of habitat, changing climates over a long period of time, and human's interventions (Gentry 1982).

According to Gentry (1982), four cultivars selected for fiber seem to have appeared from this gene reservoir: (1) *A. angustifolia* var. *deweyana* (Trel.) Gentry, named "zapupe verde," and grown in Tamaulipas and Veracruz states, Mexico; (2) *A. angustifolia* var. *letonae* (Taylor) Gentry, named "agave letón," and grown in El Salvador and Guatemala; (3) *A. angustifolia* var. *nivea* (Trel.) Gentry, grown in Guatemala; and (4) *A. sisalana* Perrine, "sisal," a possible hybrid between *A. angustifolia* and *A. kewensis*, which may have originated in Chiapas but is grown extensively in Africa and Brazil. To these four cultivars we should add (5) *A. fourcroydes* Lem., named "Henequen," grown in the Yucatán Peninsula, Tamaulipas, and Cuba (Colunga-GarcíaMarín et al. 1999), and (6) the hybrid H-11648 [*A. amaniensis* Trelease & Nowell x *A. angustifolia*) x *A. amaniensis*] (Lock 1962) extensively cultivated in Africa. The distribution of all these fiber cultivars in Mesoamerica coincides with the Maya area.

From this same gene pool, and from outside the Maya area, several cultivars have been selected that were important as a food source in pre-Hispanic times. Today, they are important sources of alcoholic beverages such as "tequila" (*A. tequilana* Weber) and the mezcales, the most famous of which come from the Mexican state of Oaxaca. Gentry (1982) considers that the separation of *A. tequilana* from *A. angustifolia* is only nominal. This multiplicity of cultivars derived from the same gene pool makes *A. angustifolia* a singular case of multiple domestication of a species throughout its geographical distribution. This multiple domestication is probably associated with its use by different human cultures, in contrasting environments, and for different purposes. This domestication pattern is very different from that of other crops of Mexican origin, such as corn and common bean, for which a unique domestication area has been defined.

The results summarized in this chapter are derived from an investigation whose main objective has been to understand the origin, variation, and evolutionary trends of henequen under human selection.

MATERIALS AND METHODS

Three types of evidence were compiled about wild and cultivated populations:

1. *Ethnobotanical evidence*—This evidence consists of the study of past and present man-*Agave* interactions, which were analyzed by ethnohistorical sources and based on ethnobotanical exploration.
2. *Morphological evidence*—This evidence was compiled through the numeric, statistic, and phylogenetic analysis of 66 morphologic characters evaluated in populations grown under both natural and homogeneous conditions. Characters included stem, leaf, inflorescence, flower, fruit, and seed characteristics.
3. *Genetic evidence*—This evidence was obtained through the analysis of three isozymatic systems: Malate Dehydrogenase (MDH), Acid Phosphatase (ACP), and Cathodic Peroxidase (PRX).

(Details of the materials and methods are explained in Colunga-GarcíaMarín & May-Pat 1993; Colunga-GarcíaMarín et al. 1993; Colunga-GarcíaMarín, Estrada-Loera, & May-Pat 1996; Colunga-GarcíaMarín & May-Pat 1997; and Colunga-GarcíaMarín et al. 1999.)

RESULTS AND DISCUSSION

Ethnobotanical evidence

Ethnohistorical analysis indicated the lack of evidence about the diversity of henequen during the pre-Hispanic Maya times, but it is assume to be at least equal to or larger than that recorded in the agronomy manuals published at the beginning of the twentieth century (de Echánove 1814; Regil and Peón 1853; Espinosa 1860; Barba 1895–1896; Bolio 1914). These manuals included seven varieties of henequen as well as the experimental cultivation of wild plants. Analysis of these manuals suggests that, under traditional agriculture, Maya peasants selected varieties for their different type of fiber as well as their adaptability to soil and precipitation conditions.

Our ethnobotanical exploration of the seven varieties revealed that only three of them could now be identified: (1) Sac Ki, or white henequen, the most

abundant variety and the one preferred by the cordage industry; (2) Yaax Ki, or green henequen, with fiber very similar to that of Sac Ki, but of lower yield; and (3) Kitam Ki, or wild boar henequen, with a very soft fiber and low yields. This variety is very scarce. Sac Ki is the variety that corresponds with Gentry's (1982) diagnosis of *A. fourcroydes*; the other two varieties have not been formally described.

Subdeciduous forest wild populations, called Chelem, are collected for their fiber and used for handicrafts. Artisans who use wild plant fibers distinguish three variants within these populations according to fiber quality: Chelem white is the one considered as more similar to cultivated variants, while both Chelem green and Chelem yellow are seen as of lower quality (in that order). Kitam Ki and wild population varieties have fibers that are preferred for textile use when there is a direct contact with the skin, such as in hammock and sandal manufacture (Colunga-GarcíaMarín & May-Pat 1993).

The loss of henequen varieties during the end of the nineteenth century and the beginning of the twentieth century resulted from the establishment of extensive plantations of Sac Ki (white henequen), the variety preferred for the cordage industry, and the elimination of the other existing varieties. The cordage industry was strongly developed in the Yucatán Peninsula as a response to the great demand for binder twine by the wheat harvest in the United States. This great demand was a consequence of the adaptation of binder twine to a harvesting machine for cutting and threshing grain in the field in 1880. The agronomy manuals at the beginning of the twentieth century explicitly encouraged producers to cultivate Sac Ki and to eliminate all other varieties. The loss of henequen varieties was accelerated by the invention in 1895 of the fiber-extracting machine for rasping and cleaning henequen, which imposed very narrow criteria for the length of leaves that could be rasped. This length was specifically that of Sac Ki. Henequen genetic erosion was hastened by the exclusive practice of vegetative propagation, which ensured that only Sac Ki germ plasm could be propagated (Colunga-GarcíaMarín and May-Pat 1993). In this way, the evolutionary trends that were not oriented towards cordage use and adaptation to the rocky soils of the north lowland Maya area were eliminated.

Ethnobotanical research uncovered 41 traditional uses for henequen. These uses comprise all morphological structures and all the anthropocentric-use categories, including food use, which was so important as a domestication incentive in other areas of Mesoamerica. The specialized use of only one product—the fiber—is a result of exclusive exploitation by the cordage industry (Colunga-GarcíaMarín and May-Pat 1993; Colunga-GarcíaMarín et al. 1993).

Morphological evidence

Morphological variation analysis under uniform grown conditions indicated that cordage-cultivated varieties (Sac Ki and Yaax Ki) differ from wild populations in similar direction and magnitude, a trend that may be described by four domestication syndromes (i.e., a combination of characteristics with anthropocentric interest, or related to the process of artificial selection). These syndromes include greater fibrosity, less thorniness, less reproductive capacity, and gigantism.

Greater fibrosity may be illustrated by the linear relationship that exists between the fresh leaf mass and the dry leaf mass. For a given fresh leaf mass, cordage-cultivated plants have 1.9 times more fiber than wild plants. This difference suggests that domestication has changed the physiological resource allocation strategy of wild plants, resulting in a more fiber-rich domesticated plant that can be harvested more efficiently. Something analogous can be observed with the other domestication syndromes. Less thorniness may be evaluated through the relationship between leaf length and the number of teeth. For a given leaf length, cordage-cultivated plants have 1.6 times less teeth than wild plants. In the same way, the diminished reproductive capacity may be illustrated by the linear relationship between the number of ovules and the number of normal seeds. For a given number of ovules, cordage-cultivated plants have 5.3 times less normal seeds than wild plants. Gigantism can be observed specially in the length and width of the leaves. Leaves from the domesticated varieties are 1.34 times larger and 1.85 times wider than those of wild ones (Colunga-GarcíaMarín, Estrada-Loera, and May-Pat 1996; Colunga-GarcíaMarín and May-Pat 1997). These syndromes have an obvious correlation with the cordage industry interests that have guided the process of henequen evolution during the last century.

The textile-cultivated variant Kitam Ki is the one variant that most resembles wild plants. In a cluster analysis using UPGMA (Unweighted Pair-Group Method using Arithmetic averages) as a grouping method, Kitam Ki grouped with wild populations. This variant differs from wild populations in two out of the four domestication syndromes—larger fibrosity (although in a much lesser degree than is observed in cordage variants) and a diminished reproductive capacity. These results suggest a process of artificial selection with an orientation and intensity mainly focused on textile use (Colunga-GarcíaMarín, Estrada-Loera, and May-Pat 1996; Colunga-GarcíaMarín and May-Pat 1997).

With respect to *A. angustifolia* populations, morphological evidence suggests the existence of two ecotypes—one including dunes and deciduous forest populations, and the other corresponding to subdeciduous forest populations. Subdeciduous forest populations have the longest fiber and the

greatest quantity of fiber. Populations from the subdeciduous forest used by artisans for their fiber were grouped in a separate cluster using UPGMA as a grouping method. The artisans' classification of Chelem varieties according to their fiber quality agrees with morphological evidence as long as the variety Chelem white has the longest fibers and the greater quantity of fiber, which exactly matches the artisans' description (Colunga-GarcíaMarín, Estrada-Loera, and May-Pat 1996; Colunga-GarcíaMarín and May-Pat 1997).

Genetic evidence

Phylogenetic analysis using parsimony, based on morphologic and isozymatic data combined, resulted in a single most parsimonious tree (Figure 24.1). Two main lineages were revealed—one for wild populations, and the other for extant henequen varieties used for their fiber. Within this last lineage, two other lineages were evidenced: (1) the lineage of cordage-cultivated plants whose sister group is Chelem white, which is the variety recognized by artisans as the most similar to them; and (2) the lineage of the textile-cultivated variety. The position of the other Chelem varieties in the phylogram suggested their hybrid origin between wild and cultivated varieties.

For all plants studied, the isozyme Malate Dehydrogenase (MDH) had the same electrophenotype, with the exception of the textile-cultivated variant Kitam Ki, which had an electrophenotype also found in four plants from the Mexican states of Veracruz and Oaxaca. On the other hand, the cordage-cultivated variants Sac Ki and Yaax Ki showed identical electrophenotypes to those of several wild plants for the three isozymatic systems. These results support the hypothesis of a Yucatecan origin of Sac Ki and Yaax Ki and the introduction of Kitam Ki from outside of the peninsula. This hypothesis is also supported by ethnobotanical evidence because of the scarce knowledge that people have about Kitam Ki, as compared with Sac Ki or Yaax Ki.

Isozymatic evidence, as a genetic diversity estimator, showed that while the wild variants had relatively high genetic variation, no variation was observed within the three henequen varieties. In *A. angustifolia*, partition of the variation levels indicated that 40% of the variation could be found between populations, and 60% within them. In contrast, all the variation in henequen varieties is found between populations, and none can be found within them. These results are to be expected in a cultivar that is always propagated vegetatively. The extremely small fraction of total isozymatic variation observed within cultivated varieties is, so far as we know, the most dramatic reported for a cultivar.

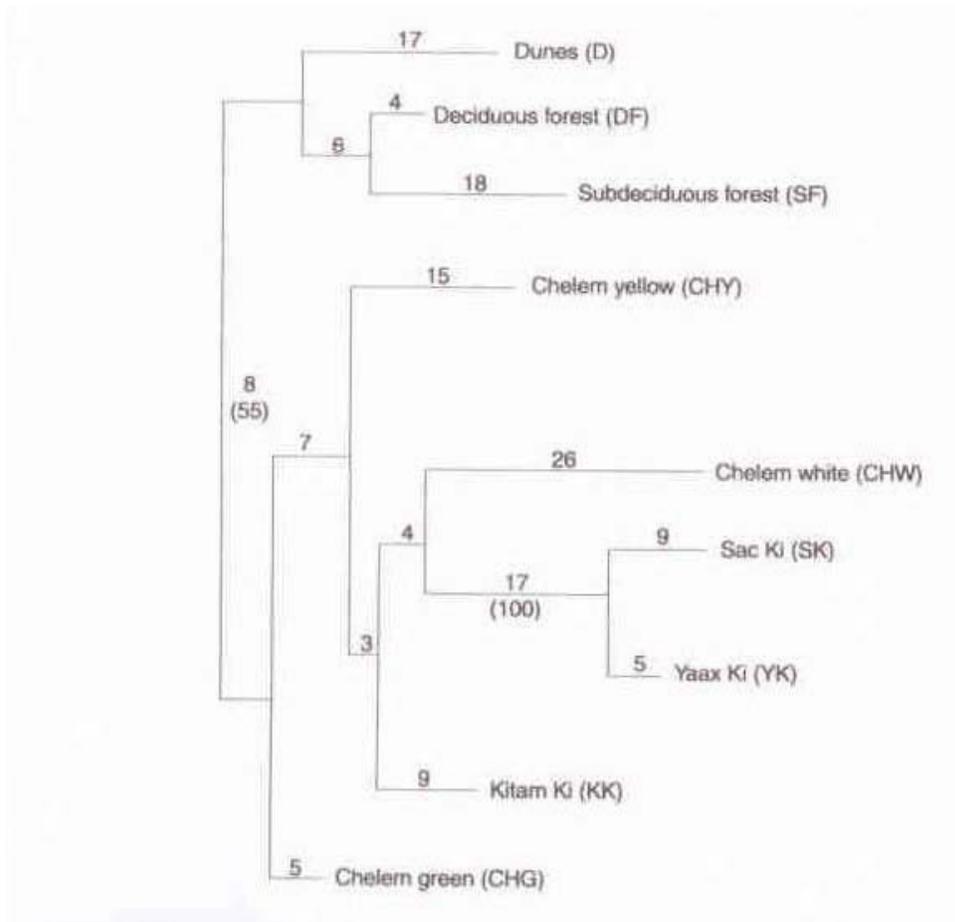


FIGURE 24.1. Phylogenetic relations of extant henequen variants (SK, YK, and KK) and wild *A. angustifolia* populations (D, DF, SF, CHY, CHW, and CHG) from the Yucatan Peninsula, based on 66 morphological characters and 27 isozymatic bands. The single most parsimonious tree derived from an exhaustive search is shown. The tree was rooted using the D, DF, and SF cluster as an outgroup. Consistency index (CI) = 0.799 (CI = 0.712 when noninformative characters were excluded); homoplasy index (HI) = 0.268 (HI = 0.310 when noninformative characters were excluded); retention index (RI) = 0.639. Tree length = 164 steps; length is shown above each branch. Bootstrap values (%) over 50, based on 1,000 replicates, are in parentheses below branches.

Results obtained in this study of the cordage-cultivated varieties Sac Ki and Yaax Ki agree with the predictions of Doebley (1989) in cases of wild-cultivated derivatives when isozymes are analyzed: (1) the cultivar falls within the variation range of the putative wild progenitor, (2) the cultivar has a subset of the allelic diversity found in the wild progenitor, and (3) the genetic variation is distributed in a different way. Cultivated plants have more variation between varieties than within them, while the opposite is true for wild plants.

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Chapter 25

Bioprospection Studies at El Edén: From Plants to Fungi

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INTRODUCTION

In 1997, a project was started to search for bioactive compounds from some of the plant communities at the El Edén Ecological Reserve, which is located in Quintana Roo, Mexico. As part of this project, fungi were isolated and identified from different insects at two plant communities within the reserve according to the work in progress by Torres-Barragán et al. The search for bioactive natural metabolites and potential microbial insecticides is motivated by the problems associated with the extensive use of chemical pesticides. These agrochemicals affect not only pest insects, but also beneficial species. Moreover, insects tend to acquire resistance to synthetic chemicals, which creates new pest problems; the presence of chemical residues also causes environmental hazards and health problems.

Evolved resistance to pesticides in insects has led to an exponential increase in the number of insect species resistant to them; some estimates place this number at more than 500 species (Mackenzie, Ball, and Virdee 1998). For example, the housefly *Musca domestica* has developed resistance to almost every chemical used against it. This problem points to the urgent need for alternatives to chemical pesticides (Mackenzie, Ball, and Virdee 1998).

In nature, mutual interactions among organisms include all direct as well as indirect effects. Some of these biotic interactions are regulated by

secondary metabolites (i.e., infochemicals) that are produced and liberated by living beings. Each organism responds in a different way to infochemicals. The result is a vast communicative interplay, which is fundamental to the fabric of life. Organisms use chemicals to lure their mates, associate with symbionts, deter enemies, and fend off pathogens. Substances that transmit information between organisms are a fundamental part of the regulatory chemicals of nature.

Molecules that have a signal value in nature have sometimes been demonstrated to be useful to humans; the wide variety of medicinals underscores this point. Major recent additions to the therapeutic arsenal include ivermectin, cyclosporin, FK-506, and taxol—all compounds that can be expected to have evolved as signaling agents (Eisner & Meinwald 1995). Many diverse benefits can be expected from an ongoing search for natural products. Through laboratory experimentation, field research, and careful observation, species can be rated by “chemical promise”; this can aid in the important task of selecting species for chemical screening. This enables the assessment of some of the hidden value of nature. Most species remain to be discovered. These unknown species are potentially of immense value and deserving of protection, lest we be forever impoverished by their loss (Eisner and Meinwald 1995).

This project is focused on bioprospection and the search for the aggregated value of biotic resources, mainly from plants and microorganisms. Our aim is not only to assist in the biochemical exploration of dry tropical ecosystems in Mexico, but also to contribute to biodiversity conservation. Biological diversity reflects and underlies molecular diversity. The molecules found in nature may be regarded as solutions to challenges that organisms have confronted and overcome during molecular evolution. As the understanding of these solutions deepens, the efficiency with which new treatments can be discovered and/or designed for human disease and new natural agrochemicals also increases.

Nature assists discovery efforts in a variety of ways. Some compounds synthesized by plants and microorganisms are used directly as drugs, or for control of some pests. As their cultures disappear, the loss of the “shaman’s” knowledge of the ethnobotanical uses of plants has been compared to the burning of the library at Alexandria. But for those of us who are beginning to understand how to read the molecules within living things, the loss of biological diversity itself is also the loss of a library—a library that contains answers to questions we have not yet learned to ask (Caporale 1995).

As part of this same project, a collection of two basic types of fungi is being made: entomopathogenic and plant-associated fungi. Both types of fungi constitute a rich germ plasm source to search for bioactive compounds and to determine their potential use as biocontrol agents in future studies.

EL EDÉN ECOLOGICAL RESERVE

El Edén Ecological Reserve is located in the Yalahau region in the northern portion of Quintana Roo, Mexico. This region contains the main ecosystems of the Yucatán Peninsula and the Caribbean. This zone was occupied by the ancient Maya culture and exhibits more biodiversity than anywhere else in the peninsula. Nowadays, this region also constitutes an important source of water and forest products for the future.

The tropical forests of the northern region of Quintana Roo are mainly dry ecosystems. These types of forests are in serious danger because of the inadequate development models adopted, the drastic changes in land uses, and the demographic growth. Dry tropical forests possess a great variety of species and biotypes and also are rich in endemisms, which make them a natural source to search not only for bioactive natural products, but also for biological insecticides that may hold the key to potential solutions of pest and disease problems (Gómez-Pompa 1998).

STUDIES ON PLANTS

Some plants were selected to evaluate their content of bioactive or allelochemical compounds. Our studies were conducted in four ways:

1. One-square area of 25 m² within each of three plant communities of El Edén (tropical forest, secondary plant community, and savanna) was sampled, and the most abundant and/or conspicuous species were collected.
2. Some species were collected in the permanent marked-out transects in order to make systematic studies on flora, fauna, microorganisms, and soils.
3. Some species were studied because of their known ethnobotanical and medicinal uses that suggested the presence of bioactive compounds.
4. Some endemic species were collected because they are unique, and their importance for biodiversity conservation is very high.

Herbarium samples of each plant are kept at the Herbarium of the University of Yucatán, Mexico.

Biodirected fractionation studies of selected plants were obtained by using seeds, phytopathogenic fungi, and brine shrimp (*Artemia salina*) as test organisms. These studies were performed according to procedures previously described (Anaya 1996; Jiménez-Arellanes et al. 1996; Castañeda et al. 1996;

Anaya and Pelayo-Benavides 1997; Anaya and del Amo 1999). Some of the main results obtained from research are discussed as follows.

Bioassays with seeds

Table 25.1 shows the main results of the bioassays performed to test the effects of aqueous leachates from leaves and fruits of some Fabaceae species on the radicle growth and germination of three test species: (1) amaranth [*Amaranthus hypochondriacus* L. (Amaranthaceae)]; (2) barnyard grass [*Echinochloa crus-galli* (L.) P. Beauv. (Poaceae)]; and (3) tomato [*Lycopersicon esculentum* Mill. (Solanaceae)]. The aqueous leachates of all the Fabaceae species (except *Mucuna* sp. on barnyard grass) significantly inhibited the radicle growth of amaranth, barnyard grass, and tomato. These results suggest the presence of allelochemical compounds in the tested leachates. Radicle growth is more affected by allelochemical stress than germination. In general, tomato was the most sensitive species, as its radicle growth was inhibited by 53 percent to 84 percent by the Fabaceae aqueous leachates. Radicle growth of amaranth was inhibited by 36 percent to 58 percent, while that of barnyard grass was inhibited by 15 percent to 74 percent. Leachates of *Bauhinia jenningsii* P. Wilson, and *Mimosa pudica* L. (leaves and fruits), as well as leaves of *Lonchocarpus* sp. and flowers of *Mucuna* sp., were the most inhibitory on the radicle growth of amaranth. Leaves and flowers of *M. pudica* were the most inhibitory treatments on barnyard grass. *B. jenningsii*, *Mucuna* sp., *Lysiloma latisiliquum* (L.) Benth., and *M. pudica* were the most inhibitory on tomato.

Table 25.2 shows the effects of the aqueous leachates of leaves of other plant species from different families with a high phytotoxicity on the test plants. Once again, the radicle growth was the most affected process by allelochemical stress compared with germination. Radicle growth of amaranth and tomato were strongly inhibited by these treatments. The most active treatments on the radicle growth of the test species were leachates from *Hamelia patens* and *Eupatorium* sp. on amaranth, leachates of *H. patens* and *Lantana camara* on tomato, and that of *Jatropha gaumeri* Greenm. on barnyard grass. Leachates of *H. patens* also inhibited germination of tomato and amaranth by 72.5 percent and 32.5 percent, respectively.

Table 25.3 shows some preliminary results of the biodirected phytochemical fractionation studies of various plants with a strong allelochemical potential. In this study, plants were used as test organisms. The inhibitory effect of organic extracts was less significant compared with that of the aqueous leachates. The most inhibitory treatments on the test plants were chloroform extracts from *Callicarpa acuminata* and *Zuelania guidonia* on amaranth; methanol and hexane extracts from *C. acuminata*, methanol extract from *Thevetia gaumeri*, and chloroform extract from *Jatropha gaumeri*, on

TABLE 25.1. Effects of the aqueous leachates of leaves and fruits of some Fabaceae plants from El Edén on the radicle growth (percent) and germination (percent) of amaranth, barnyard grass, and tomato. Data are representative of four replicates and were analyzed by ANOVA test. Data are percentages compared to a control (100 percent).

TREATMENTS	TEST SEEDS						
	Plant species	Plant part	Amaranth		Barnyard grass		Tomato
			Radicle growth	Germ.	Radicle growth	Germ.	Radicle growth
<i>Bauhinia jenningsii</i>	L	42.9*	97.5	45.1*	80.0	15.8*	80.0
<i>Bauhinia jenningsii</i>	F	41.8*	92.5	64.5*	85.0	23.3*	95.0
<i>Mucuna</i> sp.	L	58.4*	100.0	84.9	85.0	18.5*	82.5
<i>Mucuna</i> sp.	F	48.7*	90.0	54.0*	77.5	26.6*	97.5
<i>Lysiloma latisiliquum</i>	L	51.7*	92.5	38.6*	87.5	22.8*	97.5
<i>Mimosa pudica</i>	L	43.5*	100.0	32.3*	82.5	24.0*	87.5
<i>Mimosa pudica</i>	F	45.1*	92.5	26.3*	82.5	26.9*	90.0
<i>Swartzia cubensis</i>	L	59.1*	97.5	57.8*	80.0	36.5*	95.0
<i>Lonchocarpus rugosus</i>	L	48.7*	95.0	74.0*	87.5	43.0*	97.5
<i>Lonchocarpus violaceus</i>	L	58.3*	100.0	74.0*	95.0	40.7*	95.0
<i>Lonchocarpus</i> sp.	L	42.7*	100.0	45.2*	82.5	47.0*	90.0
<i>Havardia (Pithecellobium) albicans</i>	F	63.7*	95.0	50.2*	77.5	43.6*	90.0

L = leaves; F = fruits; * $p < .05$; Germ. = Germination

TABLE 25.2. Effects of the aqueous leachates of leaves of several plant species from El Edén on the radicle growth (percent) and germination (percent) of amaranth, barnyard grass, and tomato. Data are representative of four replicates and were analyzed by ANOVA test. Data are percentages compared to a control (100 percent).

TREATMENTS	TEST SEEDS					
	Amaranth		Barnyard grass		Tomato	
Plant species	Radicle growth	Germ.	Radicle growth	Germ.	Radicle growth	Germ.
<i>Thevetia gaumeri</i>	31.3*	72.5	65.7*	72.5	27.3*	87.5
<i>Eupatorium</i> sp.	29.2*	90.0	46.6*	75.0	25.7*	80.0
<i>Ipomoea</i> sp.	34.0*	92.5	53.0*	92.5	24.4*	95.0
<i>Jatropha gaumeri</i>	31.3*	100.0	31.4*	72.5	22.3*	97.5
<i>Hampea trilobata</i>	39.2*	97.5	40.0*	85.0	26.3*	97.5
<i>Malva viscus arboreus</i>	40.7*	92.5	43.1*	90.0	20.7*	97.5
<i>Allophylus cominia</i>	48.0*	100.0	54.9*	95.0	41.2*	87.5
<i>Lantana camara</i>	32.4*	77.5	41.9*	95.0	17.8*	80.0
<i>Hamelia patens</i>	23.3*	67.5	56.7*	85.0	12.9*	27.5

*p < .05; Germ. = Germination

barnyard grass; and chloroform and hexane extracts from *C. acuminata* on tomato.

Bioassays with phytopathogenic fungi

Table 25.4 shows some preliminary results of the biodirected phytochemical fractionation studies of El Edén plants with a strong allelochemical potential. In this study, phytopathogenic fungi were used as test organisms. As the data indicate, *Alternaria solani* and *Fusarium oxysporum* were the most resistant fungi to the effects of chloroform-methanol extracts from bioactive plants. The fruits extract of *Pithecellobium albicans*

TABLE 25.3. Effects of the organic extracts of aerial parts of some plant species from El Edén on the radicle growth of amaranth, barnyard grass, and tomato. Data are representative of four replicates and were analyzed by ANOVA test. Radicle growth data are percentages of growth compared to a control (100 percent).

TREATMENTS	TEST SEEDS		
	Amaranth	Barnyard grass	Tomato
Plant species (solvent)	percent of radicle growth		
<i>Acacia sedillense</i> (methanol)	65.2*	68.2*	61*
<i>Callicarpa acuminata</i> (hexane)	62.5*	52.8*	51.5*
<i>Callicarpa acuminata</i> (chloroform)	50*	60*	48*
<i>Callicarpa acuminata</i> (methanol)	57*	50*	85
<i>Jatropha gaumeri</i> (chloroform)	69.7*	59.4*	81.6
<i>Metopium brownie</i> (hexane)	92.6	91.4	68*
<i>Thevetia gaumeri</i> (methanol)	62.6*	56.9*	72.8*
<i>Zanthoxylum caribaeum</i> (methanol)	71.9*	62.4*	69.4*
<i>Zuelania guidonia</i> (hexane)	62*	88.4	81.2
<i>Zuelania guidonia</i> (chloroform)	54.4*	77.3	81.2

* $p < .05$

(Kunth) Benth significantly inhibited (25 percent) the radial growth of *A. solani* at three days of treatment. The roots extract of *Philodendron radiatum* Schott. and the stems extract of *Heliocarpus* sp. significantly inhibited *A. solani* at eight days of treatment (32 percent and 33 percent, respectively). The leaves extract of *Zuelania guidonia* inhibited the radial growth of *F. oxysporum* at three days and eight days by 35.8 percent and 32.8 percent, respectively. The leaves extract of *Croton glabellus* L. inhibited the growth of *F. oxysporum* at eight days by 25 percent. Of all fungi species tested, *Helminthosporium longirostratum* was the most sensitive to the treatments. This fungi was significantly inhibited by all chloroform-methanol extracts, except by that from *P. albicans* at three days of treatment, and *Jatropha gaumeri* leaves at eight days. The treatments that most inhibited the radial growth of *H. longirostratum* at eight days of growth were the leaves extracts of *Lantana camara* L. (66 percent), the roots extracts of *P. radiatum* (64 percent), and the leaves extracts of *Z. guidonia* (58.6 percent).

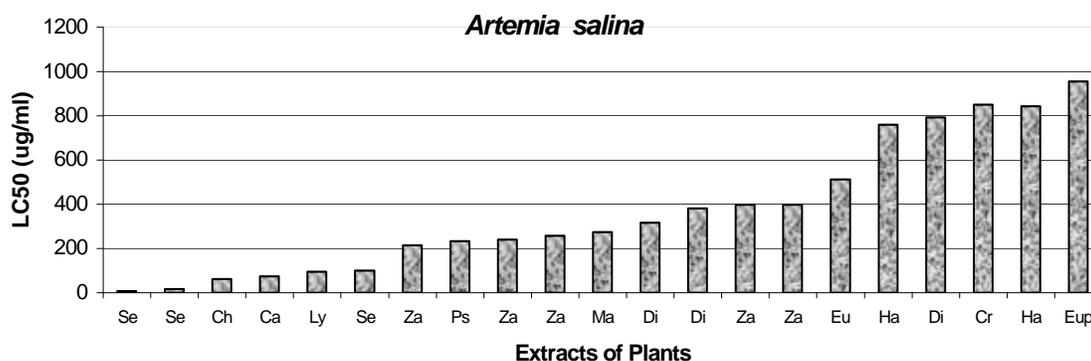
TABLE 25.4. Effects of chloroform (CHCl₃) and methanol (CH₃OH) extracts of some plants from El Edén on the radial growth of three phytopathogenic fungi. Data are percentages of radial growth compared to a control (100 percent).

PLANT SPECIES and parts used	FUNGI TEST SPECIES					
	CHCl ₃ :CH ₃ OH (1:1) Extracts	<i>Alternaria solani</i>		<i>Fusarium oxysporum</i>		<i>Helminthosporium longirostratum</i>
200 µg/ml	percent of radial growth					
	3 days	8 days	3 days	8 days	3 days	8 days
<i>Philodendron radiatum</i> –roots	81.8	68*	108.9	100	60.4*	36*
<i>Jatropha gaumeri</i> ; leaves	90.9	80.9	98.4	98.4	76.4*	81.2
<i>Sebastiania adenophora</i> ; stems	113.6	102.4	105.4	107.4	73.5*	61.5*
<i>Croton glabellus</i> ; leaves	79.6	2.3	82	75*	55.5*	53.7*
<i>Zuelania guidonia</i> ; leaves	113	100	64.2*	67.2*	52.9*	41.4*
<i>Pithecellobium albicans</i> ; fruits	75*	9.4	107.4	120	108.3	56*
<i>Byrsonima bucidaefolia</i> ; leaves	99.3	114.3	103.7	108.2	68.2*	57.3*
<i>Heliocarpus</i> sp.; stems	77	67*	100	100	74.2*	57.6*
<i>Lantana cámara</i> ; leaves	96.3	88.6	86.3	94	53.6*	34*

* p ≤ .05

Bioassays with Artemia salina (brine shrimp lethality test)

Figure 25.1 shows the principal results of the biodirected phytochemical fractionation studies of some plants of El Edén with a strong allelochemical potential. In this study, we used brine shrimp (*Artemia salina*) as the test organisms. Leaves of *Sebastiania adenophora*, roots of *Chamaecrista glandulosa* (L.) Greene (Fabaceae), leaves of *C. acuminata*, and leaves of *Lysiloma latisiliquum* (Fabaceae) constituted the group of plants with the highest toxic effect on *A. salina* (LC₅₀ less than 200 µg/ml). *Zanthoxylum*



Keys of plant species:

Se = *Sebastiania adenophora* (Euphorbiaceae) – from left to right: hexane, chloroform, and methanol leaves extracts

Ch = *Chamaecrista glandulosa* (Fabaceae) – CHCl₃-CH₃OH -1:1 roots extract

Ca = *Callicarpa acuminata* (Verbenaceae) – hexane leaves extract

Ly = *Lysiloma latisiliquum* (Fabaceae) – methanol leaves extract

Za = *Zanthoxylum caribaeum* (Rutaceae) – from left to right: hexane and methanol leaves extracts; hexane, chloroform, and methanol stem extracts

Ps = *Psychotria sp.* (Rubiaceae) – CHCl₃-CH₃OH -1:1 leaves extract

Ma = *Manilkara sapota* (Sapotaceae) – CHCl₃-CH₃OH -1:1 stems extract

Di = *Diospyros verae-crucis* (Ebenaceae) – from right to left: CHCl₃-CH₃OH -1:1 leaves and roots extracts

Eu = *Eugenia sp.* (Myrtaceae) – CHCl₃-CH₃OH -1:1 leaves extract

Ha = *Hammelia patens* (Rubiaceae) – CHCl₃-CH₃OH -1:1 leaves extract

Cr = *Croton sp.* (Euphorbiaceae) – CHCl₃-CH₃OH -1:1 roots extract

Eup = *Eupatorium sp.* (Asteraceae) – CHCl₃-CH₃OH -1:1 stems extract

FIGURE 25.1. Effects of chloroform (CHCl₃), hexane, and methanol (CH₃OH) extracts of some plants from El Edén on the survival of *Artemia salina* (brine shrimp). The effects of the extracts are expressed in LC₅₀ (µg/ml). Only those extracts with a LC₅₀ value below 1,000 µg/ml were considered.

caribaeum Lam. (Rutaceae), *Psychotria* sp. (Rubiaceae), *Manilkara sapota* (L.) P. Royen (Sapotaceae), and *Diospyros verae-crucis* Standl. (Ebenaceae) constitute the group that caused a LC_{50} less than 400 $\mu\text{g/ml}$. All other tested plant species have a LC_{50} over 400 $\mu\text{g/ml}$, but less than 1,000 $\mu\text{g/ml}$. Due to their bioactivity on brine shrimp, all these plant species could have a potential effect as insecticides and/or cytotoxics.

STUDIES ON FUNGI

Torres-Barragán et al. (in progress) made three insect collections in two zones within El Edén: the tropical forest zone and the agricultural zone in the surrounding area. Collections were performed during the rainy season (November to February) as well as during the dry season (March to October). All insect collections were transported to the laboratory at the Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), for the isolation and cultivation of all fungi found inside the insects.

A total of approximately 3,400 insects, comprising 18 insect species, were collected from the two areas. Four types of insects were from the tropical forest: houseflies, ants, bees, and termites. The main genus of fungi isolated from these four types of insects were *Penicillium* sp., *Aspergillus* sp., *Paecilomyces marquandii*, and *Verticillium* sp. Thirteen types of insects were collected from the agricultural zone: treehoppers, leafhoppers, Chili sap beetles, the coleoptera *Acalina trivitata* and *Conotelus stenoides*, whiteflies, aphids, bean grubs, fall armyworms, leaf-cutting ants, Mexican fruit flies, sap beetles, and citrus leaf miners. From these types of insects, the main fungi isolated were *Aspergillus parasiticus*, *Fusarium moniliforme*, *F. oxysporum*, and *Aschersonia* sp.

Tropical forests and other complex communities are considered stable, as the impact of a sudden population change in one species will be cushioned by the large number of interacting species and will not produce drastic effects in the community as a whole. It has been suggested that such buffer mechanisms operate in tropical forests where insect outbreaks are unknown. Coley and Kursar (2001) suggest that insect herbivores are rare in tropical forests because they are highly regulated by the third trophic level. This fact may explain the lower number of insects found in the tropical forest of El Edén. This situation contrasts with cultivated forests, where pest outbreaks are common (Mackenzie, Ball, and Virdee 1998). It was possible to confirm this in the two plant communities of El Edén where the insect collections were made (Torres-Barragán et al., in progress).

On the other hand, in the agricultural zone where pest insects are abundant, the environmental conditions are ideal for insect pest proliferation—that is, a low biodiversity of crops coupled with low amounts

of natural enemies that would otherwise control these pests. In this area, the whitefly can cause a total loss of production for both tomato crops and chili crops, mainly because of the viruses that the pests transmit to these plants (Urías-Morales, Rodríguez-Montesoro, and Silva 1995). This fact is one of the main reasons why croplands were abandoned in tropical agricultural zones, and underscores the importance of finding new alternatives for more natural pest control.

CONCLUSION

Microorganisms are essential to the health and functioning of ecosystems through mineralization and recycling of organic matter. They also play a significant role in bioproductivity, either directly via synthesis of food, medicines, and chemicals, or indirectly by making nutrients available for other primary producers. On the other hand, diverse studies on microbes from pest insects in natural protected areas have identified potential biological-control microorganisms (Charnley 1997). Detailed studies of mycoparasites population dynamics and their hosts are necessary in order to determine their potential use as biocontrol agents (Jeffries 1997).

The use of specific microbes in integrated pest management could also reduce dependence on chemical pesticides. The aim of the current investigation in this particular field is to identify those fungi from El Edén with a potential as microbial insecticides. For example, the genus *Fusarium* was one of the most remarkable fungi found in the insects of El Edén. *Fusarium* was isolated from 98.8 percent of the collected insects that showed fungal infection, with *Fusarium oxysporum* the most abundant species because it was isolated from 70 percent of the collected insects (Torres-Barragán et al., in progress) This species has received considerable attention from plant pathologists over the past 80 years because of its ability to cause vascular wilt or root rot diseases in a wide range of plants (Kistler 1997). In the 1970s, *F. oxysporum* f. sp. *orobanche* was developed in the former Soviet Union as a weed killer (Franz & Krieg 1976). One isolate of *F. oxysporum* has been evaluated as a *Striga* killer in the dryland zones of Africa where this parasitic plant causes losses of 70 percent in sorghum and maize production. In 1995, the results were dramatic: 85 percent of the *Striga* were wiped out at the seedling stage by this *Fusarium* isolate with the added advantage that it is not toxic to humans and causes no harm to cereal crops (Ciotola, Watson, & Hallett 1995).

On the other hand, a large number of *Fusarium* spp. are entomopathogenic. Highly pathogenic species are reported primarily from Homoptera and Diptera (Teetor-Barsh and Roberts 1983). *Fusarium oxysporum* is highly virulent to larvae of the mosquito, *Aedes detritus* Edw.;

to larvae of the rice green-horned caterpillar, *Melanitis leda*; and to eggs of the European corn borer, *Ostrinia nubilalis*. All these data indicate the importance of the current studies on the potential pathogenicity of the fungi isolated from El Edén insects.

Different sources of new natural products with a biocide potential have been found in some plant species and fungi of El Edén that could be used to control weeds and other pests, as well as to solve some disease problems. This project constitutes a long-term survey of the biotic chemical diversity not only of this ecological reserve, but also in the surrounding areas. In this project, methodology and research protocols were tested that could be applied to other tropical areas.

The aqueous leachates of some selected plants showed a strong phytotoxic effect. In general, the leaves are the part of the plants where this effect is more evident. Some of the most bioactive plants tested include all the Fabaceae species, *T. gaumeri*, *Eupatorium* sp., *Ipomoea* sp., *J. gaumeri*, *M. arboreus*, *H. trilobata*, *H. patens*, *A. cominia*, *L. camara*, *Z. guidonia*, *S. adenophora*, and *C. acuminata*. Families with a major phytotoxicity are Fabaceae, Apocynaceae, Asteraceae, Rubiaceae, Sapindaceae, and Verbenaceae.

In regard to defensive allelochemical compounds, Coley and Barone (1996) observe that leaves of tropical forests have both higher overall levels of defense and a greater diversity of defense compared to their temperate counterparts. This greater commitment to defense is an evolutionary response to elevated pressure from herbivores. In the tropics, mature leaves are long-lived and must therefore be resistant to both abiotic and biotic damages. Nowadays, the knowledge of the allelopathic/allelochemical potential of many plants allows them to be considered as part of the defense mechanism.

Currently, the advanced steps of the biodirected fractionation of three plant species that have compounds with a strong bioactivity on seeds, phytopathogenic fungi, and insects are being performed: *Z. guidonia*, *C. acuminata*, and *S. adenophora* (results not shown). With the collaboration of Dr. Rocio Cruz-Ortega of Instituto de Ecología, UNAM, a study is being performed of the mode of action of bioactive aqueous leachates of selected plants on protein synthesis, genetic expression, and oxidative enzymes on crop plants.

This project contributes to chemical exploration of dry tropical ecosystems in Mexico and biodiversity conservation. The scientific, economical, and historical fields of research that the long-term project at El Edén has opened are immense and promising. Each plant, animal, and microorganism within this ecological reserve constitutes a very valuable source of natural products.

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Chapter 26

Ancient and Contemporary Maya Conceptions About Field and Forest

Karl Taube

THE ORDERED WORLD

In ancient Mesoamerica, a most basic and widespread cosmological model was the four-sided world, with the intercardinal corners framing the central and pivotal *axis mundi* (“world axis”). This model can be readily documented as far back as the Middle Formative period (900–500 B.C.), when maize agriculture became a central component of Mesoamerican subsistence and economy.

In Olmec iconography, the four-sided world is portrayed by the bar-and-four dots motif (Figure 26.1a), consisting of a central vertical bar with four elements delineating the corners (Reilly 1994:257). A number of incised jade celts portray the Olmec Maize God as the central world tree, and scenes such as these probably constitute early versions of the Mesoamerican conception of the four-sided world as a maize field (Taube 2000:303). In one example, the corner elements are celtiform maize ears (Figure 26.1b). A complex Olmec-style cache from San Isidro, Chiapas, featured jade earspools as well as celts at the four directions (see Taube 2000, Figure 3).

A similar, Early Classic Maya cache discovered within Structure 10L-26 at Copán, Honduras, contained six roughly-cut earspool “blanks”—four at the corners and two near the center, with the latter probably alluding to zenith and nadir (Figure 26.2a). The center of this composition contains a jade statuette that portrays the Maize God in contortionist pose, with the legs arching up over his head (Figure 26.2b, cf. Figure 26.2c–d). The acrobat position signifies a growing tree, and is found both with depictions of the Maize God as a cacao tree as well as the well-known crocodilian ceiba *axis mundi* (Figure 26.2e–g). The Copán cache portrays the Maize God as the world tree situated in the center of the four directions.

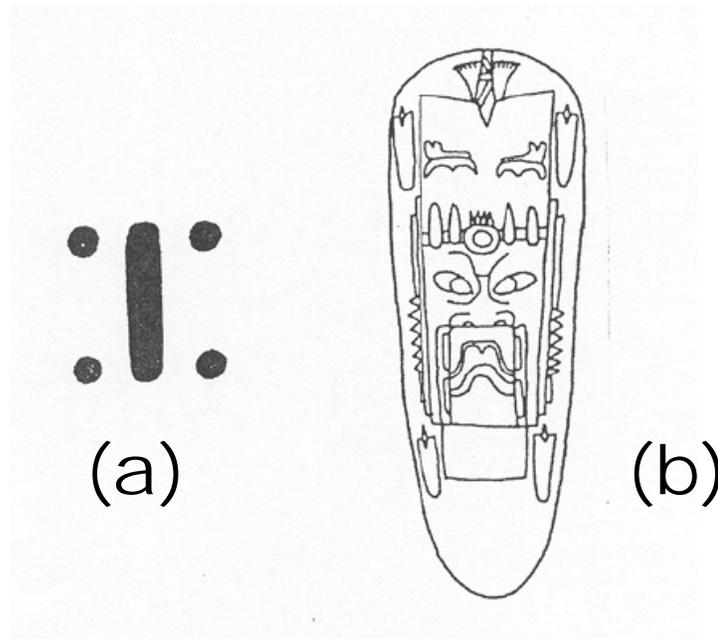


FIGURE 26.1. The bar-and-four-dots motif along with the Olmec four-sided cosmogram. a) Schematic form of bar-and-four-dots motif. b) Incised jade celt with head of Olmec Maize God as the central bar of the bar-and-four-dots motif. (Source: Modified Taube 2000, Figure 4a).

In Maya thought, the quadrangular milpa is compared to four-sided houses, towns, and other forms of socially-constructed human space. Thus, among the Yucatec, “the world, the village and the milpa are thought of as squares with four corners lying in the four cardinal points of the compass and with defined central points” (Redfield and Villa Rojas 1934:114). Hanks notes that the four sided plan relates closely to Yucatec conceptions of human space: “In most socially significant spaces, including towns, homesteads, plazas, and traditional cornfields, the four corners plus the center define the space as a whole” (Hanks 1990:299).

The Ch’orti’ compare the world to the form of four-cornered altars and maize plots (Wisdom 1940, 429–30). The Pedrano Tzotzil of Chenalhó also perceive a four-sided earth: “The world, osil balamil, is a square like the house and the fields. The sky rests on four pillars, just like those of a house” (Guiteras-Holmes 1961, 254). The K’iche’an Popol Vuh describes the cosmogonic act as the measuring of a four-sided maize field (Tedlock 1996:63–64, 220). Humans are the successful products of this maize field, whose role is to nourish and sustain the gods. A similar concept is present among the contemporary Trixano Kaqchikel of San Andrés Semetabaj, who consider the world as a maize field tended by Jesus, with world destruction constituting the supernatural “harvesting” of people (Warren 1978:33–34).

Whether it be a table, house, town, or even the cosmos, the four-sided plan refers to spatial constructions created by concerted effort, in contrast to

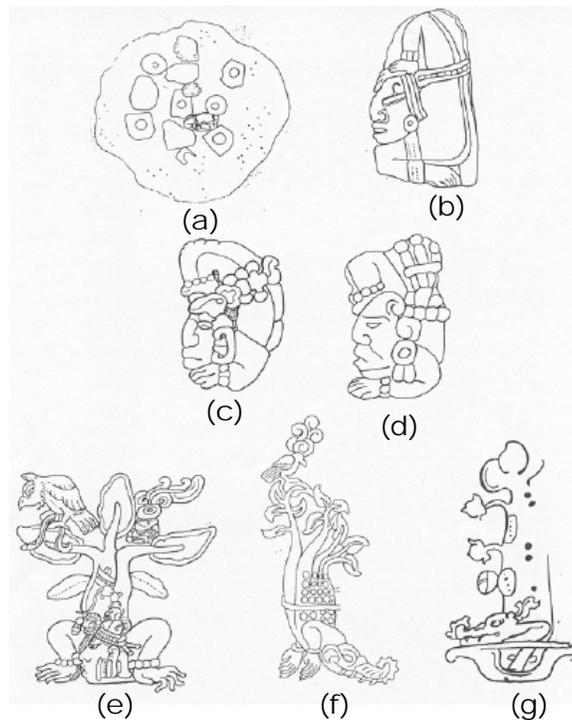


FIGURE 26.2. The Early Classic Maya Maize God as the central world tree. (a) Early Classic Maya cache featuring a jade Maize God with six earspool blanks, in an offering from Papagayo Structure 10L-26, Copán. (Source: Modified from Fash 1988, Figure 1b). (b) Detail of jade Maize God acrobat in center of Papagayo offering. (Source: Modified from Fash 1988, Figure 1c). (c) Jade Maize God contortionist with world tree on head, Salitrón Viejo, Honduras. (Source: Modified from Hirth and Hirth 1993, Figure 13.8a). (d) Jade Maize God contortionist (Source: Modified from Bliss 1957, Plate 54). (e) Maize God contortionist as cacao tree, detail of Early Classic incised vase (Source: Modified from Kerr 2000:972). (f) Late Preclassic crocodilian world tree in contortionist position, Izapa Stela 25. (Source: Modified from Taube 1993:59.) (g) Late Classic crocodilian world tree. (Source: Modified from Taube 1992, Figure 12h.)

te primordial wilderness. The Yucatec term *meyah* (or “work”) can apply to preparing the *milpa*, sweeping a house or courtyard, or purifying a space by a shaman, or *hmen* (Hanks 1990:229). The concept of work, or effort, extends to the vertical plane—not only tables and houses have four raised posts (or trees) at the corners, but also *milpas*, towns, and the cosmos. For the Ch’orti’, tree boundary markers in the *milpa* corners are compared to the corner posts of a house, with these same houseposts representing four supports of the cosmos (Wisdom 1940: 431; Fought 1972: 377–79). In the colonial Yucatec Chilam Balam community books of Chumayel, Mani, and Chumayel, a directional world tree raised after the flood is the “housepost of the sky,” with the term for raising the cosmic trees being “stood up” (*walhi*), much like

raising the beams of a house (Taube 1998:431). In Classic Maya iconography, the world corner posts are often personified as quadripartite aspects of the aged sky-bearer, Pawahtun. On a more human political level, Pawahtuns also support the corners of celestial thrones, with the seated lord occupying the central place of this four-cornered social world (e.g., Taube 1992, Figure 47a). The Pawahtun throne supports relate to the widespread Mesoamerican concept of public authority as a weighty burden (carga)—that is, an ordered society can occur only with human work and effort.

In Late Classic Maya art, the class of subordinate lords bearing the *saajal* title are often portrayed as Pawahtuns, quite probably referring to their collective role in supporting the higher office of kingship (Taube 1988a:197–98). The concept of physical labor in relation to kingship reappears in Classic Maya epigraphic statements of superordinancy, in which overseeing a subordinate ruler or polity is phrased by a glyphic compound read as *uchab'jiiy* (Houston and Stuart 1995, pers. comm.); Houston and Stuart relate this term to the Tzotzil root *chab'*, meaning “cultivate” as well as “govern, guard, or watch over” (see Laughlin 1998:I:184). A very similar concept occurs among the contemporary Trixano Kaqchikel, who conceive of three levels of supernatural cultivation: God tending the “fields” of the universe, Jesus caring for the world, and the Apostles nurturing the communities (Warren 1978:33).

An important component of the four-sided field, house, community, and world is the delineation of a clear boundary. As Hanks notes for the contemporary Yucatec Maya, “[w]ithout its perimeter, a place has no unity and is potentially dangerous” (Hanks 1990:349). Among the Yucatec, both the milpa and town are first delineated and protected by cutting a perimeter in the forest—an act known as *hol ch'ak* (Sosa 1985:243; Hanks 1990:306).

For the Chenalhó Tzotzil, the town “sides” are named by the same terms used for the upper and lower sides of the milpa (Guiteras-Holmes 1961:254–55). Along with mentioning the trees in the corners of *Ch'orti'* milpas, Wisdom (1940, 421–22) noted four living tree crosses at the four cardinal entrances of Jocotán; these boundary markers served to repel demons and evil spirits. For the Tzotzil town of Zinacantán, gods at the four directional entrances guard against illness and other dangers (Laughlin 1976:11). Similarly, the Yucatec place protective crosses at the four corners of the milpa, as well as at town entrances that are symbolically, if not actually, positioned at the four cardinal directions (Sosa 1985:243; de Jong 1999:290–91, 295). These are the places of the *b'alamo'ob'*—directional guardians of both the milpa and town who protect humanity from wild animals, demons, and evil winds (Redfield & Villa Rojas 1933:112–14; Villa Rojas 1945:101; Sosa 1985:246–248; Hanks 1990:341; de Jong 1999:293).

Although the maize field, house, community, and the created world are four sided, actual communities typically do not adopt this logistically improbable form; instead, they have rounded and organic plans. This is also plainly reflected in ancient fortifications found at El Mirador, Becan, Dos Pilas, and other sites, whose walls commonly delineate circular interiors (e.g., Webster 1979). The idealized four-sided town model defines a human and moral community.

For the Yucatec, Hanks stresses the importance of laying the milpa boundary stones in ordered, straight lines: “The stones are *tzoltá’al* ‘counted out (ordered)’ . . . and must be *toh toh* ‘straight straight’ ” (Hanks 1990:357). In Yucatec, *toh* means “straight” as well as “truth” and conditions of moral rectitude. Thus, in early colonial sources, *toh* is a “just and necessary thing,” *toh be* (straight road) “virtue,” *tohil* “justice,” *toh etz’al* “balance,” *toh kab’* “to confess, tell the truth, declare,” and *toh olal* “consolation or calmness”—all qualities that clearly relate to the social well-being and harmony of communities (Barrera Vásquez 1980:801).

Cognates of the Yucatec term *toh* are common in other Mayan languages. Thus, in Mopan, *toj* signifies “straight, good, correct, well” (Ulrich and Dixon de Ulrich 1976:202). The colonial Moran Dictionary of extinct Ch’olti glosses ‘*to*’ as “truth” (Moran 1935:67). In related contemporary Ch’ol, *toj is* “straight, just”; *toj’esat’an*, “correction of an act or letter (carta)”; and *toj’esan*, “to straighten, to guide” (Aulie and Aulie 1978: 112–13).

For colonial Tzeltal, *togh* signifies “straight” as well as socially correct states. Thus, while *toghob’* means “to straighten something” and *toghobon* “to make well,” *toghol* *unic* signifies a “virtuous man”; *tohob’tez* is “to order life”; and *tojob’tezoghb’il otanil*, “the confession” (Humberto Ruz 1986: 384–86). In colonial Tzotzil, *tojob’* means “be able to fix, behave with modesty and prudence,” and *tojil’osil* means “good government” (Laughlin 1998: I:315–16). An especially intriguing term is *tojob’tas*, which (along with signifying such morally related concepts as confession, obstructing evil, and purging) also refers to activities of human labor and construction, including polishing, leveling, preparing, restoring to former form or beauty, and laying beams (Laughlin 1998:I:315–16). In Tojolabal, *toj* means “straight” and “true”—such as *tojol winik* “true man”—with *tojb’esuman* being the term for a maker or repairer (Lenkersdorf 1979:I:352–54). Implicit in the concept of *toh* is that making milpa, houses, art, and other efforts of construction are inherently good and ethically correct human acts. On their straight paths defining the town and milpa, the Yucatec *b’alamo’ob’* defend the physical and spiritual well-being of humans and their efforts.

THE FOREST WILDS

In a seminal discussion of Maya beliefs concerning humans and the surrounding natural world, Stone (1995) notes a frequently sharp contrast between the community and the forest, which she describes as “a model of socially constructed space that cleaves along the lines of two polar spatial categories: the domestic center or community and what might be termed the wilderness, forest, or bush” (Stone 1995:15). The boundaries marking the edges of fields and communities protect humans from the many dangers of the forest wilds.

Also delineating a “fundamental distinction” among the Yucatec between forest and humanly-occupied space, Hanks notes that the forest “is a dangerous place outside of the realm of the guardian spirits posted at the cardinal corners of inhabited and cultivated space” (Hanks 1990:306). Among the tasks of shamans is dispelling evil spirits “deep into the forest” (Hanks 1990, 307). Vogt describes the Zinacanteco Tzotzil view of forest wilds, or *te'tik*, as “an undomesticated domain populated by wild plants, animals, wild animals, and demons (*pukuhetik*)” (Vogt 1976:33). The danger of the forest wilds is also reflected in the Pedrano Tzotzil regard for freshly cut materials for house construction: “They are always dangerous because they come from the forest and the bush, from the wild hills, and therefore they can eat the soul” (Guiteras-Holmes 1961:223).

In Maya thought, the wild forest is related to darkness and the night. According to the Pedrano Tzotzil Manuel Arias Sohom, the social space of the *milpa* is protected by light, in contrast to the forest region of snakes and demons: “In the cultivated fields there is neither shadow nor darkness, it is open land and we are not afraid; in the forest it is dark and there are snakes sink holes, caves, the *xpakinte'* the *ik'al* and we are afraid” (cited in Guiteras-Holmes 1961:287).

Similarly, the *Ch'orti'* regard gloomy forest regions as the realm of spooks and demons (Wisdom 1940:426). The sun protects one from such evil beings by casting them away to “where the mountains lie, where there are no human beings” (Fought 1972:489–90). Stross (1978) notes that Tzeltal contrast the daylight world of humans with the distant, nocturnal realm of wilderness: “Daytime, the home, and social behavior represent safety, while nighttime, far from home, and asocial behavior represent danger” (Stross 1978:36).

The relation of the forest to evil and darkness is nicely encapsulated in the Yucatec term *lob'*. In Yucatec, Itzá, and colonial Tzotzil, *lob'* signifies such powerfully negative concepts as “bad, evil, perverse, and ruined” (Barrera Vásquez 1980, 454–56; Hofling and Tesucún 1997, 416; Laughlin 1988, I:247). But along with being the basic term for pernicious “evil” in Yucatec, *lob'* also denotes dense, knotted forest growth—“brambly, full of

underbrush, entangled” (Barrera Vásquez 1980:454–55). In terms of landscape, a lob’ b’eh is a rough road closed with growth; *lob’chahal*, the growing of wild plants in the milpa; and lob’ k’ax, thick and closed forest. In addition, lob’ also can signify darkness (Barrera Vásquez 1980:219). The concept of lob’ as evil and wild entangled undergrowth is diametrically opposed to the Yucatec concept of toh as straightness and moral rectitude.

As a dense and dark covering laden with thorny vines and biting creatures, the forest is a thick, heavy presence that hangs over the human intruder. Hanks notes that during the milpa cutting, the initial *hol ch’ak* perimeter is an “open path,” with the farmer then passing “under” to cut the interior bush (Hanks 1990, 357). In Yucatec, one is “under the forest” (*yanal k’ax*) (Hanks 1990, 311) in contrast to being “in” or “at” a town or milpa (Hanks 1990, 306). The colonial Chilam Balam of Chumayel mentions the Itzá banished under the forest, “when the Itzá went beneath the trees, beneath the bushes, beneath the vines, to their misfortune” (Roys 1933:136). Hanks (1990) notes that, in Yucatec, “under” has negative connotations in contrast to “over” (e.g., the phrase *yoo’ beh*, or “over road,” which can signify being on a correct path). This also recalls the ancient *sak b’eho’ob’*, or “white roads”—raised masonry causeways that commonly extend in straight lines for many kilometers across the landscape. The term *sak b’eh* neatly contrasts with “black road”—*ek’ b’eh*, the word for a narrow, uneven trail. Not surprisingly, another name for such a treacherous path is lob’ b’eh (Barrera Vásquez 1980:150).

The forest wilds are related to concepts of lowness, caves, and the underworld. According to Wisdom (1940), the Ch’orti’ correlate “below” with “the low, dark, and secluded spots where evil deities dwell” (Wisdom 1940:428). Stone (1995) notes that as an alien, amoral place filled with fierce beasts and demons, the forest wilderness is closely related to caves and the underworld (Stone 1995:16–18, 42). In Pedrano Tzotzil belief, “The forest and the bush, the caves and sinkholes are feared by man, because in them he lacks the protective light and warmth of the sun” (Guiteras-Holmes 1961:287). In addition, caves are the antithesis of toh—being winding, natural features with rounded chambers that lack corners and straight, flat walls. In contrast to public ceremonies of the community, much cave ritual concerns curses and pacts with evil beings (e.g., Warren 1978:80).

To the Aztec, the ancestral Chichimec lived in caves in the remote wilderness, as illustrated in the Mapa de Quinantzín and other sources. According to Burkhart (1986), the wandering Chichimecs “symbolized both the past and the periphery of settled space” (Burkhart 1986:11). In a very similar vein, Stone (1995) notes that the Maya relate the remote forest wilds to the ancient, mythological past—a place of demonic beings from before the present creation (Stone 1995:15–16). Thus, among the Chamula Tzotzil, the regions most distant from the town center are most related to ancient,

supernatural beings (see Gossen 1974b). In Pedrano Tzotzil belief, the world was originally a forest realm of fierce demons: “They used to rob . . . They killed the people. That came to pass at the time when the earth was covered by the forest” (Guiteras-Holmes 1961:189). According to the Tzeltal of Tenejapa, such forest denizens as form changers, demons, and monsters “were more plentiful in the distant past than they are now” (Stross 1978:36). The concept of forest beasts and monsters being of the ancient past is not a modern construct, and is already present in the sixteenth century Popol Vuh. At the first dawning, the supernatural forms of pumas, jaguars, and venomous snakes were turned to stone by the sun, which protects us from these beasts (Tedlock 1996:161).

The wilderness is identified with ancient peoples as well as mythic beings. The Trixano Kaqchikel consider the ancient Maya to have lived in the wilds with animal pelt clothing, which is a concept strikingly similar to Aztec beliefs concerning their Chichimec ancestors (Warren 1978:36, 39). Among the Maya, ancient forest ruins are commonly regarded with both fear and deference. In Yucatán, a common belief persists that ancient mounds are inhabited by *aluxob'*, or mischievous goblin-like beings that must be treated with care and respect (Redfield and Villa Rojas 1934:119–20; Villas Rojas 1945:103; de Jong 1999:269–70).

The Yucatec Maya regard the great jungle-enshrouded site of Coba with special awe. Villa Rojas (1945:153) recorded the belief that at night, one can hear the music and cries of ancient Itzá living under the ruins. While living in the community of San Juan de Dios in 1984, I was asked whether I was frightened by the great snakes, or *noh chano'ob'*, that fly out of the lakes of Coba. Among the contemporary Quiché and Kaqchikel, offerings are made at their respective capitals of Uxatlán and Iximché. At Uxatlán, there is a deep, man-made cave where diviners can communicate with supernatural beings, including royalty of ancient times (Tedlock 1982:140). The reverence given to these ancient capitals is intensified by the fact that they are in forested areas isolated from daily human life.

Along with being identified with ancient beings, the forest is also a place of native resistance against conversion and Christianity. During the colonial period, many Yucatec escaped into the forest to escape Spanish domination (Farriss 1984:72–79). This strategy is plainly stated in the *Chilam Balam of Chumayel*: “There is no reason or necessity for you to submit to the archbishop, you can go and hide yourself in the forest” (Roys 1933:123).

Contemporary Maya performances portray characters who avoided the Spanish by fleeing into the forest, including Lacandon characters portrayed during Tzotzil Carnival (Bricker 1973:48–49; 129–30, 139–40). Whereas the Tzotzil regard the Lacandon beings as amoral foreigners, the Quiché have a forest character that embodies K'iche'an resistance to colonial rule. Known variously as Mam, K'oxol, or Tzitzimitl, this being is the guardian of wild

animals and the initiator of shamans (Tedlock 1982:147–48). According to the *Popol Vuh*, K'oxol escaped into the forest with the stone animals during the first dawning (Tedlock 1996:161, 304–05). In the historic drama known as the *Dance of the Conquest*, the brave king Tecum Umam dies and another K'iche'an king converts, but K'oxol divines the conquest and again escapes into the wilds to give birth to Tecum Umam's child: the customs survived the conquest by going into the woods, where the lightning-striking hatchet of the Tzitzimitl continues to awaken the blood of novice diviners and where the child of Tecum still lives (Tedlock 1996:150). It is this very being that diviners contact in the cave at Utatlán, which also contains a miniature corral of his many animals.

Far from passive and detached from the human world, the Maya forest and its denizens try continuously to invade and battle its fields and towns. Laughlin notes that among the Zinacanteco Tzotzil, wild plants have emotions, and “get angry” when they are felled, and “laugh” when they overtake a maize field (Laughlin 2000:106). In contrast, cultivated plants that flourish are “happy,” and “industrious” (Laughlin 2000:106). Much like the Yucatec concept of *lob'*, wild overgrowth has negative moral connotations, “weeds do not have good souls, they are not sensible, responsible . . .” (Laughlin 2000:105). Wild plants also attack tools left overnight in the forest, causing the worker to be fatigued the following day (Laughlin 2000:105).

In Tzotzil belief, wild animals are allies of the bush: “The creatures of the forest are man's enemies and seek to destroy his life” (Guiteras-Holmes 1961:287). In Tzotzil tales of Chenalhó and Chamula, Deer and Rabbit magically cause the forest to regrow over the newly-cut field of the sun. As punishment, the sun pulled their ears to the length they are today (Guiteras-Holmes 1961:315; Gossen 1974b, 307). A sixteenth-century version of this myth appears in the *Popol Vuh*, when, at night, wild animals restore the forest cut for the Hero Twins' milpa (Tedlock 1996:109–10). In this episode, the powers of the wilds are restored in the darkness of night.

In contrast to the carefully delineated world of humans, the forest and its inhabitants ignore boundaries. With the forest, there is the constant encroachment of weeds in the field and in the communities, while plants also hide snakes and other pernicious animals. In addition, wild animals appear to wander with little direction. As Burkhart (1986) notes, this can be ethically wrong in Mesoamerican thought (Burkhart 1986:113); in the *Popol Vuh*, a major fault of the wooden men was their tendency to wander without aim or thought (see Tedlock 1996:70, 234–35). Burkhart (1986) notes that among the sixteenth-century Aztec, children were warned against following the “road of the rabbit and deer”—that is, the same shiftless route of prostitutes (Burkhart 1986:113, 122). A sixteenth-century Aztec account has the following description of “feral”: “in the grassland, in the wasteland his animality manifests. He wanders about as a rabbit, as a deer. He goes about insensately,

he strays heedlessly” (Maxwell and Hanson 1992:179). Following weak and meandering trails in the dark forest, animals disregard the social and moral laws of humans.

Scenes in pre-Hispanic art reveal that the ancient Maya also regarded the forest as a fearful, dangerous place. At Chichén Itzá, an explicit portrayal of the menacing bush appears in a mural from the Upper Temple of the Jaguar (Figure 26.3). Dating to roughly the tenth century A.D., this scene portrays a figure standing before a house, with the forest behind teeming with fierce beasts, including an apparently roaring puma and two rattlesnakes—one of which is coiled as if to strike.

In Maya lore, snakes are one of the most widely feared creatures of the bush, clearly due to the very real risk they pose to travelers passing through dense growth. One tree has a snake wrapped around the trunk (a convention also appearing in Late Classic Maya art), with the tree trunk marked with the head of the patron of the month, Pax (Figure 26.4b, c, e). This tree often appears in hunting scenes, indicating its forest significance (Figure 26.4c, e). In the case of the Calcehtok Vase, a serpent, deer, and human figures flank the tree (Figure 26.4c). The human figures have their arms sharply bent in the Classic Maya position of “woe.” Houston (2000, personal communication.)

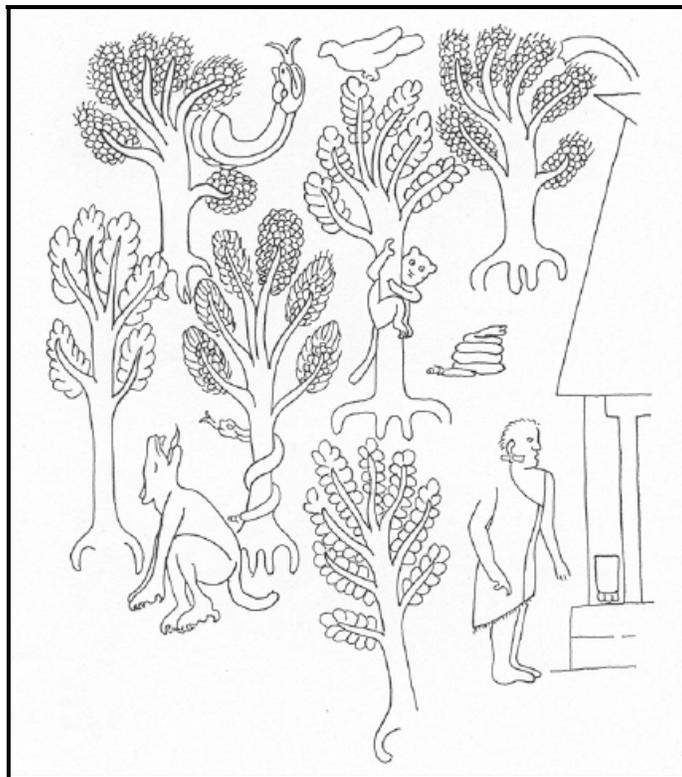


FIGURE 26.3. Early Postclassic portrayal of the forest, featuring serpents and wild beasts. Detail of a mural from the Upper Temple of the Jaguars, Chichén Itzá (Source: Modified from Maudslay 1889–1902, III: plate 40).

notes that, in the Dresden Codex, this gesture has the phonetic value *loob'*— here in texts denoting bad or evil auguries (Figure 26.4d). One Late Classic Maya vessel portrays a severed human head with the tree and the serpent, which appears to be striking (Figure 26.4b). It is quite likely that the Classic Maya motif of the serpent-wrapped tree is a condensed symbol of the forest and its hazards.

One of the better-known Classic Maya mythological scenes concerns an episode recorded in the sixteenth-century *Popol Vuh* of a monster bird shot down by the Hero Twins, Xbalanque and Hunahpu. Along with protecting their milpa from animals, the Hero Twins of the *Popol Vuh* were monster slayers, including the great bird Vucub Caquix, which they shot out of his favorite fruit tree (Tedlock 1996:77–81). A common scene on Classic Maya

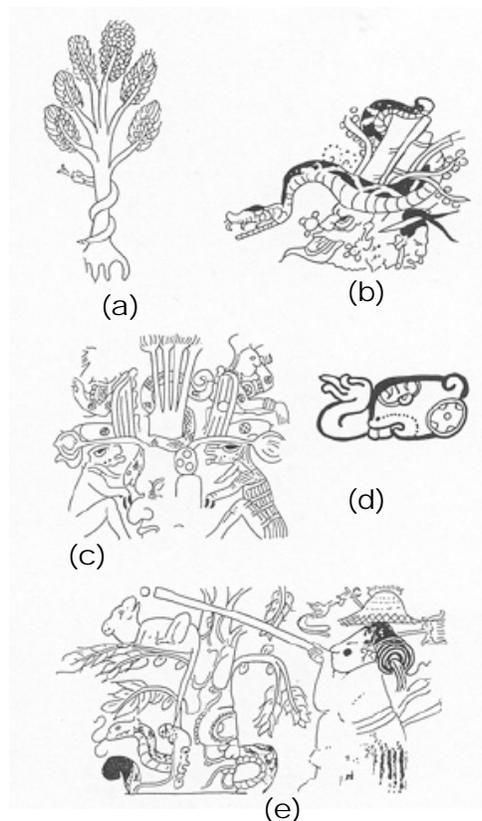


FIGURE 26.4: The Classic Maya motif of the serpent-wrapped tree as a forest symbol. (a) Detail of mural from the Upper Temple of the Jaguars (see Figure 26.3). (b) Pax God tree with probable striking serpent and severed head (Source: Modified from Taube 1988b, Figure 12.7c). (c) Pax God tree flanked by serpent, deer, and human figures with bent arms in the Classic Maya *loob'* position (Source: Modified from Taube 1988b, Figure 12.7d). (d) Glyphic compound epigraphically read as *loob'* (Source: Modified from Codex Dresden, p. 8a.) (e) Classic period Hero Twin Hun Ajaw shooting iguana in tree with a blowgun. Detail of Late Classic vase (Source: Modified from Robicsek and Hales 1981, vessel 110).

vessels, this episode even appears on Late Preclassic Izapa stelae dating to near the beginning of the Christian era (see Coe 1989:163; Taube 1993:65–66).

Although the meaning of this important episode remains poorly understood, a remarkable Late Classic Maya vase places the vanquishing of the monster bird in the broader context of the forest. The vase portrays the Classic Maya period Hero Twins standing with blowguns before the hovering bird, now partly transformed into the powerful and aged Itzamnaaj (see Kerr 1992:413; for detail of bird, see Hellmuth 1987, Figure 719). A series of 11 forest animals present tamales and vessels of drink to the Hero Twins (Figure 26.5). Of the readily identifiable animals, there are two deer, a monkey, an armadillo, a gopher, a puma, a jaguar, a peccary, and a squirrel. The placement of the monkey with a tree determines this is a forest scene. In Maya texts, the pairing of tamale and water signs (i.e., food and drink) denote a feast (Houston and Stuart 2001:69–70). The shooting of the monster bird from its tree may concern the mastery and domination of the forest, with the animals offering prepared food in tribute to the victorious Hero Twins.

A thematically related Late Classic Maya vessel depicts the partly-transformed avian Itzamnaaj and a seated deer before the Hero Twins (Figure 26.6). The deer, the primary game animal of the forest wilds, appears in a secondary position to the Classic Maya form of Xbalanque, who sits upon a mat throne. Rather than his brother (known in Classic Maya texts as Hun Ajaw), Xbalanque is the enthroned twin.

Both the Classic Maya period Xbalanque and Hun Ajaw are often referred to as the Headband Twins, owing to the frequent presence of the rulership headband on their brows. Hun Ajaw serves as the personified form of the day glyph Ajaw, meaning “king,” and embodies the office of human kingship. In contrast, his brother corresponds to the jaguar—the major “king” of the forest. Not only does the K’iche’an name Xbalanque correlate to a widespread Mayan term for jaguar (balam), but the Classic Maya form displays jaguar pelt markings on the face and body. In the Postclassic codices, hunters can display the same jaguar pelt facial markings, as seen in the Codex Paris (p. 10), where the figure is named Wuk (seven) Zip, which is the name of a Maya hunting god (Taube 1992, 60–63, Figure 28h–j; for Wuk Zip reading, see Fox and Justeson 1984, 39).

The Hero Twins may well denote two realms of authority: (1) Hunahpu, the king of the human community, and (2) Xbalanque, the king of the forest. In West Africa, where there is also a sharp distinction between the bush and human social space, the ruler of the community is often paired with the leopard of the forest. Thus, among the Benin of Nigeria, the first king Osigo was “king of the home,” and the leopard, “king of the bush” (Ben-Amos 1976:244).

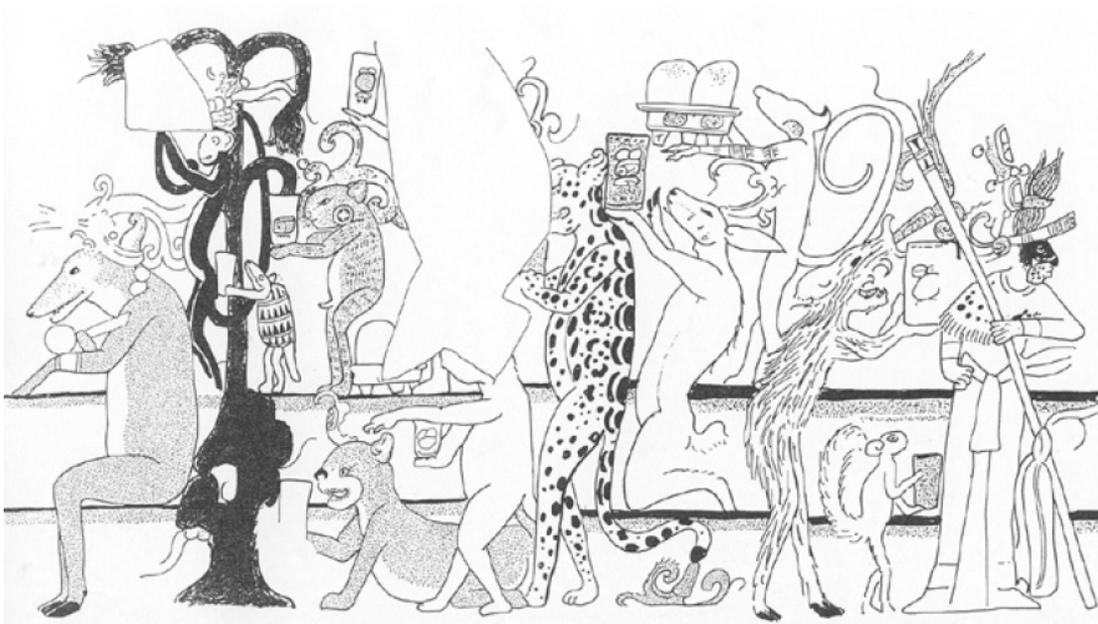


FIGURE 26.5. Forest animals presenting food and drink to the Hero Twins. Detail of Late Classic Maya vase. (Source: Drawn by author from the Foundation for Latin American Anthropological Research slide archive at Dumbarton Oaks, Washington, D.C.)

Aside from Xbalanque, there was a more specific Classic Maya god of game animals. Yucatec colonial sources mention a being known as Ah Wuk Yol Zip, or “he of seven heart Zip” (Thompson 1970:308). As Thompson noted, the contemporary Yucatec consider Zip to be the protector of deer (Thompson 1970:308; see also Redfield and Villa Rojas 1934:117–18; Villa Rojas 1945:103; de Jong 2000:139). Aside from the epigraphic reference to Wuk Zip on Codex Paris page 10, this name also appears on Codex Dresden page 13c (Figure 26.7a). The aged deity illustrated in this scene is clearly the hunting god, who grasps a deer displaying the lob’ gesture of woe. Wuk Zip has an antler, a large lower lip, and the “death collar” found with the Maya god of death. The prominent black body striping found with this being also appears on Classic Maya hunters (see Kerr 1989:74). Along with black spots and hand-print body markings, the striping probably served as camouflage in the mottled light of the forest.

Portrayals of the hunting god are relatively common in Classic Maya epigraphy and art (Figure 26.7b–g). As with the Dresden example, he displays ancient, craggy features, as well as deer ears, antlers, and a frequently extended lower lip—probably alluding to the goat-like manner in which deer pluck vegetation with their mouths. Quite commonly, he displays the spiral eye found with gods of night and darkness (Figure 26.7b, c, f; see Houston and Taube 2000:284–85).



FIGURE 26.6. Partly transformed avian Itzamnaaj and seated deer before enthroned Classic Maya form of Xbalanque (Source: Modified from Kerr 1994:641).

In Classic Maya scenes, the deity often wears hunting costume and accoutrements, such as a grass skirt, a broad-brimmed hat, while sometimes holding a conch trumpet, which is probably used both to flush game and to communicate during communal hunts (Figure 26.7d, g; see also Figure 26.4e). In one Late Classic Maya vessel scene, the hunting god blows his conch trumpet in front of the aforementioned Pax god tree, thereby indicating his forest location (Figure 26.7g). Copán Stela B provides an especially fascinating spatial context for this being. The text describes king Waxaklahun Ub'aah K'awiil impersonating the hunting god, who is identified by a prominent lower lip, an aged face, deer ear, and antler (Figure 26.7c; for Classic Maya god impersonation, see Houston and Stuart 1996). Stela B portrays the ruler standing in the cave maw of a mountain that is epigraphically labeled “Macaw Hill” (Stuart and Houston 1994:23, 26). Classic Maya vessel also portray the hunting god within a structure marked with stacked zoomorphic mountain masks (see Robiscek and Hales 1981: vessel 14). In contemporary Maya lore, the master of animals and the hunt lives in a mountain cave. Among the Itzaj, the Lord of the Deer is an old man who lives at the base of a hill with his ranch of wild animals (Hofling 1991:136–53). For the Quiché, K'oxol is both the caretaker of animals in his hill cave at Uatlán and the spirit of the sacred mountain of the east (Tedlock 1982:147–48). Similarly, the K'ekchi' Tzultakah—lords of the forest, and the caretakers and guardians of wild animals and game—reside in mountain caves (Thompson 1970:273–5). Copán Stela B reveals that the concept of the master of game residing in a hill cave was indeed present during the Classic Maya period.

Aside from game and dangerous beasts, the bush is a place of supernatural demons. Redfield and Villa Rojas describe the Yucatec Maya conception of these terrifying forest beings:

They are the subjects of fearful stories, and ideas about them suggest the uncanniness of the bush. These include animals that are not animals, but witches that have taken animal forms; animals that have exchanged forms with one another; huge animal monsters; and evil things in human form (Redfield and Villa Rojas 1934:121).

According to Wisdom (1940:405), the Ch'orti' conceive of seven demons who live in remote regions and serve as "protectors of wild plants and animals." For the Pedrano Tzotzil, there is Poslob, an evil jaguar being that eats the 'way' animal souls of people (Guiteras-Holmes 1961:293).

Quite frequently, forest demons are beings of lust and amoral behavior. In part, this is probably because the woods are a common place for trysts—far from the watchful eyes of neighbors and the community. Among the Tzotzil, there is the *h'ik'al* (or "black man"), a hypersexual forest demon whose

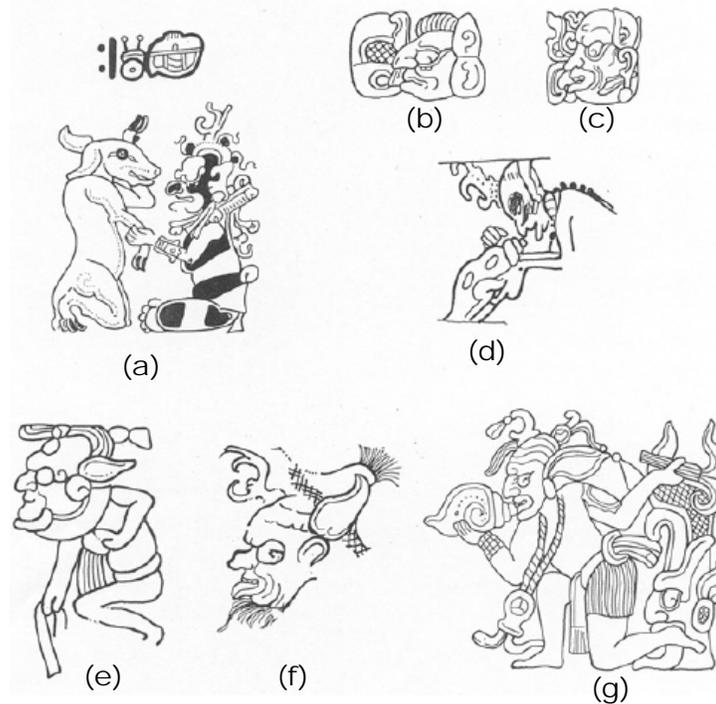


FIGURE 26.7: The Classic Maya hunting god, Zip. (a) Deer with hunting god epigraphically named Wuk Zip. (Source: From Codex Dresden, p. 13c.) (b) Classic Zip god with black prefix from Dos Pilas Hieroglyphic Stairway 4. (c) Zip god with deer ear and antler from Copán Stela B. (d) Zip god with antler and deer ear blowing conch trumpet (Source: Modified from Robicsek and Hales 1981, Vessel 37). (e) Terminal Classic Zip god with deer ear (Source: Modified from Kerr 1990:198). (f) Zip god with deer ear, antler, and hunting hat, Bonampak Room 3 (Source: Modified from Taube 1997, 39). (g) Zip god holding torch and blowing conch trumpet before Pax god tree. Detail of larger scene (Pax god tree not shown). (Source: Modified from Kerr 1990:307).

massive penis causes women to die in pregnancy (Blaffer 1972:19–54). For Yucatec Maya, the X'tab'ay is the nocturnal forest being most identified with wanton sexuality. She typically appears as a ceiba-dwelling, beautiful woman with long hair who can transform herself into a tree or snake. Men tempted by her charms either lose their souls, die, or become insane (Redfield and Villa Rojas 1934:122, 207; Villa Rojas 1945:104; Souza 1970:112). Wisdom (1940:407, n. 57) compares this being to the Ch'orti' Siguanaba, the protector of fish who appears as “sweetheart” on paths at night and makes the victim insane. Among the Tzotzil, there is the being known as Xpak'inté', a female forest demon who tempts drunks and other hapless victims (Guiteras-Holmes 1961:179; Gossen 1974b, 309; Stross 1978:38). Laughlin provides a vivid description of this most unpleasant creature:

She is believed to be able to take the appearance of one's wife to lure a hapless drunk into a clump of magueys. The back of her head is hollow. Her hair is made up of poisonous caterpillars . . . When the drunk touches her sexual parts they turn into excrement. When he strikes her she turns into a tree (Laughlin 1975:264).

Capable of transforming into trees, both the X'tab'ay and the Xpak'inté are essentially personifications of the amoral and pernicious nature of the forest.

In Classic Maya iconography, the host of beings that best fit a “demon” category are the ‘way’ spirits (Houston and Stuart 1989; Grube and Nahm 1994). Houston and Stuart (1989:5) note that, in Mayan languages, the term ‘way’ denotes “to sleep” or “dream,” as well as denoting an animal spirit co-essence or soul—known as chanul or wayihel in Tzotzil, and *lab'* or wayohel in Tzeltal (see Pitt-Rivers 1970, 186). Although the Classic Maya ‘way’ spirits refer to this aspect of the human soul, there is another soul or life force pertaining to breath (Houston and Taube 2000:267–70). Whereas the breath spirit relates to flowers and beauty, the Classic Maya ‘way’ characters are typically hideous, frightening creatures that clutch bowls of bones, eyeballs, severed hands, and other gore as their food. In addition, they are frequently deathly beings, or jaguars and other wild, forest creatures. The long roster of ‘way’ characters collected by Grube and Nahm (1994) is virtually a bestiary of animal names, including the terms for jaguar, deer, spider monkey, peccary, coati, tapir, rat, bat, snake, centipede, and even leaf-cutter ant. Moreover, a number of Codex Style vessels portray the ‘way’ spirits with the hunting god emerging from the mouth of a “serpent deer,” or boa (Robicsek and Hales 1981:Vessels 31, 33, 35, 36, 48b). Simply put, the Classic Maya ‘way’ demons are forest spirits.¹

Our understanding of Classic Maya period *way* spirits is based primarily on Tzotzil ethnography; in Tzotzil lore, the ‘way’ are explicitly beings of the forest wilds. Vogt (1976) notes that in Zinacanteco thought there are two souls—the innate and impersonal *ch’ulel* spirit, and the animal soul of the forest, the “unruly, uncontrollable ‘wild’ and impulsive side of their behavior” (Vogt 1976:33). Similarly, the Pedrano Tzotzil conceive of two souls, the indestructible *ch’ulel* and the vulnerable *wayhel* animal soul identified with the forest, darkness, and the night (Guiteras-Holmes 1961:296, 270, 288, 296, 299). When the sun sets, the *wayhel* become wild and attack one other, resulting in illness and death (Guiteras-Holmes 1961:301–02). During Chamula Carnival, monkey-men impersonators threaten to kill people by taking them to the forest and feeding them their own animal spirit souls, a form of self-inflicted spiritual cannibalism (Bricker 1973:95).

According to the Pedrano Tzotzil, the highly antisocial sentiment of envy causes *wayhel* souls to do harm (Guiteras-Holmes 1961:158). Similarly, whereas the ritual guides of the Trixano Kaqchikel cargo ceremonies operate in public rites of the community, individual sorcerers perform in the isolated forest wilds in rites concerning accidents or illnesses, which are misfortunes believed to be caused by envy (Warren 1978:65–66).² In Trixano belief, wild animals and shadows are sources of disease (Warren 1978:79). According to the Ch’orti’, disease comes from underworld “were-animal” spirits, or *nahual* (Fought 1972:331–33). In Yucatec belief, sorcerers summon diseases from the underworld in the form of particular insects and other small creatures (Redfield & Villa Rojas 1934:178). Stuart (1998, pers. comm.) notes that a number of Classic Maya ‘way’ characters, such as Fire Heart Death and Red Bile Death, appear to personify particular diseases. Representing the vulnerable and personal aspect of human souls, the Classic Maya period *way* spirits were both targets and sources of witchcraft.

In Classic Maya ritual, artificial scaffolds portrayed symbolic forests. One Jaina style figure depicts a figure, dressed as a human deer, bound atop a scaffold ornamented with leaves (Figure 26.8a). This sculpture portrays human sacrifice in the metaphoric context of the hunt, with the speared victim as a deer (Taube 1988b:332). The leaf-covered scaffold is a symbolic portrayal of the forest where hunts occur. A number of Late Classic Maya scenes depict complex leafy bowers ornamented not only with leaves, but also with symbols of death and sacrifice, such as crossed bones and severed heads. In addition, leaf-covered structures can appear in scenes depicting jaguars, hunters, and other forest beings (Figure 26.8b–d).

The most elaborate known example of the leafy bower appears in a stucco facade at Tonina (see Yadeun 1993, Figure 23). In this case, *way* spirits

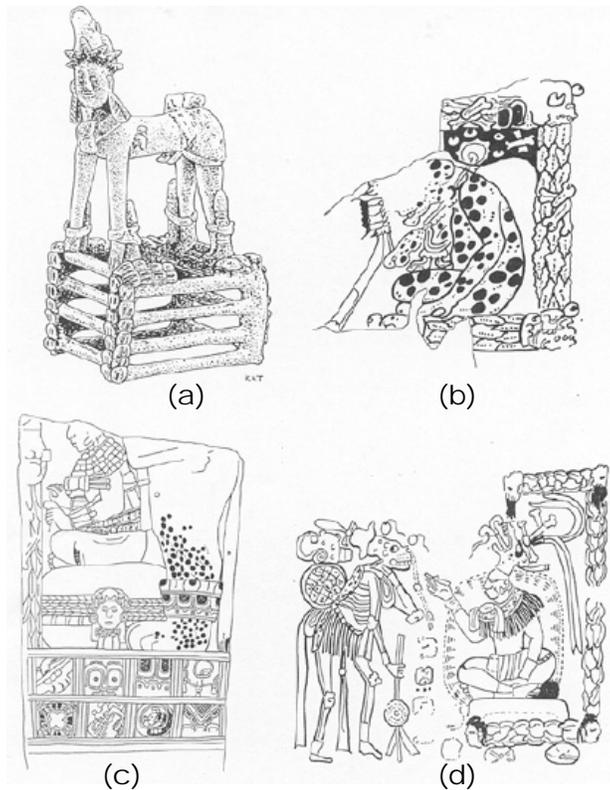


FIGURE 26.8. Late Classic Maya leafy arbors as ritual portrayals of the forest. (a) Victim dressed as deer bound atop a leafy scaffold (*Source*: Modified from Taube 1988b, Figure 12.4). (b) Leafy arbor with skulls and crossed bones containing seated jaguar (*Source*: Modified from Hansen 1994:97). (c) Seated ruler in leafy arbor backed by massive jaguar, Piedras Negras Stela 10. (*Source*: Modified from Maler 1901, Plate 19.) (d) Deer hunter way in front of leafy bower. Detail of Late Classic Maya vase (*Source*: Modified from Kerr 1992, 446).

appear in and behind the structure, much like furtive beings seen briefly in the forest trees. The base is marked with twisted serpent bodies, recalling the writhing serpent that appears in Classic Maya depictions of the forest (see Figure 26.4). One portion of the frieze depicts the Hero Twin Hun Ajau battling the demon bird. A dead bird in the small of his back indicates his role as a hunter. As with the aforementioned scenes, skulls and severed heads hang in the bower. Such leafy bowers constitute Classic Maya forms of the Aztec *tzompantli*, a symbolic tree laden with skulls for fruit (Taube 1994:228–29). Clearly enough, the Popol Vuh tree holding the head of Hun Hunahpu is a mythical version of the *tzompantli*. Excavations in front of the Tonina facade revealed a line of postholes, probably for supporting an actual skull rack bower (see Yadeun 1993:42).

According to the Popol Vuh, the sacrificial tree of Hun Hunahpu stood near the ball court, recalling the *tzompantli* platform next to the Great Ball

Court at Chichén Itzá. Classic Maya ballplayers are frequently portrayed as forest beings, wearing hunter hats or headdresses of deer and other bush animals (Hellmuth 1991). Hellmuth (1991, Figure 11) calls attention to one vessel depicting a ball player wearing the headdress of the old hunting god. Among the Classic Maya, ball courts were symbolic entrances to the underworld; as cave-like places of bloody competition, danger, and death, Classic Maya ball courts may have to be considered as rarefied, potent versions of the forest wilds.

THE WILDERNESS AND THE CLASSIC MAYA POLITICAL LANDSCAPE

Among both ancient and contemporary Maya, the forest is a dangerous, uncontrollable place of demons and fierce, biting beasts. Although the Classic Maya may well have closely cared for and managed forests of valued woods, fruit trees, medicines, and other products, the fearsome *way* spirits suggest a more distant, wilder realm. It is quite likely that forest wilderness was often in buffer zones, or “no man’s lands,” between competing polities. Thus, aside from demons and dangerous creatures, the wilderness was probably feared as a frequent place of raids and battles. The colonial Yucatec *Chilam Balam of Chumayel* describes a battle ending in “the heart of the forest,” and a mural from Chichén Itzá depicts a pitched battle in red, forest-covered hills away from human habitation (Roys 1933:157; Coggins 1984, Figure 17). The hazards of journeying in the wilds is vividly illustrated by a Late Classic Maya vessel that portrays a raiding party attacking a group of unarmed travelers, including women and infants (see Kerr 1997:802). Wearing the broad-brimmed hats of hunters and travelers, two of the attacked men attempt to defend themselves with small stones against the well-armed warriors. Two zoomorphic witz mountains denote the mountain wilderness context of this scene.

With its feared beasts, demons, and the very real threat of raids and capture, the forest surely was a major force for social cohesion during the Classic Maya period, with people preferring the safety of the community rather than the dangers of the wilderness. To be banished and forced into the bush was a situation of terrible consequence that placed one in moral as well as physical peril.

Mention has been made of the fleeing of the Itzá “under” the forest, and this is not the only account of banishment in the *Chumayel* (see Roys 1933:77, 122, 133). People are described eating food of the wilds, much like animals: “They shall find their food among the trees, they shall find their food among the rocks” (Roys 1933:77). This combination of wood (*che’*) and stone (*tunich*) is also the Aztec term for castigation (*tetl cuahuitl*), such as is meted

out to drunks, adulterers, and other moral deviants (Seler 1902–1923:II:934). In fact, the *Chilam Balam of Chumayel* mentions the beating of things with “wood and stone” (Roys 1933:99), and, in the *Popol Vuh*, the irresponsible and thoughtless wooden men banished to the forest as monkeys were also struck “by things of wood and stone” (Tedlock 1996:72).

The Maya murals of Mulchic may portray a Classic Maya version of this episode, Great Chaak figure stand before a scene of large stones raining upon people in the forest (Figure 26.9). Overcome with panic and virtually nude, they tumble over one another like frightened game. Individuals forced out of communities lose both their moral and geographic center, which are essential qualities that make them human.³

The most elaborate portrayal of forest battle appears in Room 2 of Structure 1 at Bonampak Chiapas. The background of this scene is a swirling mass of green outlined with parallel red lines. According to Thompson (1955), this motif alludes to “scrublike vegetation such as one sees around a modern Maya village” (Thompson 1955:51)—in other words, secondary growth at the periphery of the community, with dense and twisted foliage recalling the Yucatec *lob’*. The warrior costumes of Bonampak Room 2 pertain directly to the forest. As in the case of ballplayers, the men wear headdresses of forest beings, such as jaguars, deer, peccary, wild birds, and skeletal demons, along with the brimmed hats of hunters. Aside from the Bonampak scene, such headdresses are common in Classic Maya art, and designate warriors as denizens of the bush.

Along with warriors and hunters, Maya kings had a distinct relation with the forest, as they were capable of passing beyond political and natural boundaries to visit or conquer distant realms. With this unique ability, they were identified with the jaguar (the “king” of the forest)—a concept vividly expressed by royal litters and palanquins topped by jaguar beings. First appearing on Stela 21 of Late Preclassic Izapa, such jaguar vehicles are common in Classic Maya art, including figurines (see Thompson 1939, plate 23; Schele 1997, plate 16).

The most elaborate portrayals of jaguar palanquins appear on wooden lintels from Temples I and IV of Tikal (see Jones and Satterthwaite 1982, Figures. 70, 73; see Figure 26.10a-b). In the lintel scenes, the seated rulers are backed by massive supernatural jaguar figures (Figure 26.10a). The accompanying texts describe major Tikal victories against Calakmul and Naranjo (Martin and Grube 2000:44–45, 78–79).⁴ The jaguar palanquins reveal that, during the Classic Maya period, Maya kings prowled the landscape as fierce beasts guarding and extending their domain.



FIGURE 26.9. The routing and killing of panicked men in the forest. Note Chaak figures to left, and large stones apparently falling on figures, possibly a Late Classic Maya form of destruction of wooden men. Detail of Late Classic Maya mural, Mulchic (Source: Modified from Barrera Rubio 1989, Figure 1).

THE FOREST AND SUPERNATURAL POWER

According to Helms (1992:220–21), the ability of ancient Panamanian chiefs to travel in the forest endowed them with special supernatural powers. Similarly, ancient Maya rulers had the special ability to journey to the forest and distant lands—powers that could have been expressed by particular forest animals, such as the jaguar, as well as rare and exotic goods and materials. Stone (1995) notes that in Mesoamerican thought, caves of the forest wilds are the dwelling places of beings of fantastic wealth, who “control not just water and weather, but the most coveted fruits of nature, including land, game, and agricultural products” (Stone 1995:39).

Maya lore is filled with tales concerning pacts made with forest beings, who, although dangerous, can provide supernatural powers and wealth (e.g., Redfield and Villa Rojas 1934:121; Villa Rojas 1945:103-04; Tedlock 1982:149; Stone 1995: 39). Although isolated caves or hills are important forest loci for communicating with such forces as gods of rain, wind, and the hunt, aspects of the forest wilderness are also included in the human realms of the fields and community. Thus, among the Yucatec, the largest trees are spared from milpa clearing, thereby providing shade for young, growing maize (Redfield and Villa Rojas 1934:43). Similarly, a ceiba tree often appears in the center of Yucatec communities as the symbolic central axis, despite the fact that it also can be the nocturnal haunt of the X’tabay demon (see Souza Novelo 1980:108).

Forest imagery and symbolism commonly appears in the monumental art and architecture occupying the center of Classic Maya cities. It has been noted

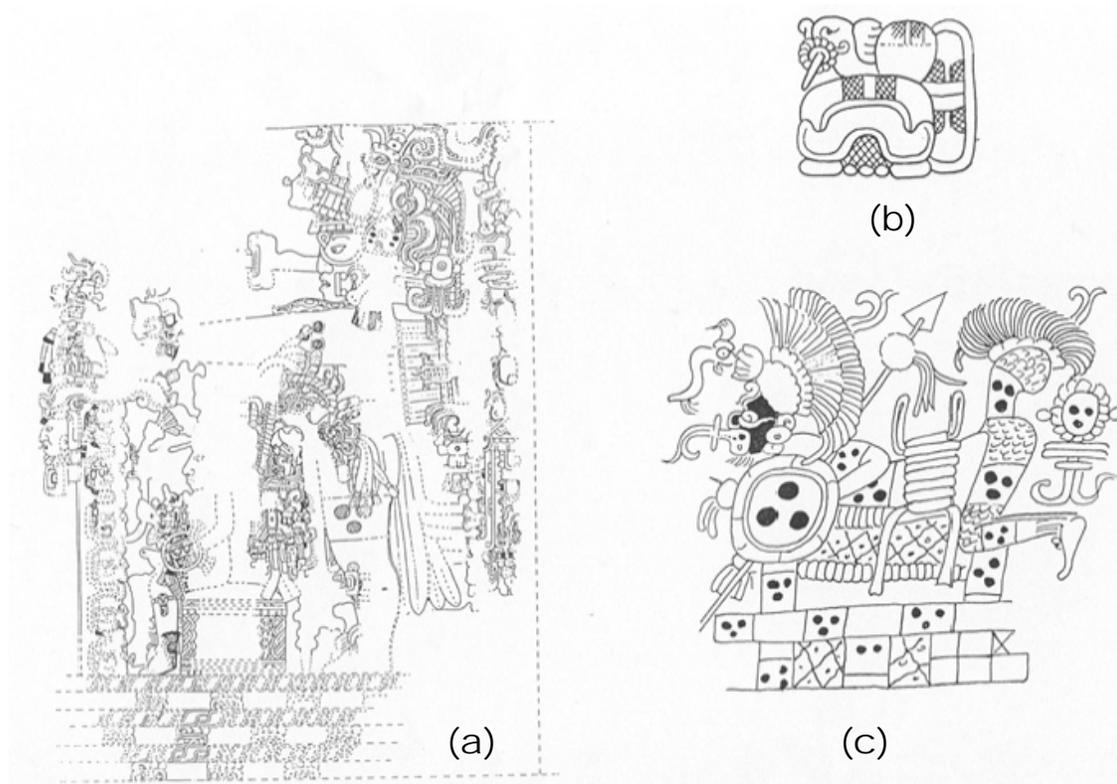


FIGURE 26.10. Late Classic Maya portrayals of the hummingbird jaguar palanquin of Naranjo. (a) Palanquin backed with massive jaguar figure. Note the remnants of a hummingbird beak and a pierced flower protruding from its face. Lintel 2 of Temple IV, Tikal (*Source*: Modified from Jones and Satterthwaite 1982, Figure 73). (b) Glyph for Lintel 2 palanquin with hummingbird. Note brow cruller and pierced flower on beak (*Source*: Modified from Jones and Satterthwaite 1982, Figure 73). (c) Hummingbird jaguar palanquin on vessel illustrating the early Naranjo king Aj Wosal (*Source*: Modified from Kerr 2000:1003).

that the ball court displays the symbolism of the forest and caves. In fact, the bringing of captives for the ballgame and consequent sacrifice is a vivid portrayal of channeling dangerous alien powers—in this case the foreign captives—for the spiritual well-being of the community.

Aside from the hunting god of Stela B, other forest characters appear in the monumental architecture of Copán. The East Court features a stairway with a pair of dancing jaguars flanking the central image of the Jaguar God of the Underworld. William Fash (1995, personal communication) notes that a massive sun god head was probably placed at the opposing east side of the court (for sculpture, see Maudslay 1889–1902:I:plate 10b). Whereas the eastern head refers to the diurnal world, the western deity and his attendant jaguars symbolize the night. Another pair of forest beings flank the sides of the Reviewing Stand in the West Court. With their rattles and old, simian

features, these figures can be identified as a specific ritual clown character, “a fantastically ugly, aged and wrinkled were-monkey” (Taube 1989:366).

As with contemporary Maya performance, Classic Maya rituals clowns are frequently amoral forest beings. Their appearance may often have been timed to period-ending events, such as the termination of the K’atun. The text upon which the West Court performers stand concerns the period ending date 9.17.0.0.0 13 Ahau 18 Kumk’u. The incised peccary skull from Copán features a stela and altar in a cave quatrefoil surrounded by forest beings, including a were-monkey clown with his rattle, an enema-bearing jaguar, peccaries, and a deer facing a skeletal hunter ‘way’ (see Fash 1991, Figure 52). The K’atun ending date 8.17.0.0.0 1 Ahau 8 Ch’en accompanies the stela, precisely 1 Bak’tun before the Reviewing Stand text.

The Postclassic Codex Dresden illustrates forest performers at the termination of the 365-day year (the final five days known as Wayeb in Yucatec). The upper portion of the New Year passage appearing on Codex Dresden pages 25 to 28 features opossum performers striding with rattle staffs, dancing fans, and belt tinklers. Aside from its appearance as ritual entertainer in the Classic Maya period, the opossum is mentioned as a ritual clown in the colonial Book of the Chilam Balam of Tizimin (Taube 1989:353, Figures 24.1–2). These grizzled, shambling beings represent creatures of the forest entering at the directional entrances of the community during Wayeb celebrations. Wild animals are also featured in the New Year passage appearing on Codex Paris pages 19 and 20, including a jaguar attacking a human victim. According to the colonial account of de Cogolludo (1954:353), the Wayeb is especially feared as a time when people would be attacked by snakes and wild beasts. During the Wayeb, forest beings invade the world of humans.

Contemporary Maya traditions provide a vivid insight into the meaning of the ritual invasion of the forest during the Wayeb and other period-ending rites. Among the Tzotzil, there is the five-day festival of Carnival ending with Ash Wednesday. In Chamula thought, Carnival is explicitly equated with their calendric five-day Wayeb, here known as ch’ay k’in, or “lost fiesta” (Gossen 1974a:229–30, 233–34). During Carnival, raucous and aggressive forest beings (i.e., the monkey impersonators known as maxetik) dominate the community (Bricker 1973:84–126). As Bricker (1973) notes, Chamula Carnival constitutes “a period of license and evil which marks the end of the old year” (Bricker 1973:126). A number of maxetik carry stuffed animals representing animal spirit souls; with these animals, they jokingly threaten to destroy one’s soul in the forest (Bricker 1973:95).

At Chenalhó, Carnival is also the time of amoral forest beings, including monkeys, jaguars, Lacandon characters, and demons (Bricker 1973:127–44). In Zinacantan, the major period of forest animals and demons is not Carnival, but the January celebrations of San Sebastián, marking the annual change of

cargo officials (Bricker 1973:46–67; Vogt 1976:159–78). As with Chamula Carnival, stuffed animals are also carried, although here they represent the shameless and lascivious wives of errant cargo holders.

The forest creatures appearing in the Tzotzil celebrations of Carnival and the Zinacanteco festival of San Sebastián clearly have a number of social functions and meanings. For one, the wild animal and demon impersonators are both entertaining and frightening; in Classic Maya art, animals engaged in drink and dance are frequently depicted with a certain degree of humor (e.g., Taube 1989, Figure 24.1–2). In addition, the forest characters are important sources of social commentary, who not only point out the misdeeds of particular individuals in the community, but also by their ridiculous and bestial behavior stress essential moral qualities of humans beings. In a similar manner, Maya beliefs concerning forest demons, such as the Yucatec X'tab'ay temptress, enforce proper modes of conduct. Thus, the seven forest apparitions described by Wisdom (1940:404–05) for the Ch'orti' serve as “the enforcers of moral life.” Stross notes that Tzeltal demon tales serve as warnings and lessons for correct human behavior, “rules as it were, for getting along and staying alive” (Stross 1978:37).

Aside from their ritual roles as entertainers and social commentators, the forest beings of ancient and contemporary Maya celebrations express a profound message of human existence. In a telling statement, Vogt notes that a major theme of the festival of San Sebastián is “the reprehensible but inescapable ‘animalism’ in all Zinacantecos” (Vogt 1976:175). Of course, this inherent “animalism” is also expressed by the ‘way’ animal spirits, which constitute the “wild” forest aspect of humans. Although the precise etymology of the term “Wayeb” remains obscure, it probably alludes to dreams and the night. In Yucatec, ‘way’ can signify “to see visions as in dreams”; *wayak'*, to mean “dream”; and ‘way’ to be a “journey that is done at night” (Barrera Vásquez 1980:916–17).

Although labor and daylight are of the ordered world, other necessary aspects of human existence are dreams and the night, which are qualities of the forest. In a discussion of the Tz'utujil Maya of Santiago Atitlán, Stanzione notes: “Without proper rest us humans go crazy and eventually die, without dreams we often find no reason to live” (Stanzione 2000:42). For the Tz'utujil, dreams are important source of information to shamans and midwives (Stanzione 2000:42). In Zinacantán, during dreams “the souls of plants interact with man ‘beneath the earth’s surface’ ” (Laughlin 2000:105). From such dreams, shamans, midwives, and bonesetters get their powers to cure (Laughlin 2000:105). Aside from providing plant knowledge, dreams also reveal the identity and character of one’s animal soul (Pitt-Rivers 1970:190; Laughlin 1976:5). According to Laughlin, dreaming is an essential part of Zinacanteco existence: “They dream to life a full life. They dream to

save their lives” (Laughlin 1976:3). In Maya thought, humans contain the forest in their beings, a force that manifests itself in nocturnal dreams.

Just as the ordered world was made by the gods at creation and is reasserted by humans in their diurnal efforts, constructed order ultimately tires and reverts to natural chaos. The burdens of time and public service to the community are heavy loads that eventually must be laid to rest. Implicit in the creation of the ordered world is the creation of time. Thus, in Classic Maya belief, the creation of the present Long Count cycle concerned the setting of the three hearthstones constituting the center of the four-sided world (see Freidel, Schele, and Parker 1993, ch. 2). In contrast, the dark forest and its beings embody the timelessness beyond and before the creation of the ordered world and time.

According to Ochai, the term for the Tzotzil Wayeb, *ch’ay k’in*, could be interpreted as “the period without sun” (Ochai 1984:217–18) and is a ritual form of an extended night—a return to primordial time when powerful beings from the fringe of creation enter the community. Ochai (1984:221) notes that during ancient Yucatec Wayeb and Tzotzil Carnival, the invasion of chaos renews and revives the cycle of time. In Maya thought, darkness and the night are often related to supernatural power. Stone (1995) notes that the colonial Quiché kept idols were kept in dark places to conserve their spiritual force, and it is quite likely that ancient Maya temples or “god-houses” functioned similarly (Stone 1986:17). According to Wisdom, darkness protects sacred objects among the contemporary *Ch’orti’*, and the favored areas to contact supernaturals are “dark rooms or in dark places in the forest” (Wisdom 1940:431). As a primordial region of darkness, the forest wilds are a continual source of supernatural power. Much as the bush covers and replenishes fallow fields, forest beings restore the spiritual power of the human world during calendrically timed ritual events.

CONCLUSION

Hanks notes that “the forest belongs to the Maya and they to it” (Hanks 1990:389). Along with the maize fields, the forest is in the domain of men, while the household and community belong to the realm of women. Thus, two of the major activities of the forest—hunting and war—are performed by men. The ritual penetration of the static and passive community by aggressive, sexually-charged forests beings could well be a symbolic form of conception and regeneration. Although a place of fear and danger, the forest is an essential and necessary part of human existence. Aside from its material benefits of food, medicine, and goods, the forest wilds are a continuous source of inspiration and reflection. A fascinating nest of contradictions, the forest both threatens and reinforces social cohesion, and sharply delineates the

border of the created world of humans. Although the beasts and demons that inhabit the bush are amoral, their absurd behavior and threat of danger reinforce fidelity, sobriety, and a broad range of other social values.

Many Maya conceptions of the forest are undoubtedly part of a very widespread and ancient complex concerning the dynamic and complex relation of humans to the surrounding natural world. In central Mexican thought, the wilderness is also a frightening, dangerous place (Stone 1995:16). Among the contemporary Yaqui and Mayo of Sinaloa, the annual pre-Lenten dramas concerning the Passion of Christ feature the temporary invasion of the community by amoral animal demons (e.g., Crumrine 1977:90–94).

Similar ritual invasions of the forest are also known in native traditions of North America. Thus, among the Iroquois, there is the False Face Society, who wear masks designed from dreams and visions of forest spirits (Fenton 1987:27–29). Beings of both illness and curing, False Faces have important roles in Iroquois communities during the Midwinter celebration, as well as the spring and autumn purification of the houses. As with Maya forest spirits, the False Faces are ancient—“no one ever sees them now”—and live in distant wilds, which, in this case, is far, far to the west (Fenton 1987:144). Among the Kwakiutl of British Columbia, there is the great *tseka* Winter Ceremonial featuring performers impersonating spirits and animals of the forest that fill the community with spiritual power (Boas 1966:171–298).

Although it would be tempting to consider the Mesoamerican and North American community forest celebrations as deriving from a shared tradition of the distant past, such ceremonies are found with many sedentary peoples around the world. Thus, powerful and frequently malevolent bush spirits are a common feature of masked dances in west African communities (Anderson and Kreamer 1989). For the Dan of Liberia, the *gle* masks are potent embodiments of forest beings who are envisioned in dreams (Johnson 1986:5). Masked forest spirit performances are also widespread in Melanesia. Among the Elema of the Papuan Gulf, there is the *kovave* cycle of male initiation, during which the youths impersonate semi-comical bush spirits for a month within the village until the masks are finally burned and the participants acquire their adult human status (Meyer 1995:127). Although this paper is only an initial effort in discussing contemporary and ancient Maya conceptions of the forest in relation to human space, a cross-cultural study of native views of forest and village would surely reveal a broad spectrum of significant shared traits and parallels.

In traditional Maya thought, the forest is indifferent to the human world and even the forces of creation; it is a place that always was and always will be. However, this is a static and internal perspective that does not include current economic and political conditions in Latin America and the world. A satellite image published by National Geographic in 1989 graphically portrays the natural and social devastation from thousands of highland Guatemala

Maya being forced out of their ancient centers to live under the forest (Garrett 1989, 474–75). Due to development and the steady increase in human population, the remote edge of the Maya world is not the forest, but modern industrialized society. Unless steps are taken to preserve this critical but increasingly limited region, the Maya forest will indeed become a remote place of dreams, imagination, and the past.

NOTES

1. The recognition of the Classic Maya ‘way’ beings as forest spirits may help explain the relation of the Classic Maya Xbalanque to his twin Hun Ajaw. Rhonda Taube (2001, personal communication) notes that the jaguar pelt Hero Twin may constitute the ‘way’ of Hun Ajaw. Thus, the jaguar pelt body marking also appears on the ‘way’ logograph, which is no more than an Ajaw glyph, half covered by the pelt (see Houston and Stuart 1989, Figure 1). In Classic Maya writing, the stylized Ajaw sign substitutes freely with the portrait glyph of Hun Ajaw. While Hun Ajaw is the lord of the community and the day, his ‘way’ twin rules the forest and the night.

2. Houston (2001, personal communication) notes that one painted text from the cave of Naj Tunich contains a couplet referring to the seeing of both a road and a way (see Stone 1995, Figures 8–65d).

3. To the Aztec, banished kings and others were said to follow the road of the rabbit and deer, the same twisted and treacherous path of prostitutes (Burkhart 1986:125; Maxwell and Hanson 1992:177).

4. For Lintel 3 of Temple IV, the palanquin was a trophy taken from Naranjo (Martin and Grube 2000:78–9). The hieroglyph for this vehicle is a hummingbird with the brow “cruller” of the Jaguar God of the Underworld and a beak piercing a flower (Figure 26.10b). The remains of a similar beak and pierced blossom can be seen on the palanquin figure, which also displays the “cruller” brow element (Figure 26.10a). This palanquin also appears on a Tepeu 1 vessel illustrating the early Naranjo king Aj Wosal with his warriors (Figure 26.10c; see Kerr 2000:1003). It is quite likely that the Naranjo vessel portrays the hummingbird jaguar palanquin—or a form of it—before its capture by Tikal.

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PART V:
PLANTS AND PEOPLE

Chapter 27

Geographical and Historical Variation in Hurricanes Across the Yucatán Peninsula

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Brian Hall

INTRODUCTION

Disturbance is a continual though varying theme in the history of the Yucatán Peninsula. Ancient Maya civilizations cleared and modified much of the forested landscape for millennia, and then abruptly abandoned large areas nearly 1,000 years ago, allowing forests of native species to reestablish and mature (Turner 1974; Hodell, Curtis, and Brenner 1995). More recently, late twentieth century population growth has fueled a resurgence of land-use activity including logging, slash-and-burn agriculture, large mechanized agricultural projects, tourism, and urban expansion (Turner et al. 2001; Turner, Geoghegan, and Foster 2002). Throughout this lengthy history, fires have affected the region—ignited purposefully or accidentally by humans, and occasionally by lightning (Lundell 1940; Snook 1998). And, as indicated by ancient Maya records, historical accounts, and contemporary observations, intense winds associated with hurricanes have repeatedly damaged forests and human settlements (Wilson 1980; Morales 1993).

Despite the generally acknowledged importance of natural and human disturbance in the Yucatán Peninsula, there has been little attempt to quantify

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the spatial and temporal distribution of this activity, or to interpret its relationship to modern vegetation patterns (cf. Lundell 1937, 1938; Cairns et al. 2000). As a consequence, we have relatively little information regarding the major drivers of regional patterns in vegetation structure and composition. In order to undertake such analyses, it is necessary to develop quantitative descriptions of the variation in soils, climate, and disturbance geographically and over long periods of time (Turner, Geoghegan, and Foster 2002).

In this study, hurricane impacts across the Yucatán Peninsula over the last 150 years. In particular, we seek to document regional differences in hurricane disturbance regimes—that is, the observed variation in frequency and distribution of winds of different intensity (cf. Heinselman 1973; Foster and Boose 1995; Boose, Chamberlin, and Foster 2001). Our analysis is based on the detailed meteorological records maintained by the U. S. National Hurricane Center (see as bellows). These records, which contain track and maximum wind speed data for Atlantic hurricanes since 1851, enable us to reconstruct the general pattern of wind speed, direction, and damage associated with each historical storm using a meteorological model (HURRECON) developed at Harvard Forest and available on the Harvard Forest Web site.

Hurricanes may exert a strong impact on forest ecosystems and human activities. Therefore, a quantitative estimate of the variation of these impacts through time and space should enhance the understanding of long-term landscape dynamics, as well as current patterns of vegetation, and should aid in anticipating future impacts by hurricanes in this region.

METHODS

The study region consisted of the Mexican states of Campeche, Yucatán, and Quintana Roo, which comprise the upper two-thirds of the Yucatán Peninsula (Figure 27.1). An intensive compilation and analysis of historical records, which was pursued in earlier studies of New England and Puerto Rico (Boose, Chamberlin, and Foster 2001) but which would be far more difficult for the peninsula because of its small and rural population, was beyond the scope of this project. Therefore, the approach taken was to reconstruct hurricanes over the last 150 years using the best available meteorological data and model parameters that were found to work well for hurricanes in Puerto Rico.

Meteorological data

The primary source of meteorological data was the HURDAT (Hurricane Data) database maintained by the U.S. National Hurricane Center (Neumann,



FIGURE 27.1. The study region within the Yucatán Peninsula, with major political boundaries and place names identified (see text).

Jarvinen, and Pike 1987; NOAA 1994). Recently, HURDAT has been updated to include location and maximum one-minute sustained wind speed (i.e., averaged over a one-minute period) every six hours for all known Atlantic hurricanes since 1851 (NHC 2001). HURDAT was used to identify all storms that approached within 300 km of the study region with sustained winds of hurricane force (33 m/s) or greater. A total of 105 hurricanes from 1851 to 2000 were selected for meteorological reconstruction and analysis (Table 27.1).

Hurrecon model

A simple meteorological model (HURRECON), based on published empirical studies of many hurricanes and developed in previous studies of historical hurricanes in New England and Puerto Rico (Boose, Foster, and Fluet 1994; Boose, Chamberlin, and Foster 1997, 2001), was used to reconstruct the impacts of each storm. HURRECON uses information on the track, size, and intensity of a hurricane, as well as the cover type (land or water), to estimate surface wind speed and direction. The model also estimates wind damage on the Fujita scale by using the correlation between maximum quarter-mile wind velocity (i.e., maximum wind velocity sustained over a quarter-mile distance) and wind damage proposed by Fujita (1971).

TABLE 27.1. Dates, meteorological characteristics, and reconstructed damage for the 105 hurricanes investigated in this study.

Hurricane No.	Date	Name	SS Cat	Track	Fmax
Y1852	5	Oct 7-8	2	O	F1
Y1857	4	Sep 28	2	N	F1
Y1861	2	Aug 17	1	O	nd
Y1864	3	Aug 31	1	S	F1
Y1865	4	Sep 11	2	O	F1
Y1866	2	Aug 16	1	N	F1
Y1868	3	Oct 7	2	O	F1
Y1870	11	Oct 31- Nov 2	1	N	F1
Y1873	5	Oct 4-5	2	O	F2
Y1877	4	Sep 28-29	1	O	F1
Y1878	2	Aug 14-15	1	O	F0
Y1879	3	Aug 20	1	N	F1
Y1880	2	Aug 9	2	N	F2
Y1882	2	Sep 7	1	O	F0
Y1886a	2	Jun 18-19	1	O	F1
Y1886b	3	Jun 28 1	2	N	F1
Y1886c	4	Jul 15-16	1	O	F0
Y1886d	7	Sep 19	2	O	F0
Y1887a	2	Jul 25	2	N	F1
Y1887b	7	Sep 17	2	N	F1
Y1887c	11	Oct 15-16	1	O	F0
Y1888	4	Sep 6-7	1	N*	F1
Y1889	6	Sep 17-18	2	S	F1
Y1892	7	Oct 12-13	1	S	F1
Y1893a	2	Jul 6	1	S	F0
Y1893b	8	Sep 4-5	1	N*	F0
Y1893c	10	Sep 28-29	1	N	F1
Y1894	4	Oct 5	3	O	F1
Y1895	2	Aug 26-27	2	N	F1

Hurricane	No.	Date	Name	SS Cat	Track	Fmax
Y1896a	4	Sep 27-28		3	O	F0
Y1896b	5	Oct 7-8		1	O	nd
Y1902	4	Oct 5-8		1	W	F1
Y1903	2	Aug 12-13		2	N	F2
Y1906a	5	Sep 24		1	O	F0
Y1906b	8	Oct 16-17		3	O	F0
Y1909a	3	Jul 18-19		1	O	nd
Y1909b	5	Aug 25-26		3	O	F2
Y1909c	7	Sep 17-19		3	O	F0
Y1910a	2	Sep 11		2	O	F0
Y1910b	4	Oct 16		3	O	F0
Y1912	5	Oct 12-13		2	N	F1
Y1913	1	Jun 24-25		2	N	F1
Y1915a	2	Aug 15		3	O	F1
Y1915b	5	Sep 27-28		3	O	F1
Y1916a	1	Jul 3-4		2	O	F1
Y1916b	4	Aug 17		3	O	F2
Y1916c	6	Sep 1-2		1	S	F1
Y1916d	13	Oct 15-16		2	N*	F2
Y1916e	14	Nov 14-15		1	O	F1
Y1917	3	Sep 26		3	O	F0
Y1921	6	Oct 23-24		3	O	F1
Y1922	4	Oct 18-20		1	N*	F1
Y1924	7	Oct 18-19		3	O	F0
Y1926	3	Aug 22-23		1	O	nd
Y1931a	5	Sep 10-11		3	S	F2
Y1931b	6	Sep 14-15		1	N*	F0
Y1933a	2	Jul 3-4		2	O	nd
Y1933b	14	Sep 12-14		1	N	F1

Table 27.1 (continued)

Hurricane No.	Date	Name	SS Cat	Track	Fmax	
Y1933c	15	Sep 22-23	2	N	F2	
Y1934	2	Jun 8-9	1	N	F1	
Y1938a	2	Aug 13	2	N	F1	
Y1938b	3	Aug 25-26	2	N	F1	
Y1941a	2	Sep 20-21	1	O	F0	
Y1941b	4	Sep 28	1	S	F0	
Y1942a	2	Aug 27-28	2	N	F2	
Y1942b	10	Nov 8-9	2	S	F1	
Y1944a	4	Aug 22-23	1	N	F1	
Y1944b	8	Sep 20-21	1	N	F1	
Y1945	10	Oct 4	1	S	F0	
Y1946	5	Oct 6-7	2	O	F0	
Y1947	2	Aug 12-13	1	N*	F0	
Y1948	8	Oct 4-5	2	O	nd	
Y1950	2	Aug 28	Baker	1	O	nd
Y1951	3	Aug 19-20	Charlie	4	N	F2
Y1953	8	Sep 24-25	Florence	3	O	F1
Y1955a	8	Sep 16-17	Hilda	2	N	F2
Y1955b	10	Sep 28	Janet	5	N	F3
Y1960	2	Jul 15	Abby	1	S	nd
Y1961a	1	Jul 24	Anna	1	S	F0
Y1961b	3	Sep 6-8	Carla	3	O	F2
Y1961c	9	Oct 31	Hattie	4	S	F2
Y1964a	10	Sep 29-30	Hilda	3	O	F0
Y1964b	11	Oct 13	Isbell	1	O	nd
Y1966	9	Oct 6-7	Inez	4	O	F2
Y1967	2	Sep 17	Beulah	2	N	F2
Y1969a	3	Aug 15-16	Camille	4	O	F0
Y1969b	6	Sep 3-4	Francelia	2	S	F0

Hurricane	No.	Date	Name	SS Cat	Track	Fmax
Y1969c	15	Oct 19-23	Laurie	1	N	nd
Y1970a	3	Aug 1-2	Celia	3	O	F0
Y1970b	6	Sep 10-11	Ella	1	N	nd
Y1971	6	Sep 10-11	Edith	1	S	F0
Y1972	2	Jun 17-18	Agnes	1	N	nd
Y1973	3	Aug 19-21	Brenda	1	N*	F1
Y1974a	6	Sep 2-6	Carmen	4	N	F3
Y1974b	9	Sep 19-20	Fifi	2	S	F0
Y1978	8	Sep 18-19	Greta	2	S	F1
Y1980a	1	Aug 7-8	Allen	5	O	F3
Y1980b	10	Nov 11-12	Jeanne	1	O	nd
Y1988	8	Sep 14-15	Gilbert	5	N	F3
Y1993	7	Sep 19-20	Gert	1	S	nd
Y1995a	15	Oct 1-3	Opal	1	N*	F0
Y1995b	17	Oct 10-16	Roxanne	3	N	F2
Y1996	4	Aug 20	Dolly	1	N	F1
Y1998	13	Oct 27-28	Mitch	5	S	F1
Y2000	15	Oct 1-3	Keith	4	S	F2

Hurricane = year of storm; letters (a, b) indicate multiple storms in same year.

No. = tropical storm number in HURDAT.

Date = date of landfall or closest approach to the Yucatán Peninsula.

SS Cat = Saffir-Simpson category at time of greatest impact.

Track = offshore (O) to north or east; landfall in northeast (N) peninsula (Quintana Roo); landfall in southeast (S) peninsula (Belize), or further south; or offshore to west (W) of peninsula. Storms that reintensified after crossing the peninsula and caused greater reconstructed damage in western or northern areas are marked with an asterisk.

Fmax = maximum reconstructed damage in the states of Campeche, Yucatán, or Quintana Roo. See text for description of F-scale ranges.

nd = no damage.

Model equations are given below. Wind velocity and direction are measured relative to the Earth's surface, and angles are measured in degrees. Parameter values used in this study are given in parentheses.

The sustained wind velocity (V_s) at any point P in the northern hemisphere is estimated as follows:

$$V_s = F[V_m - S(1 - \sin T)V_h/2] [(R_m/R)^B \exp(1 - (R_m/R)^B)]^{1/2} \quad (1)$$

In equation (1), F = a scaling parameter for the effects of friction (water = 1.0, land = 0.8), V_m = maximum sustained wind velocity over water anywhere in the hurricane, S = a scaling parameter for asymmetry due to the forward motion of the storm (1.0), T = the clockwise angle between the forward path of the hurricane and a radial line from the hurricane center to point P , V_h = the forward velocity of the hurricane, R_m = the radius of maximum winds (50 km), R = the radial distance from the hurricane center to point P , and B = a scaling parameter controlling the shape of the wind profile curve (1.3).

The peak wind gust velocity (V_g) at point P is estimated from V_s as follows:

$$V_g = GV_s \quad (2)$$

In equation (2), G = the gust factor (water = 1.2, land = 1.5). The maximum quarter-mile wind velocity (V_p) is estimated from G and V_s using Fujita's method (Fujita 1971, equ. 12).

Wind direction (D) at point P is estimated as follows:

$$D = A_z - 90 - I \quad (3)$$

In equation (3), A_z = the azimuth from point P to the hurricane center, and I = cross isobar inflow angle (water = 20° , land = 40°). In the southern hemisphere, T is the counterclockwise angle between the forward path of the hurricane and a radial line from the hurricane center to point P , and $D = A_z + 90 + I$.

Parameter values for F , G , and I were adopted directly from published sources, and these values and the value for S were found to work well for hurricanes in New England and Puerto Rico (Boose, Chamberlin, and Foster 2001). The parameters B and R_m , which control the width of the modeled storm (for a given value of V_m), were assigned values found to be most common for hurricanes in Puerto Rico.

Fujita scale

The Fujita system for characterizing wind damage in tornadoes and hurricanes, used by the U.S. National Weather Service for tornadoes (Grazulis 1993), was found in earlier studies to be an effective method both for quantifying actual wind damage and for reconstructing the ecological impacts of historical storms (Boose, Chamberlin, and Foster 2001). The Fujita scale ranges from F0 (minor damage in gale force wind) to F5 (extreme damage in the most severe tornadoes). In assessing actual wind damage, Fujita values are assigned based on specific levels of damage to common cultural and biological features in the landscape. Corresponding sustained wind speeds proposed by Fujita for the lower levels of damage encountered in hurricanes are as follows: F0 = 18–25 m/s, F1 = 26–35 m/s, F2 = 36–47 m/s, and F3 = 48–62 m/s (assuming a wind gust factor of 1.5 over land; Fujita 1971, 1987). These values were used in this study to convert reconstructed peak wind velocity to predicted wind damage on the Fujita scale.

As a general rule for mature forest stands, F0 damage means loss of leaves and small branches, F1 damage means isolated blowdowns (small gaps), F2 damage means extensive blowdowns (large gaps), and F3 damage means most trees are blown down (Fujita 1971, 1987). These impacts, however, are strongly dependent on forest structure and composition, and the short-stature, dry forests of the Yucatán Peninsula may be more resilient than average and suffer less damage for the same range of wind speeds.

Compilations

HURRECON provides estimates for individual sites (as tables) and for entire regions (as GIS maps in IDRISI format; Eastman 1997). Model runs were completed for two individual sites: (1) Zoh Laguna, a small town in the south-central peninsula, and (2) Cancún, in the northeastern tip (see Figure 27.1), using a time step of five minutes and assuming the cover type to be land. Regional estimates were made at 7.5-km resolution using a time step equal to the minimum time required for each hurricane to traverse one grid cell (7.5 km x 7.5 km) within the regional study window (lat. 15.5–22.5° N , long. 86–92° W).

Maps of reconstructed damage for individual hurricanes were compiled to generate maps showing the number of storms at a given minimum intensity (F0, F1, F2, or F3) and the maximum F-scale intensity for each grid cell. Each frequency map was then divided by hand into three to five regions, and a mean return time was calculated for each region (rounded to the nearest five years for values greater than ten years).

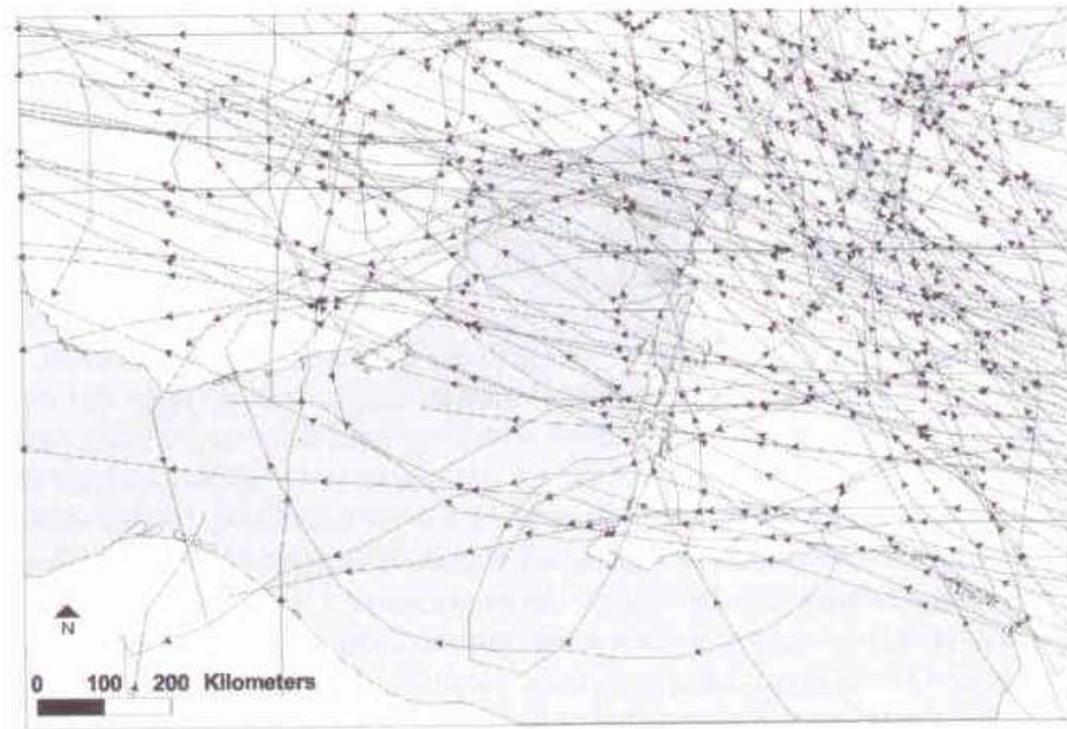


FIGURE 27.2. Tracks of 105 hurricanes investigated in this study during the period 1851-2000.

RESULTS AND DISCUSSION

Meteorological characteristics

The intensity of the hurricanes studied ranged from category 1 to category 5 on the Saffir-Simpson scale at the point of greatest impact to the Yucatán Peninsula (see Table 27.1), based on the maximum sustained wind speed (V_m) values in HURDAT. Forty-six hurricanes (44 percent) were category 1 ($V_m = 33\text{--}42$ m/s), 31 hurricanes (29 percent) were category 2 ($V_m = 43\text{--}49$ m/s), 18 hurricanes (17 percent) were category 3 ($V_m = 50\text{--}58$ m/s), 6 hurricanes (6 percent) were category 4 ($V_m = 59\text{--}69$ m/s), and 4 hurricanes (4 percent) were category 5 ($V_m = 70+$ m/s).

The track map for all 105 hurricanes shows that most hurricanes approach the Yucatán Peninsula from the east-southeast, with the greatest density of storms offshore to the north or east, or landing on the northeastern part of the peninsula (Figure 27.2). All but one of the hurricanes studied may be assigned to one of three broad patterns of hurricane tracks and consequent wind damage (see Table 27.1; the exception was Y1902, whose anomalous track lay to the west of the Yucatán Peninsula):

1. *Offshore (O) to north or east.* Forty-five hurricanes (43 percent) passed offshore to the north and east of the Yucatán Peninsula (Figure 27.3a–c). Because most of their circulation remains over the warm waters of the Caribbean Sea and the Gulf of Mexico, such hurricanes show little or no change in intensity as a result of passing near the peninsula (cf. Bender and Ginis 2000). Impacts on the Yucatán Peninsula, which experiences the somewhat weaker (left) side of these storms, are usually moderate; however, very intense hurricanes that come close to shore, such as Hurricane Allen (Y1980a; Figure 27.3c), may cause significant damage along the northeastern coast.
2. *Landfall in northeastern (N) peninsula.* Forty hurricanes (38 percent) made landfall in Quintana Roo in the northeastern part of the peninsula (Figure 27.3d–f). In general, these storms weaken as they pass over the peninsula, although they frequently reintensify upon reaching the Gulf of Mexico. Twenty percent of the hurricanes in this group reintensified to the point where the greatest reconstructed impacts were on the western and northern parts of the peninsula (see Table 27.1). Hurricanes in this group have the potential to cause the greatest wind damage across the study region, especially along the eastern coast.
3. *Landfall in southeastern (S) peninsula.* Nineteen hurricanes (18 percent) made landfall in Belize in the southeastern part of the peninsula, or further south (Figure 27.3g–i). Many of these storms weaken and dissipate over the mountains of Mexico or Guatemala, although a few cross over to the Pacific; others curve to the north and enter the Gulf of Mexico, where they may reintensify. These storms generally have moderate impacts across the study region, although significant damage can occur in Belize and occasionally on the northern coasts of Guatemala and Honduras.

Temporal patterns

Over the period 1851–2000, there was considerable variation in hurricane activity from year to year. Sixty-two hurricanes were estimated to have caused significant damage (F1+) across the study region, yielding an average return interval of 2.4 years. In nine separate years there were two such hurricanes; in one year (1916) there were five. The maximum interval between two such storms was 9 years (note that these are regional values and do not apply to any given site). On a decadal scale, the number of F1+ hurricanes ranged from two storms (1850s, 1920s, 1980s) to nine storms (1910s) per decade (Figure 27.4). Similar multidecadal variation in hurricane frequency was observed in studies of New England and Puerto Rico (Boose, Chamberlin, and Foster 2001) and is

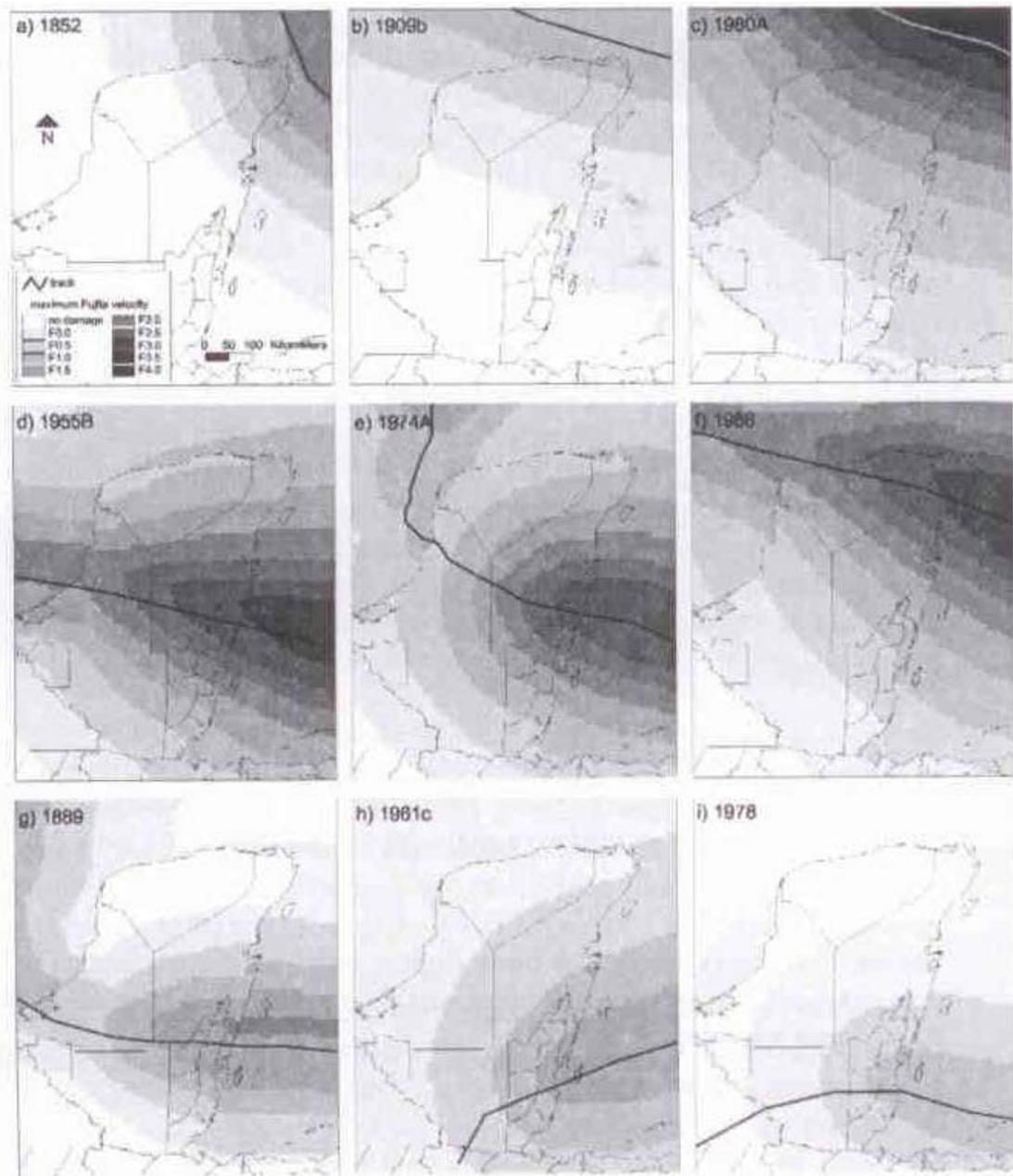


FIGURE 27.3. Representative and important storms illustrating three broad patterns of hurricane tracks and consequent wind damage: (a-c) offshore to north or east, (d-f) landfall in northeastern peninsula (Quintana Roo), and (g-i) landfall in southeastern peninsula (Belize) or farther south. Maps show reconstructed damage on the Fujita scale in 0.5-class increments. See Table 27.1 for a complete list of all hurricanes.

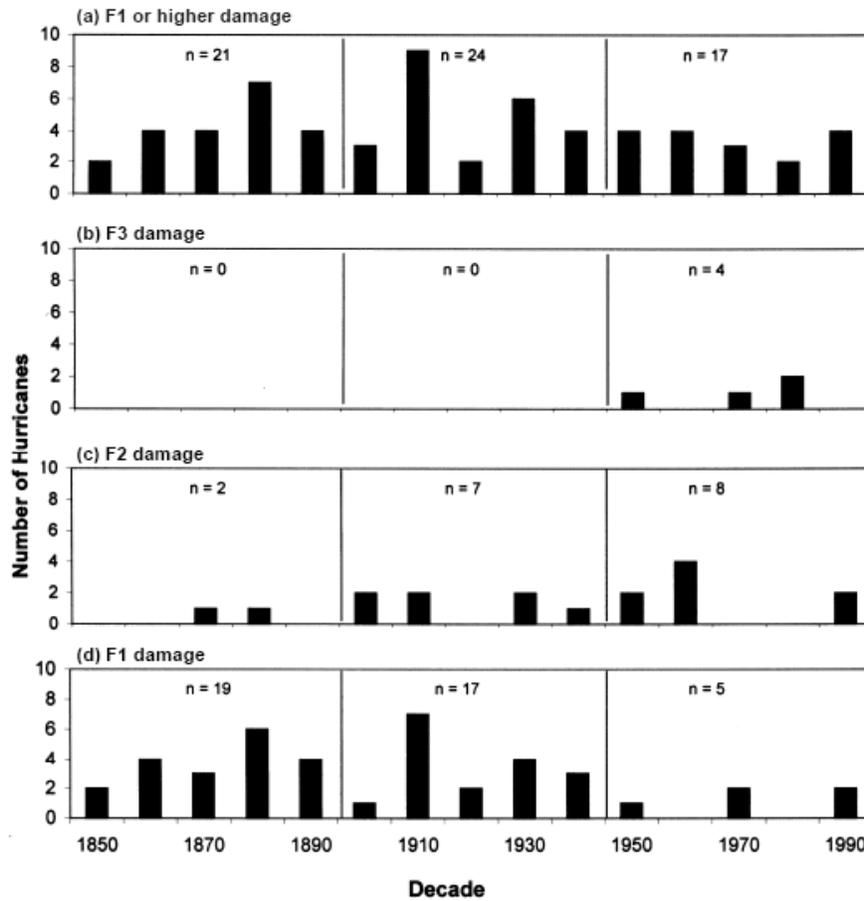


FIGURE 27.4. Number of hurricanes by decade over the entire study area, with maximum reconstructed damage on the Fujita scale equal to (a) F1 or higher, (b) F3, (c) F2, and (d) F1.

well-documented for Atlantic hurricanes in general (Neumann, Jarvinen, and Pike 1987).

The total number of F1+ hurricanes since 1851 was fairly constant at a half-century scale, suggesting that few if any hurricanes escaped historical notice during this period (Figure 27.4). Similar results were found for hurricanes in New England and Puerto Rico during the same period (Boose, Chamberlin, and Foster 2001). There was a significant increase, however, in reconstructed hurricane damage in the Yucatán Peninsula: all four hurricanes causing F3 damage occurred after 1950, while there were considerably fewer F2 storms during the period 1851–1900 and only five F1 storms since 1950.

A similar trend can be seen in the overall intensity of the hurricanes studied: all category 4 and 5 hurricanes (on the Saffir-Simpson scale) occurred since 1950, while the fraction of category 3 hurricanes was significantly higher in 1901–1950 than in 1851–1900 (Figure 27.5). To some extent, this

trend may reflect limitations in the HURDAT database itself; for example, nineteenth-century hurricanes were frequently classified as category 2 in the absence of other information, resulting in a disproportionate number of category 2 hurricanes during this period (C. Landsea, pers. comm.). Thus, the intensity of some early hurricanes may be underestimated in HURDAT. At the same time, the historical records from New England (380 years) and Puerto Rico (500 years) suggest that 150 years may not be long enough to detect long-term trends for the most intense (and rare) hurricanes (Boose, Chamberlin, and Foster 2001). More historical and paleoecological research is needed to resolve these issues.

Analysis of the seasonal distribution of hurricane activity in the study region showed that 80 percent of the F1 hurricanes and all of the F2 and F3 hurricanes occurred in the months of August, September, and October (Figure 27.6). This distribution closely matches the observed pattern in New England, while in Puerto Rico nearly 85 percent of the F1+ hurricanes occurred in the two months of August and September (Boose, Chamberlin, and Foster 2001).

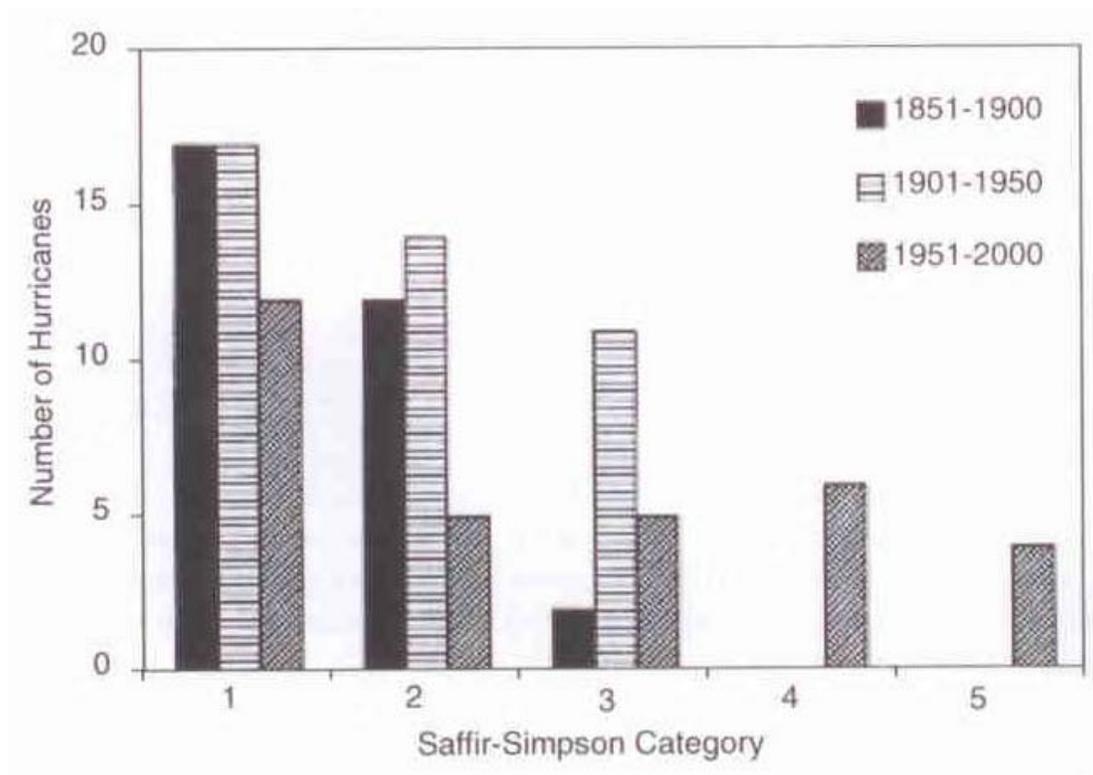


FIGURE 27.5. Number of hurricanes by Saffir-Simpson category (at time of greatest impact to the Yucatan Peninsula) for three 50-year periods. All 105 hurricanes investigated in this study area included.

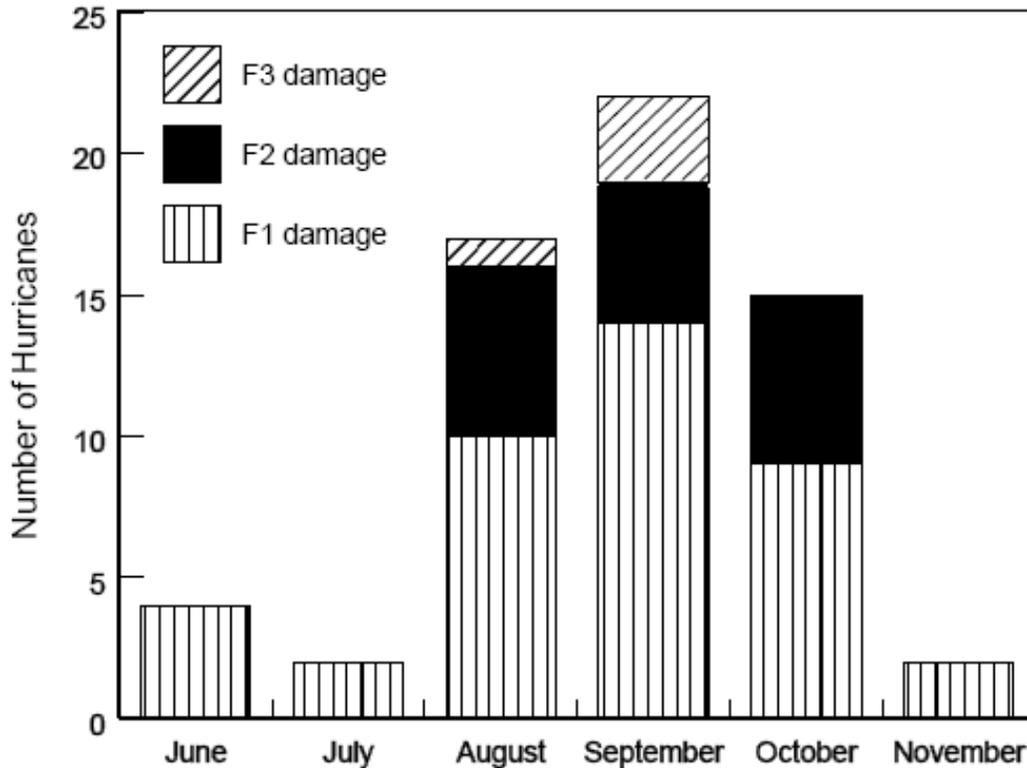


FIGURE 27.6. Seasonal distribution of hurricanes with reconstructed damage on the Fujita scale of F1 or higher during the study period (1851–2000), showing the date of landfall or closest approach to the Yucatán Peninsula.

Spatial patterns

Regional maps of reconstructed hurricane frequency (Figure 27.7), maximum damage (Figure 27.8), and average return interval (Figure 27.9) show a significant gradient in both frequency and intensity from northeast to southwest across the study region over the last 150 years. This gradient results from (1) the greater number of storms to the north, (2) the east to west movement of most hurricanes across the area, and (3) the tendency for most hurricanes to weaken significantly after landfall.

As a consequence there is a significant variation in hurricane disturbance regime across the region. For example, F3 damage, which resulted from four hurricanes (see Figure 27.3c–f) during the period 1851–2000, was concentrated in eastern and northeastern areas, with the most extreme damage (F3.5) limited to the northeastern tip of the peninsula. At the same time, southwestern parts of the study region did not experience damage above F1 over a period of 150 years. Based on these data, the northeastern tip of the peninsula can expect massive forest damage (F3) about every 75 years (on average), while extensive wind damage may be quite rare in southwestern

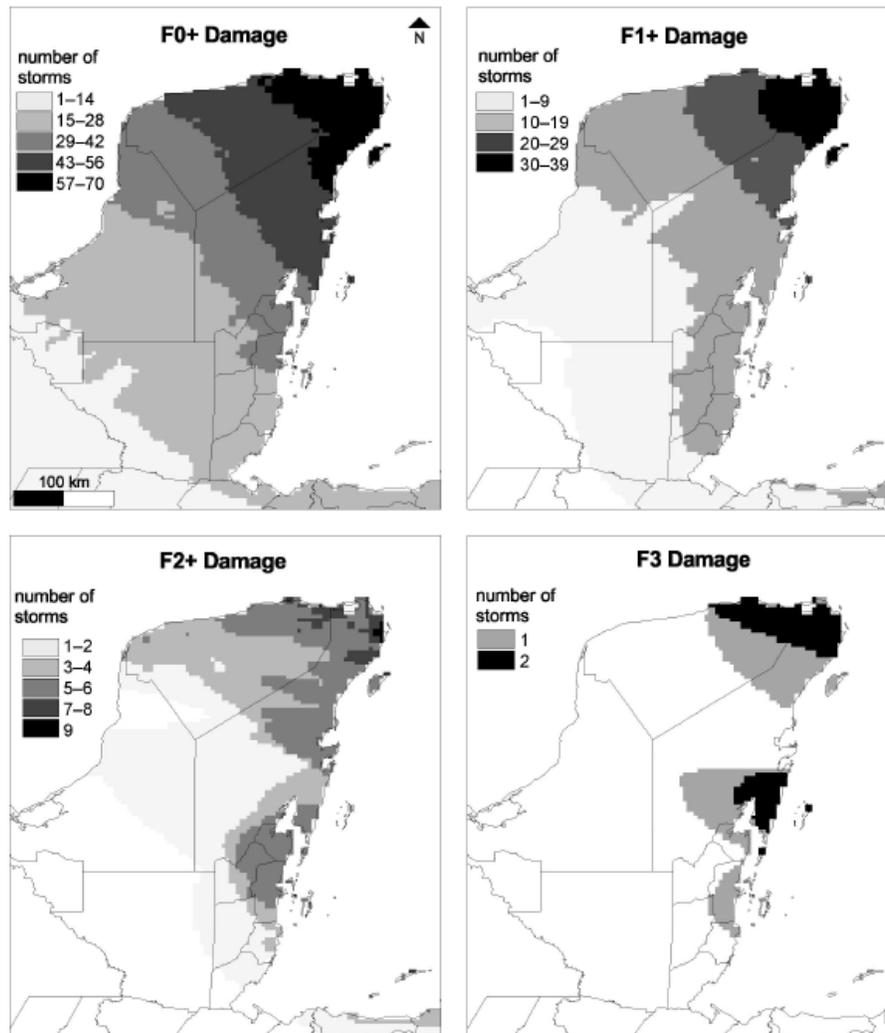


FIGURE 27.7. Regional gradients in reconstructed hurricane damage, showing the number of hurricanes at different damage levels during the study period (1851-2000).

areas. Note that the number of F0 storms is probably underestimated because the hurricane selection criteria were designed to identify all hurricanes producing F1+ damage in the study region.

This regional variation is further illustrated through a comparison of reconstructed hurricane impacts in Zoh Laguna and Cancún (Figure 27.10). Although separated by only 400 km, the two sites have strikingly different hurricane histories. During the period 1851–2000, Zoh Laguna experienced only one F2 hurricane and six F1 hurricanes, while the maximum reconstructed damage was F2.5 from Hurricane Janet (Y1955b). During the same period, Cancún experienced two F3 hurricanes, eight F2 hurricanes, and thirty F1 hurricanes, while the maximum reconstructed damage was F3.6 from Hurricane Allen (Y1980a) and F3.5 from Hurricane Gilbert (Y1988).

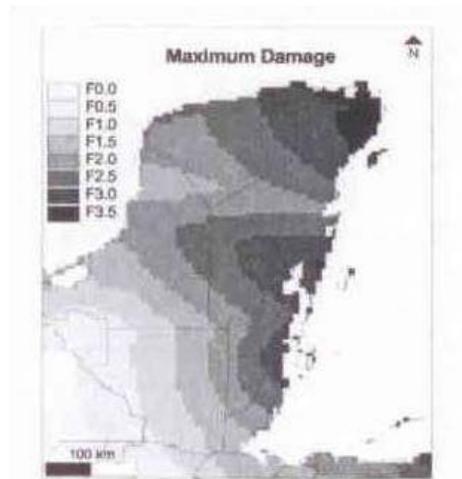


FIGURE 27.8 Regional gradients in maximum reconstructed damage on the Fujita scale in 0.5-class increments during the study period (1851-2000).

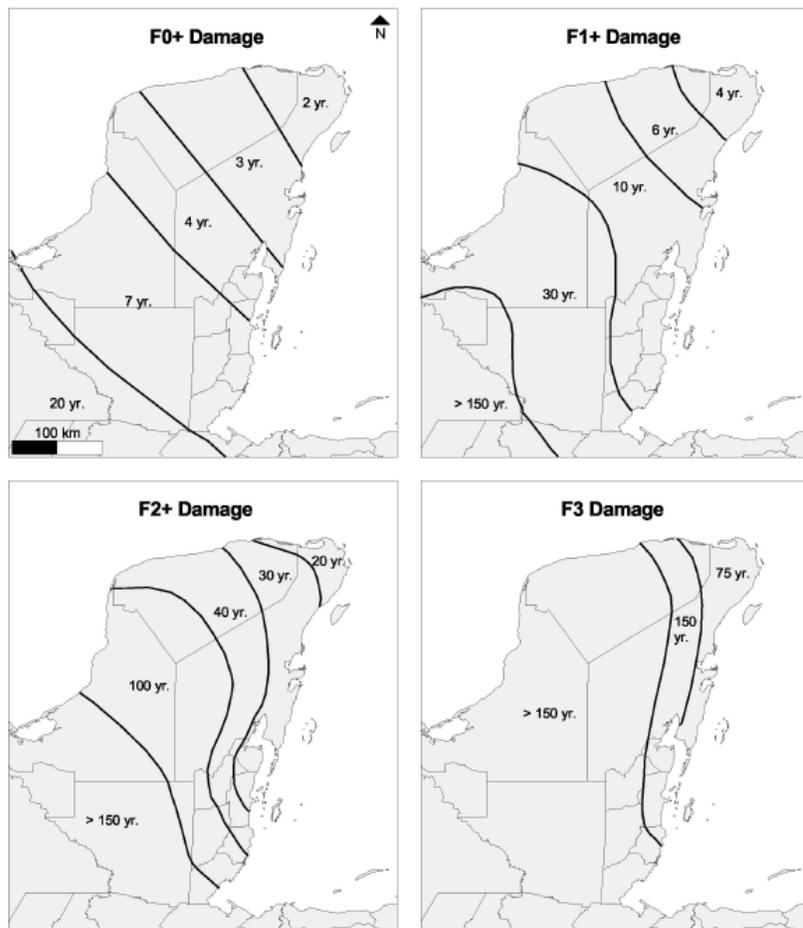


FIGURE 27.9. Smoothed regional gradients in reconstructed hurricane damage, showing average return intervals at different damage levels during the study period (1851-2000).

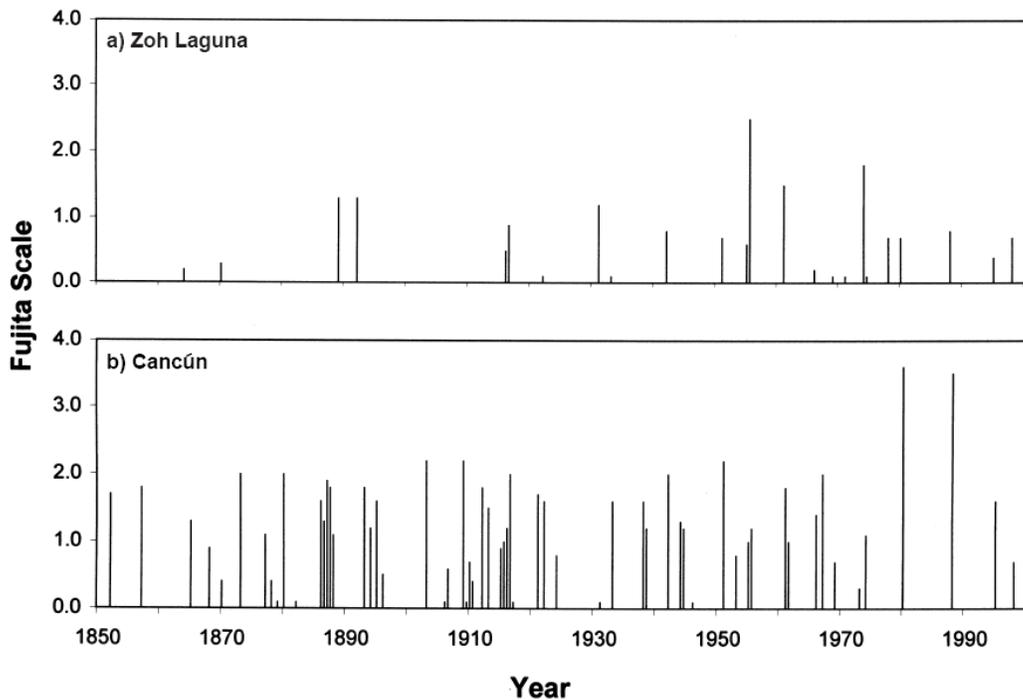


FIGURE 27.10. Timelines of reconstructed hurricane damage on the Fujita scale, by year, for two sites: (a) Zoh Laguna in the south-central Yucatan Peninsula, and (b) Cancún in the northeastern tip of the Yucatan Peninsula. (See Figure 27.1 for locations.)

The ecological role of hurricanes

Hurricanes play a number of important ecological roles in the Yucatán Peninsula, but these roles vary geographically as well as temporally with the intensity and history of human and other natural disturbances. As a consequence of millennia of disturbance by wind, fire, humans, and wildlife, the majority of species inhabiting the native forests of the region have a variety of biological mechanisms ensuring their rapid recovery as well as the rapid resumption of forest ecosystem processes after disturbance.

Among the disturbances mentioned, wind damage probably exerts the shortest-lived impacts and alters ecosystem processes the least (cf. Foster et al. 1997). Wind, even of the greatest intensity, primarily affects above-ground forest structure and small areas of soil: uprooting trees, breaking boles and branches, and indirectly damaging understory plants through treefall (Cooper-Ellis et al. 1999). Often a majority of the damaged trees survive this damage and—through reiteration, vegetative reproduction, and seedling establishment—rapidly reestablish a forest canopy and structure (cf. Brokaw and Walker 1991; Tanner, Kapos, and Healey 1991; Whigham et al. 1991). The amount of soil disturbance is generally low, except for extremely steep

terrain where mass movement can occur. Consequently, forest composition, microenvironments, and ecosystem processes usually undergo quite modest changes (Boucher 1990). Although forest damage following a hurricane may appear (and often is characterized as) “catastrophic,” biotic repair mechanisms (i.e., plants, fungi, and microbes) enable the forest to maintain important functional processes such as nutrient cycling, carbon uptake, and hydrological regulation while rapidly rebuilding its former structure (Lodge and McDowell 1991; Bowden et al. 1993; Steudler et al. 1996).

At the same time, the varied structural patterns created by the vagaries of hurricane damage on a plant-to-plot or landscape scale may provide habitat diversity in a region that is otherwise characterized by low structural variation (cf. Foster and Boose 1992). Nonetheless, the lack of topographical relief across most of the Yucatán Peninsula eliminates a major source of landscape patterning—variable wind exposure (Foster, Knight, and Franklin 1998; Foster, Fluet, and Boose 1999; Boose, Chamberlin, and Foster 2001). At a regional scale across the peninsula, the gradient of hurricane frequency and intensity broadly parallels latitudinal gradients in elevation, soil depth, depth to water table, and forest height (Wilson 1980). Therefore, disentangling the relative role of disturbance history (wind, fire, human), soil factors (depth, fertility, moisture), and climate (precipitation) in controlling variation in forest height, structure, and composition remains a major and generally unaddressed challenge (Turner, Geoghegan, and Foster 2002).

Fire and human land use represent potentially more severe impacts than wind (Steudler et al. 1996; Foster et al. 1997). Fire can effectively kill a greater extent of the above-ground biomass so that, even with rapid reiteration and sprouting, the rate of recovery of leaf-area index (i.e., a measure of how long it takes foliage, from the top of the canopy to the forest floor, to return to previous levels of coverage), forest canopy, and species composition may be slower than after blowdown (García, Rodríguez, and Chavelas 1996). Hot fires have the potential to ash much of the surface organic matter, and thereby volatilize large amounts of limiting nutrients such as nitrogen. In the very shallow soils of the Yucatán Peninsula, these processes may be accompanied by erosional losses and the resulting changes in soil fertility and structure may be very slow to recover. Historical human activity has generated major impacts on soils and vegetation across vast portions of the peninsula, and these continue to influence modern vegetation patterns and processes (Beach 1998; Lundell 1938). Ongoing land use associated with improved transportation and access, increasing populations and tourism, and government-supported development schemes is generating profound changes in land cover and regional environmental conditions (Turner et al. 2001).

Although hurricanes exert less impact on forest ecosystems than fire or land use, the interactions among these factors can be very important. In particular, there is good evidence that, in the wake of intensive hurricanes, a tremendous build-up of fine and coarse fuels occurs that may increase the potential for severe and extensive fires (Harmon et al. 1995; Snook 1998). The combination of these two disturbances creates long-lasting changes in forest communities (Whigham 2002). Consequently, there is a great need to complement the type of regional study presented here with research that would evaluate the frequency and geographic coincidence of multiple disturbance events (Foster, Fluet, and Boose 1999).

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Chapter 28

Anthropogenic Vegetation: A Garden Experiment in the Maya Lowlands

Scott Atran

INTRODUCTION AND OVERVIEW: THE GARDEN EXPERIMENT

Using a variation on an experimental model from biology, we distinguish the influence of certain socio-cultural factors (social networks, cognitive models) from economic (sources and level of income), demographic (family and population size), and ecological factors (habitat and species) in environmental management and maintenance. In a “garden experiment,” when members of a species have different phenotypes in different environments, samples are taken from both environments and replanted in only one. If differences still exist, then they are likely genetic (two genotypes); if not, then they are probably environmental (one genotype producing two phenotypes). Similarly, plausible evidence for the importance of culturally transmitted factors on behavior is data showing that groups of people who have different social histories and collectively identifiable mental make-ups behave differently in the same physical environment.

Physical and psychological measures show that three groups living off the same rainforest habitat exhibit strikingly distinct behaviors, cognitions, and social relations relative to the rainforest. Only the area’s last native Maya (Petén Itza’, or Itza’) reveal systematic awareness of ecological complexity involving animals, plants, and people, as well as practices that clearly favor rainforest regeneration. Spanish-speaking immigrants (Ladinos) prove closer to native Maya (Itza’) in thought, action, and social networking than do immigrant Maya (Q’eqchi’). There is no overriding “local,” “Indian,” or “immigrant” relationship to the environment.

Results indicate that exclusive concern with rational self-interest and institutional constraints do not sufficiently account for “commons” behavior, and that cultural patterning of cognition and access to relevant information are significant predictors of behavior. Indeed, for male Itza’, the perceived influence of rainforest spirits contributes to the behavioral and mental models of the local ecology. Possibly Itza’ (and others) “negotiate” with species as intensional (subjectively defined) and relational entities, such as enemies or friends, and do not simply treat them as extensional, replaceable objects, such as items in a shopping mall.

THE COMMONS SETTING

“The Tragedy of the Commons” and other similar social and ecological dilemmas are basically variants of a deep problem in decision and game theories known as “The Prisoner’s Dilemma” (Hardin 1968; Bromley 1992). Consider a group of n persons who share a common territory of fixed size on which they hunt (or graze) animals. Each hunter (or herdsman) has one of two choices: (1) he can cooperate with the others by not overhunting (grazing) on the commons; or (2) he can hunt (graze) in a way that is advantageous to him, but which ultimately results in the overuse and destruction of the common resource. The second option appears more rational in the short term; the temporary advantage to one who overhunts (grazes) always outweighs the short-term disadvantage to the hunter (or herdsman) when that disadvantage is distributed equally among the other hunters (herdsmen) ($1/n$). If all cooperate, the common resource is preserved; but if the rationale of “The Prisoner’s Dilemma” prevails, however, no one will have an incentive to cooperate, and all will defect.

Field and laboratory studies by anthropologists (Atran 1986; Berkes et al. 1989), psychologists (Thompson and Gonzalez 1997), and political scientists (Ostrom et al. 1994) indicate that individual calculations of rational self-interest collectively lead to a breakdown of a society’s common resource base unless institutional or other normative mechanisms are established to restrict access to cooperators; in other words, it is irrational to continue to act to sustain a diminishing resource that others increasingly deplete. This is so even when people’s “basic needs” are satisfied (Boniecki 1977), no matter how small the group or how informed the group is of the looming tragedy (White 1994). Earlier observations, however, have suggested that exclusive concern with economic rationality and institutional norms might not sufficiently account for behavioral differences among groups in lowland Mesoamerica (Atran and Medin 1997).

This study concerns three cultural groups in the same municipality in Guatemala’s Department of El Petén: (1) native Itza’ Maya, (2) Spanish-speaking immigrant Ladinos (mixed European and Amerindian descent), and

(3) immigrant Q'eqchi' Maya. Each group founded, and is centralized within, a distinct locality: Itza' in the town of San José, Ladinos in the settlement of La Nueva San José, and Q'eqchi' in the hamlet of Corozal. Interviews were conducted in Itza', Spanish, and Q'eqchi', respectively. In 1960, a military government opened Petén (one third of Guatemala's territory) to colonization. Satellite imagery indicates 40 percent of Petén's quasi-rainforest cover was destroyed and 10 percent was degraded between 1960 and 1990, as the population increased from 21,000 to over 300,000 (now nearly 1 million) (Schwartz 1995; Sader 1999). In 1990, under a "debt-for-nature" swap, Guatemala's government included remaining rainforests north of lat. 17°10' N in a United Nations sponsored Maya Biosphere Reserve. The three groups lie within the Reserve's official "buffer zone" between that latitude and Lake Petén Itza to the south.

San José has 1,789 inhabitants. Most identify themselves as Itza', although only a minority speak the native tongue. The Itza', who ruled the last independent Maya polity, were reduced to forced labor (*corvée*) after their conquest in 1697. San José was founded in 1708 as one of a handful of Spanish "reductions" for concentrating remnants of the native Itza' population (and fragments of related groups). Itza' represent the last Lowland Maya with demonstrable ties of genealogy (Atran 1993) and practice to pre-Columbian Maya civilization in Petén's northern forests (Atran 1999; Atran and Ucan Ek' 1999), where the population once exceeded the region's current level by an order of magnitude (Culbert and Rice 1990).

Nearly all 625 inhabitants of neighboring La Nueva are Ladinos. Most drifted into the area in the 1970s as nuclear families stemming from various towns in southeast Guatemala.

Q'eqchi' speakers, a Highland Maya group, settled the hamlet of Corozal at the same time. Although Q'eqchi' also filtered in as nuclear families, they migrated in two waves that transplanted partial Highland communities to Corozal: (1) directly from towns in the vicinity of Cobán (capital of the Department of Alta Verapaz due south of Petén), or (2) indirectly from Alta Verapaz via the southern Petén town of San Luis (home to a mixed community of Q'eqchi' and Lowland Mopan Maya). Most of the 395 inhabitants speak only Q'eqchi', which is not mutually intelligible with Itza'. The Q'eqchi' now comprise the largest and most linguistically isolated ethnic group in Petén (Stewart 1980; Grünberg and Ramos 1998).

AGROFORESTRY BEHAVIORS

All three groups practice agriculture and horticulture, hunt game, and extract timber and non-timber forest products for sale in commercial markets.

Each household (about five persons) has usufruct (i.e., the right of cultivating and enjoying products of the land without owning it) on 30 manzanas (21.4 hectares) of ejido land (municipal commons), paying yearly rent of 2–4 quetzales (the equivalent of \$0.30–\$0.70) for each manzana cleared for swidden plots, known as milpa (agricultural land), where the predominant crop is maize. Yearly variation in crop patterning can be substantial, owing in part to microclimate and drastic rainfall fluctuation. For example, at the height of the growing season, July rainfall in Flores (Petén's capital) went from 121 mm in 1993 to 335 mm in 1996; in nearby Tikal, rainfall increased from 58 mm to 137 mm during that same period.

People can hold plots in scattered areas and can change plots. Plots from all three groups may abut. Hunting is tolerated on neighboring plots, but access to a neighbor's crops and trees warrants sanctions. Analysis of variance (ANOVA) studies suggest that mean family size, per capita income, and number (and kind) of income sources do not differ reliably for the three groups.

Multiple converging measures of soils, biodiversity, canopy cover, reported human impact, and cognitive models of human-plant-animal relationships indicate that Itza' promote forest replenishment, Q'eqchi' foster rapid forest depletion, and Ladinos fall somewhere in between (Atran et al. 1999). In this study, one hectare (ha) plots of agricultural land (milpa), fallow land (guamil), and forest reserve for every informant in each group. For each plot we measured plot size, species diversity, tree count (minimum circumference > 0.30 m at 1–1.5 m from ground), coverage (m² foliage for each tree crown), and soil composition (10 cm and 20 cm depths, including analysis of soil structure, pH, percent organic matter, and ten essential chemical elements). Measurements of behavior patterns and their consequences for soils corroborate patterns from reported behavior, suggesting that Itza' agroforestry practices encourage a potentially sustainable balance between human productivity and forest maintenance; Q'eqchi' depletion practices are destructive in the short term; and Ladino practices are intermediate—neither as harmful as Q'eqchi', nor as productive as Itza'.

The differences among Itza', Ladinos, and Q'eqchi' in terms of the amount of land cleared for cultivation, the fallow length, and the number of plant species cultivated is summarized in Table 28.1. The results show that Itza' clear less land, fallow longer, and cultivate more than twice as many plant species as Ladinos or Q'eqchi'. Itza' also use a much more variable yearly mix of crops. Crop diversity, coupled with awareness of greater ecological complexity and reciprocity among plants, animals, and people favors forest regeneration by Itza'. If we consider rate of forest destruction (D) to be a function of land cleared per year, then projected results from our sample plots indicate the Q'eqchi' destroy more than five times as much forest

TABLE 28.1. ANOVA of Petén swidden (milpa) practices, where (R) = reported two-year average, and (O) = observed in third year.

	N	Crops per Year	Years of Land Use	Hectares (ha) Cleared	Years Fallow	Species per Year
Itza' (R)	16	2	2.3	1.6	4.7	7.8
I (O)	10			2.0		9.7
Ladino (R)	16	2	1.8	2.6	3.6	3.3
L (O)	10			2.4		6.4
Q'eqchi' (R)	12	1	1.0	4.1	3.3	3.6
Q (O)	10			3.6		6.2
Other Q'eqchi	*		1.6	3.7	3.3	2.5

* Average of five Q'eqchi settlements (Fagan 2000).

as Ladinos, whereas Ladinos destroy less than twice as much as Itza': $F(2,41) = 25.04$, $p < .0001$, $D(I) = .753$, $D(L) = 1.39$, $D(Q) = 3.92$ (see Atran et al. 2002 for formula).

MENTAL MODELS OF FOLKECOLOGY

Factor-analytic use of mental models shows that cognitive preferences strongly reflect, and reliably predict, behavior regularities. For every informant in each sample group, we asked the following question: “Which kinds of plants and animals are most necessary for the forest to live?” Among hundreds of locally known species, informants nominated a small sample of some two dozen plant and animal species (see Table 28.2). When, as happened for each group, there was a cultural consensus in the formal sense (i.e., a single factor solution in a principal components analysis) we were justified in aggregating individual responses into a “cultural model” (Romney, Weller, and Batchelder 1986; López et al 1997).

For each plant in the list, we asked informants to explain how it affected each animal in the list, and vice versa. A preliminary coding system represented each species pair in terms of one of five folkecological relations that can be roughly glossed as “mutualist” (+1, +1), “commensalist” (+1, 0), “parasitic” (+1, -1), “destructive” (-1, 0 or -1, -1), or “neutral” (0, 0). Itza' recognized significantly more mutualist and commensalist relationships than did Ladinos, whereas Q'eqchi' recognized almost no such relationships.

TABLE 28.2. Petén plants and animals

Ref.	Plant name	Scientific name	Ref.	Animal name	Scientific name
	FRUIT TREES			ARBOREAL ANIMALS	
P1 *	ramon	<i>Brosimum alicastrum</i>	A1	bat	Chiroptera
P2 *	chicozapote	<i>Manilkara achras</i>	A2	spider monkey	<i>Ateles geoffroyi</i>
P3 *	ciricote	<i>Cordia dodecandra</i>	A3	howler monkey	<i>Allouatta pigra</i>
P4 *	allspice	<i>Pimenta diocia</i>			<i>A. palliata</i>
P5 *	strangler fig	<i>Ficus obtusifolia</i>	A4	kinkajou	<i>Potus flavus</i>
		<i>F. aurea</i>	A5	coatimundi	<i>Nasua narica</i>
	PALMS		A6	squirrel	<i>Sciurius deppei</i>
P6 *	guano	<i>Sabal mauritiiformis</i>			<i>S. aureogaster</i>
P7 *	broom palm	<i>Crysophilia staurocata</i>			
P8 *	corozo	<i>Orbignya cohune</i>		BIRDS	
		<i>Scheelea lundelli</i>	A7	crested guan	<i>Penelope purpurascens</i>
P9	xate	<i>Chamaedorea elegans</i>	A8	great curassow	<i>Crax rubra</i>
		<i>C. erumpens</i>	A9	ocellated turkey	<i>Meleagris ocellata</i>
		<i>C. oblongata</i>	A10	tinamou	<i>Tinamou major</i>
P10	pacaya	<i>Chamaedorea tepejilote</i>			<i>Crypturellus</i> spp.
P11	chapay	<i>Astrocaryum mexicanum</i>	A11	toucan	<i>Ramphastos sulfuratus</i>
			A12	parrot	Psittacidae in part
			A13	scarlet macaw	<i>Ara macao</i>
	GRASSES / HERBS				
P12	herb/underbrush	(various families)	A14	chachalaca	<i>Ortalis vetula</i>
P13	grasses	Cyperaceae/ Poaceae	A15	pigeon/dove	Columbidae

Ref.	Plant name	Scientific name	Ref.	Animal name	Scientific name
	OTHER PLANTS			RUMMAGERS	
P14 *	mahogany	<i>Swietenia macrophylla</i>	A16	collared peccary	<i>Tayassu tacaju</i>
P15 *	cedar	<i>Cedrela mexicana</i>	A17	white-lipped pecc.	<i>Tayassu pecari</i>
P16 *	ceiba	<i>Ceiba pentandra</i>	A18	paca	<i>Cuniculus paca</i>
P17 *	madrial	<i>Gliricidia sepium</i>	A19	agouti	<i>Dasyprocta punctata</i>
P18 *	chaltekok	<i>Caesalpinia velutina</i>	A20	red-brocket deer	<i>Mazama americana</i>
P19 *	manchich	<i>Lonchocarpus castilloi</i>	A21	white-tailed deer	<i>Odocoileus virginianus</i>
P20 *	jabin	<i>Piscidia piscipula</i>	A22	tapir	<i>Tapirus bairdii</i>
P21 *	santamaria	<i>Calophyllum brasilense</i>	A23	armadillo	<i>Dasybus novemcintus</i>
P22 *	amapola	<i>Pseudobombax ellipticum Bernoullia flammea</i>		PREDATORS	
P23 *	yaxnik	<i>Vitex gaumeri</i>	A24	jaguar	<i>Felis onca</i>
P24 *	kanlol	<i>Senna racemosa</i>	A25	margay	<i>Felis wiedii</i>
P25 *	pukte	<i>Bucida buceras</i>	A26	mountain lion	<i>Felis concolor</i>
P26 *	water vine	<i>Vitis tiliifolia</i>	A27	boa	<i>Boa constrictor</i>
P27	cordage vine	<i>Cnestidium rufescens</i>	A28	fer-de-lance	<i>Bothrops asper</i>
P28	killer vines	(various epiphytes)	A29	laughing falcon	<i>Herpetotheres cachinnans</i>

* Species counted in study of tree frequencies (= 44%, 50% and 54% of trees in Itza', Ladino and Q'eqchi' parcels, respectively)

For each species, we also asked what its value was for people, and what people's effect was on the species. The species' value for people was coded for "use" or "cash"; human impact on species was assessed on a scale from negative (-1) through neutral (0) to positive (+1). Each group had sufficient statistical consensus among informants to warrant aggregating individual responses within the group into a cultural model, and also for aggregating individual responses across all groups into a metacultural model.

Itza' stated that classes of animals differentially affected classes of plants, whereas Ladinos reported more universal affects. To illustrate, plant kinds were collapsed into four categories (Fruit Trees, Palms, Grasses/Herbs, and Other Plants), as were animal categories (Arboreal Animals, Birds, Rummagers, and Predators). ANOVA reveals a plant-by-animal interaction: $F(9,99) = 26.04, p < .0001$. Post hoc measures reveal this to be significant only for Itza'. On a qualitative level, although both groups acknowledged that animals have a large impact on fruit trees, Itza' differed from Ladinos in understanding this relationship. Ladinos see animals as harming plants by eating fruit. Itza', however, have a more nuanced appreciation of the relationship between seed properties and processing: If the seed is soft and the animal cracks the fruit casing, the animal is likely to destroy the seed and thus harm the plant; but if the seed is hard and passes through the animal's body rapidly, then the animal is apt to help the plant by dispersing and fertilizing the seed.

Itza' folk ecological models also relate directly to observed behavior. Regression analysis for Itza' revealed that ratings of human impact (the extent to which people report their actions as helping or hurting particular species) and weed status (factoring out plants considered to be weeds) predicted (normalized) frequencies of trees counted in informant parcels: $r^2 = .46; F(2,20) = 7.58, p = .004$; both predictors $\leq .01$. No comparable relation emerged for Ladinos or Q'eqchi'. Regression analysis also revealed different predictors of human impact on plants for each group. For Itza', ecological centrality (number of associations in a group's consensual ecological model for a given plant) and combined utility (value of a plant for wood, shelter, and cash combined) predicted a human impact signature: $r^2 = .44; F(2,25) = 9.13, p < .001$; both predictors $< .01$. Thus, ecological importance and combined utility predicted which plants the Itza' seek to protect. For Ladinos, cash value was the only reliable predictor of impact: $r^2 = .34, F(2,25) = 6.55, p < .01$. The correlation between cash use and impact was positive, indicating that Ladinos protect plants having cash value. For Q'eqchi', none of these variables predicted an impact signature; the (nonsignificant) correlations were also consistently negative, indicating the Q'eqchi' tend to destroy valuable plants (see Table 28.3).

A recent study comparing these Itza' data to avagere for several Q'eqchi'

TABLE 28.3. Rankings of human impact on plants and ecological centrality

<i>Itza'</i>			<i>Ladino</i>			<i>Q'eqchi'</i>		
Impact	Centrality	Plant	Impact	Centrality	Plant	Impact	Centrality	Plant
1.00	0.64	ramon	0.75	0.20	ceiba	0.33	0.04	guano
1.00	0.62	chicle	0.58	0.15	pacaya	0.25	0.09	corozo
0.83	0.11	cedar	0.58	0.10	xate	0.08	0.07	grasses
0.83	0.48	ciricote	0.55	0.16	allspice	0.00	0.17	amapola
						0.00	0.02	cordage
0.83	0.11	mahogany	0.50	0.47	ciricote			vine
0.75	0.20	xate	0.42	0.61	chicle	0.00	0.00	chapay
0.67	0.05	ceiba	0.33	0.12	madrial	0.00	0.04	ciricote
						0.00	0.08	broom
0.67	0.40	guano	0.33	0.64	ramon			palm
0.67	0.09	madrial	0.17	0.14	cedar	0.00	0.01	jabin
0.67	0.36	allspice	0.17	0.36	guano	0.00	0.00	kanlol
0.58	0.25	amapola	0.17	0.25	grasses	0.00	0.07	madrial
0.58	0.13	chapay	0.08	0.30	mahogany	0.00	0.02	pacaya
0.58	0.09	corozo	0.00	0.29	amapola	0.00	0.00	allspice
		broom				0.00	0.01	
0.58	0.30	palm	0.00	0.17	water vine			pukte
0.58	0.20	pacaya	0.00	0.22	corozo	0.00	0.21	ramon
0.50	0.34	grasses	0.00	0.00	yaxnik	0.00	0.02	santamaria
0.42	0.07	chaltekok	-0.13	0.14	pukte	0.00	0.01	yaxnik
0.42	0.17	jabin	-0.14	0.01	chaltekok	0.00	0.05	herbs
						-0.08	0.15	strangler
0.42	0.06	manchich	-0.18	0.11	santamaria			fig
					cordage	-0.08	0.03	
0.25	0.16	santamaria	-0.25	0.06	vine			water vine
0.17	0.37	herbs	-0.25	0.25	herbs	-0.08	0.00	chaltekok
		strangler			broom	-0.08	0.01	
0.08	0.47	fig	-0.33	0.09	palm			killer vines
0.08	0.28	yaxnik	-0.44	0.13	jabin	-0.25	0.05	ceiba
-0.25	0.16	pukte	-0.50	0.20	chapay	-0.25	0.01	manchich
-0.33	0.07	water vine	-0.60	0.00	manchich	-0.25	0.03	xate
-0.33	0.01	cordage	-0.67	0.60	strangler	-0.58	0.13	chicle

<i>Itza'</i>			<i>Ladino</i>			<i>Q'eqchi'</i>		
Impact	Centrality	Plant	Impact	Centrality	Plant	Impact	Centrality	Plant
		vine			fig			
-0.58	0.09	killer vines	-0.67	0.24	killer vines	-0.67	0.12	cedar
-0.58	0.03	kanlol	-0.75	0.06	kanlol	-0.75	0.09	mahogany

communities supports the reliability of the different cropping patterns reported above (Fagan 2000). Remote sensing confirms the pattern of deforestation along Q'eqchi' migration routes for Petén (Sader 1999). Unless checked by some means (e.g., fixed concessions, relocation of Q'eqchi' outside the area, etc.), the high deforestation and soil erosion rates, together with open immigration into Petén, is likely within a generation to have an avalanching effect on the ecosystemic integrity of the entire Biosphere area.

In this context, Itza' appear to behave "irrationally" insofar as their restraint subsidizes another group's profligacy: the more cooperators produce for "free riders," the more the free-riding group is able to expand and lay waste (Axelrod and Hamilton 1981). But within the more localized municipal context, Itza' seem ecologically rational in that their behavior is "attracting" another group (the Ladinos) toward effective cooperation and sustainability. In fact, until massive immigration began, generations of Ladinos had assimilated so much Itza' agroforestry technique over the last three centuries that the farming and forest-tending practices of these Ladino "Peténeros" were reported to be virtually indistinguishable from those of Itza' (Schwartz 1990). Indeed, some Ladino Peténeros have continued rituals devoted to the Maya rain god, chaak, although Itza' rituals have stopped.

COMMUNICATION NETWORKS

Social network analysis supports the close relationship between Itza' and Ladinos. For each community we began with 6 men and 6 women not immediately related by kinship or marriage. Each informant was asked to name, in order of priority, the 7 people outside of the household "most important for your life," as well as in what ways the people named in this *social network* were important. Several days later, each informant was then asked to name, in order of priority, the 7 people "to whom you would go if there were something that you do not understand and want to find out about the forest/fishing/hunting." Informants were asked about the kind of information they would seek in these *expert networks*. (The decision to restrict the number of people named in each case to 7 is based on previous cross-cultural studies.) After performing these tasks with initial group of informants,

we used a “snowball method” to extend these ego-centered networks to the wider context of patterned social communication in which they operated. Social interaction and expert networks were elicited from the first and last persons named in the social network.

The greatest overlap in the two networks occurred among Itza’ and the least among Q’eqchi’. For Itza’, 14 of the most cited social partners are among the 22 most cited forest experts. Although the Itza’ social network is not highly centralized, the most cited social partner is also the second most cited forest expert, whereas the top forest expert is also the third most cited social partner. For Ladinos, 11 of the most cited social partners were among the 25 most cited forest experts. Of these 11, all were Ladino men. Ladino women tend to mention Ladino men as experts; however, the top Ladino experts most often cite the same Itza’ experts as the Itza’ do themselves, suggesting diffusion of information from Itza’ experts to a select group of socially well-connected Ladino men. For Q’eqchi’, who have by far the most densely connected and centralized social networks, only 6 of the most cited social partners are among the 18 most cited forest experts (these are cited much less often as experts than outside institutions).

Thus, the three groups markedly differ in their social and expert network structures, with different consequences for the flow of information about the forest. The Q’eqchi’ networks suggest that information pertinent to long-term survival of the forest comes from outside organizations with little long-term experience in Petén. What outside information there is seems unlikely to penetrate deeply into the Q’eqchi’ community because it is not conveyed by socially relevant actors. For Itza’, expert information about the forest appears integrally bound to intimate patterns of social life as well as to an experiential history traceable over many generations, if not millennia. For Ladinos, expert information is also likely to be assimilated into the community.

Because Ladino experts are socially well-connected, information from Itza’ experts has access to the greatest number of multiple interaction pathways. To test this learning hypothesis, we regressed *gender* and *frequency of being cited as an expert* against Ladino first factor scores in the combined Itza’-Ladino cultural consensus model. The r^2 on Ladino scores was .63 [$F(2,10) = 6.97, p = .02$] with gender ($p = .02$) and expertise ($p = .008$) both reliable.

Over time, socially well-connected male Ladinos converge towards the consensus of Itza’ experts. For example, judgments of hundreds of plant-animal interactions by the Ladino most highly rated as an expert by other Ladinos comprised a proper subset of the pairwise judgments made by the Itza’ who was most highly rated by the top Ladino himself and by the other Itza’. It is highly improbable that Ladinos who approximate Itza’ response patterns actually observe and copy Itza’ dealings with the species pairs in

question. Rather, individual male Ladinos seem to project fragmentary observations of Itza' behavior to a richly textured cognitive model of folk ecology *by inference*, rather than imitation (for details, Atran et al. 2002). In contrast, Ladino women make plausible but unwarranted inferences that Itza' do not. For example, in the absence of direct observation of furtive, nocturnal felines, it is plausible to believe that they would hide out under the protective cover of leafy fruit trees to prey upon other animals that feed on the fruit. Female Ladinos who seldom venture into the forest or inquire about it overwhelmingly (75%) infer that felines seek out fruit trees. Male Ladinos (17%) and Itza' (16%) know better because they go into the forest.

DIFFERENT VALUES

Such mental models have no explicit or normative rule structures (Atran 2000). Even the gloss of "ecological reciprocity" simply points to, rather than describes, the diverse relationships involved. In fact, of 14 Itza' informants, 11 claim to share more of their values about plants and animals with Q'eqchi' than with Ladinos; in addition, two Itza' attest to sharing values equally with both groups, whereas one Itza' disclaims sharing values with either group. Further valuation studies underscore this bias.

For each plant species, we asked informants from each of the three groups to rank the species in order in terms of their importance according to members of their own community, members of the other two communities, God, and the forest spirits. Itza' overestimated the agreement between their responses and those of the Q'eqchi', but underestimated agreement with Ladinos; similarly, Q'eqchi' also overestimated agreement with Itza'. For example, the correlation between Itza' beliefs about Q'eqchi' preferences and Itza' beliefs about their own preferences (i.e., [Iq, Ii], $r = .94$) differs appreciably from the correlation between Itza' beliefs about Q'eqchi' preferences and Q'eqchi' beliefs about their own preferences ([Iq, Qq], $r = .74$). By contrast, the correlation between Itza' beliefs about Ladino preferences and Itza' beliefs about their own preferences ([Il, Ii], $r = .90$) does not differ appreciably from the correlation between Itza' beliefs about Ladino preferences and Ladino beliefs about their own preferences ([Il, Ll], $r = .93$). Similarly, ([Qi, Qq], $r = .84$) – ([Qi, Ii], $r = .62$) = .22, whereas ([Lq, Ll], $r = .92$) – ([Lq, Qq], $r = .84$) = .08. Interestingly, Ladino beliefs about what they think to be Itza' preferences correlate almost perfectly with Ladino beliefs about God's preferences ($r^2 = .96$). Ladinos say that the Itza', like God, commune with the forest in mysterious ways.

Only Itza' see the forest spirits as actively protecting the forest: Itza' rankings from the point of view of the forest spirits are significantly related to

Itza' models of human impact as well as ecological centrality (see Atran et al. 2002). For example, multiple regressions show that male Itza' consensus on spirits, together with the overall Itza' consensus on combined use (wood + shelter + cash), account for most of the variance in human impact: $r^2 = .70$, $F(2,18) = 20.71$, $p = .0001$, with spirits and use equally reliable predictors ($ps < .01$). The most reliable combination of predictors for what male Itza' believe the spirits think are ecological centrality and God (both $ps < .01$): $r^2 = .65$, $F(2,18) = 17.0$, $p = .0001$. Ladinos and Q'eqchi' state their belief in forest spirits, and even provide normative accounts of spirit life similar to those of Itza'. Yet, in these two groups, belief in spirits is not reliably linked to forestry practice.

When asked, Itza' express the belief that they will be punished if they violate spirit preferences. For the Itza', it appears that the spirits are intermediaries or "spokesmen" for the forest species, although there is wide individual variation in response to what the spirits say about any given species. This has intriguing implications for ecological decision theory and game theory in that individual Itza' may be basing their cognitive and behavioral strategies for sustaining the forest more by playing a game with spirits than by playing a game with other people. Spirit preferences may represent a cultural (aggregated statistical) summary of sustained human-species interactions over many generations.

Finally, we asked representatives of 17 nongovernmental organizations (NGOs) at a workshop on the Maya Biosphere Reserve (December 1999) to rank the same trees as did Itza', Ladinos, and Q'eqchi' (in terms of importance to forest life). For the NGOs, there was marginal consensus, with one slightly negative first-factor score ($-.076$): ratio eigenvalue 1:2 = 2.73, variance = 45.6 percent. The most valued species for NGO representatives are, in rank order: mahogany, tropical cedar, allspice, and chicle. These are the most important trees for the extractive economy and export market. NGO preferences partially predict the consensus on preferences expressed by Ladinos ($r^2 = .72$) and Itza' ($r^2 = .44$) (recall that for the Q'eqchi' there was no consensus); however, the worst predictor of NGO rankings is Itza' male rankings of spirit preferences ($r^2 = .06$, ns) and Itza' ratings of ecological centrality ($r = -.229$)

CONCLUSION: SPIRITUAL GAMES

In sum, these studies show that different cultural groups subject to equal common resources pressures respond with strikingly different culturally patterned behaviors and cognitions. These studies also suggest a nonobvious role for religion in helping human societies to resolve "The Tragedy of the Commons" and other ecologically-pertinent forms of "The Prisoner's

Dilemma.” Supernatural agents not only may serve to guarantee trust and foster cooperation between non-kin as standard theories of social commitment assume (Frank 1988), but such agents may also act to allow humans to engage nonhuman resources in relations of “indirect reciprocity” (Alexander 1987) so as to better monitor and accommodate nature’s requirements for continuing “Her” human support.

Evidence from this “garden experiment” does not indicate the primacy of norms, institutions, or moral rules in explaining cultural differences in regard to “The Tragedy of the Commons.” Indeed, the Itza’ community is the most socially atomized and least expressive of cooperative norms. Nevertheless, it is the one whose individuals best act to maintain the common environment. The Q’eqchi’ community is most socially interconnected and ceremoniously institutionalized, but is least likely to preserve the resource base, perhaps because the community is so culturally hermetic (Schackt 1984). Most surprising, immigrant Ladino households, which tend not to share prior kinship or cultural bonds with one another, much less with native Itza’ Maya, come to measurably resemble native Itza’ Maya in thought and action.

This relates to the seemingly intractable problem of “upscaling” lessons of local commons to increasingly mobile and multicultural societies. Even in a relatively open-access environment (e.g., one with uncontrolled immigration), if there is ready access to relevant information, then ecologically sound behaviors may be learned by relative newcomers who have no institutional compulsion, cognitive predisposition, or cultural tradition favoring commons survival. (Having the time to learn, though, poses a daunting problem: rates of cultural and environmental degradation in neotropical areas are awesome by any standard, owing to global economic and political processes that function similarly across such areas.) These findings also call into question an operating principle of agent-based normative models (Axelrod 1997)—namely, societies that do not share normative values (e.g., Itza’ and Ladino) are less likely to interact and converge than societies that do share normative values (e.g., Itza’ and Q’eqchi’).

Finally, these findings bear specifically on Maya studies. Earlier research on Itza’ focused primarily on maize production (Cogwill 1962) to better understand the cereal basis for ancient Maya civilization (Reina 1967). But there is increasing argument that tree tending and multicropping were important to pre-Columbian Maya civilization (Gómez-Pompa, Flores, and Sosa 1987) and perhaps critical to the survival of Lowland Maya over two millennia of intermittent and catastrophic upheaval (Flannery 1982). Our findings provide data to develop this line of research. They also raise the possibility that a better understanding of intricate cultural patterns favoring environmental maintenance may enhance their value and reduce Lowland Maya chances for extinction in the next millennium.

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Chapter 29

Traditional Knowledge of Plant Resources

Eugene N. Anderson

INTRODUCTION

Thanks to the work of a great number of scholars, Maya knowledge of the environment has been thoroughly recorded. The “traditional ecological knowledge” (or TEK) of the Mexican Maya groups is probably better documented than that of any other indigenous groups in the world. (Knowledge of Highland Guatemalan Maya TEK lags far behind, but this situation, fortunately, is changing for the better.)

The reasons are not hard to find. First, the Maya remain numerous, diverse, and politically important; they are still prevalent throughout much of south Mexico and Guatemala. Second, they are a vocal and sophisticated set of communities. They share their knowledge relatively readily and easily. Their names for local fauna and flora have been widely assimilated into Spanish and even into English (e.g., “cacao” from the widespread root *kakaw*, “shark” from Yucatec *xok*, etc.)¹ Third, the glories of Maya civilization—ancient and modern—has led to important scholarly attention.

HISTORY OF RESEARCH

The Maya written record of plant and animal names can now be traced to Classic Maya times (ca. 400–800 A.D.). The word *kakaw* shows up on

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countless vessels, some of which actually contain chocolate residue. Kings' names such as "First Crocodile" and "Yellow Peccary" (Harrison 1999; Martin and Grube 2000) provide evidence of which animals were regarded as powerful and spiritually charged. Martin and Grube (2000:15) list jaguar, quetzal, macaw, snake, crocodile, turtle, and peccary as common name-animals; less common are shark, gopher, and other fauna. Many animals served as waay—transformation-animals of shamans, or spirit-animal companions of people in general. It is not known whether plant names were used much, but Central Mexican native peoples have always used flower names for girls. Xochitl, which is Nahuatl for "flower," is common even in Los Angeles, California. The Maya probably used flower names as well.

The Lowland Maya archaeobotanical record is notoriously poor, but fortunately not so poor as it once was. In fact, in a recent review, David Lentz reports 118 plant genera or species identified from Classic Maya sites (Lentz 1999:6–9). Most of these are plants now used for food, fiber, or medicine, although some were probably mere wild plants of the area, and others may be contaminants (genera such as *Echinochloa* and *Paspalum*, recorded in Lentz's table, are common introduced weeds).

When the Spanish convinced themselves that they had conquered the Maya (a delusion they were frequently to regret), they quickly began compiling dictionaries. Excellent early-Colonial dictionaries (from the late sixteenth, seventeenth, and the eighteenth centuries) of most major Maya languages are available. Study of plant and animal names in these dictionaries has been spotty, but, at least for Yucatec Maya plant names, solid identifications are now possible.

With the coming of modern anthropological research, the study of Maya ecological knowledge entered a new era. This was due above all to three huge projects: (1) The Carnegie Institute of Washington's research on Maya archaeology and ethnography in the 1920s and subsequently; (2) the Harvard (later Harvard-Chicago-Stanford) Chiapas Project in the 1950s through 1970s; and (3) the research of Arturo Gómez-Pompa and his associates, beginning in the 1980s (e.g., Gómez-Pompa, Flores, and Sosa 1987) and continuing today (e.g., Herrera 1994; Ross-Ibarra and Molina 2000).

The Carnegie Institute research led to the classic ethnographic work of Robert Redfield and his associates (Redfield and Villa Rojas 1934). This eventually led to the collection of a great amount of data on food (Benedict and Steggerda 1936), milpa agriculture, and other relevant matters.

Meanwhile, interest in ethnohistory led to support for the epochal work of Ralph Roys. Roys brought ethnobotany (a new field) to Latin America and almost singlehandedly created the field of ethnohistory. Among other things, he studied Colonial medical texts. To understand the plant names, Roys

worked with botanist Paul Standley and others. He appended a prototype ethnobotanical dictionary of Yucatec to his study of Maya medical texts (Roys 1931). This book, an incredible achievement, has unfortunately come to have a rather stultifying effect on the field. The tendency has been to assume “Roys did it all,” and to ignore later work (notably Barrera, Barrera, and López 1976) or the possibility for further research. Also, Roys’ inadequacies, such as identifying huhub as *Pinus caribaea* (Roys 1931, 246) without noting its use for wild *Spondias purpurea*, have been perpetuated without checking. Roys went on to produce an edition of the ethnobiologically rich Colonial Maya text, *Ritual of the Bacabs* (Roys 1965), recently reedited in Spanish by Arzápalo (1987).

The Harvard Chiapas Project, organized by Evon Vogt, led directly or indirectly to a great deal of research on all matters ecological. In particular, it stimulated the work of Brent Berlin, who has become a leading authority on Maya ethnobotany (Berlin 1992 reviews most of the relevant literature). The Chiapas Project is largely outside the scope of this chapter, but Berlin’s long shadow is still felt. Not only did he set the pattern for a great deal of ethnobiological research in Mayaland, but I am a Berlin student. (I also took courses with Vogt.) Berlin’s botanist collaborator, Dennis Breedlove, went on to work with Robert Laughlin on the greatest Maya ethnobotany to date, a study of the Tzotzil of Zinacantan (Breedlove and Laughlin 1993).

Finally, a third great project was organized by Arturo Gómez-Pompa (see e.g., Gómez-Pompa, Flores, and Sosa 1987). This project stemmed originally from work by Mexican botanists and anthropologists, notably E. Hernandez Xolocotzi (1985), Alfredo Barrera Vásquez, Alfredo Barrera Marín, and Rosa Maria López Franco (Barrera, Barrera, and López 1976; see also texts usefully collected by Vázquez 1981). Their work was crystallized in the research done at INIREB-Mérida in the 1980s, and later in collaborative work by the University of California at Riverside (UCR) and the Universidad Autónoma de Yucatán. This led to my own Maya work. Much of this research was published by INIREB (notably Mendieta and del Amo 1981), and by INIREB and later UADY in the series “Etnoflora Yucatanense”; particularly long and detailed works in this series include Sosa et al. (1985), Sanabria (1986), and Herrera (1994). Other UADY publications include Sosa and Salvador (1993).

Recently, a large number of Mexican governmental and nongovernmental agencies have organized and published research on Yucatec ethnobotany. Among a number of organizations and publications, notable is work of ECOSUR (e.g., Pulido and Serralta 1993) and of Silvia Terán and Christian Rasmussen (1994; Terán, Rasmussen, and Cauich 1998). Many other works on Maya culture or agriculture touch on ethnobiological knowledge to varying degrees. A recent valuable contribution is Anne Bradburn’s list (1998), which is appended to Victoria Bricker’s dictionary of

Yucatec. Medical botany has been examined (Ankli, Sticher, and Heinrich 1999).

Moreover, the neighboring Itzaj Maya, speaking a dialect of Yucatec, have been studied extensively by Scott Atran (1993, 1999a, 1999b) and a dictionary compiled by Charles Andrew Hofling and F. Tesucún (1997). This material deserves extensive discussion; see Atran's paper in this book. "Anthropogenic Vegetation: A Garden Experiment in the Maya Lowlands."

Finally, relevant to all these concerns are the recent editions of colonial dictionaries (Acuña 1993; Andrews Heath 1980; Arzápalo 1996) and synthetic works drawing on them (Álvarez 1997; *Diccionario Maya Cordemex* 1980).

CHUNHUHUB: USES FOR PLANTS

As the material found in the publications referenced above is far too extensive to be examined here, the analysis will be confined to the research conducted in and around Chunchuhub, Quintana Roo, Mexico.

As with many Maya towns, Chunchuhub has an ethnobiological name: which means: "Trunk of the wild plum tree." Wild plums (*Spondias purpurea*), still abound in the community. Thus, the name remains as appropriate as ever, although it goes back to pre-Hispanic times. It may even be the Classic Maya name of the site, which has been almost continuously inhabited since at least early Classic times—although there was a long break between the War of the Castes and resettlement by ex-"rebel Maya" in the 1940s.

In spite of encroachment by pan Bimbo, white sugar, and refrescos, Chunchuhub still depends on its own home-grown maize. Among the more traditional cultivators, maize still makes up about 75 percent of the diet, as it has among the Maya for countless centuries (White 1999). Until the very recent rise to eminence of white flour and white sugar, there was no "second most important" plant. Beans (mainly *Phaseolus vulgaris*, of the general type informally called "black turtle") and chiles (*Capsicum annuum* and *C. frutescens*, as well as the habanero, which is probably *C. chinense*) are daily fare. Sweet potatoes are the major famine food. Oranges, mangoes, papayas, squash (several species), and tomatoes grace the table very frequently. Less common, but important, are white potatoes, mameys (*Pouteria mammosa*), chicosapotes (*Achras sapota*), cabbage, cilantro, and various other plants. Achiote (*Bixa orellana*), a pre-Columbian plant of ritual significance, remains the commonest condiment after chile. Important is the abal (*Spondias* spp.), whose fruit, when dried, has a special name, k'ul (*Diccionario Maya Cordemex* 1980, 421). This name is sometimes generalized to other dried (and

often powdered) fruit, including mamey and chicosapote as well as abal, which was stored in the old days in case of shortages.

In all, in this study 122 locally grown plants used for food were recorded. Some of these are grown only for fun; for instance, people grow sugar and sometimes white potatoes, but most such foods are imported. (Another 17 species are brought in from outside; of these, only wheat is important. The rest are minor condiments.) The Maya love to try anything and everything, and individuals have experimented with such unlikely plants as grapes and apples. One man proudly showed me his grapevine; it bore no fruit in the tropical climate, but it was a lovely plant to look at and enabled everyone in the neighborhood to know what a real grapevine looked like.

By far the most diverse set of plants are the medicinals. In this study, 330 plants used medicinally were recorded (many have not been identified to date), and this number may be only a small fraction of the whole. Traditional curers (*jmeen*) seem able to find uses for every plant and often have discovered new ways of utilizing bark, leaves, and roots. As in most studied cases, a high percentage of these plants are dooryard herbs and weeds. Some are grown deliberately; every extensive garden includes rue (*Ruta chalepensis*), mint (*Mentha* spp.), aloe vera (*Aloe* sp.), and epazote (*Chenopodium ambrosioides*). Others are used simply because they are easily available.

On the other hand, the most highly regarded medicinals are largely deep-forest plants: elemuy (*Malmea depressa*, a diuretic and thus believed to be a kidney medicine), wako ak' (*Aristolochia maxima*, a stomach medicine and general tonic), tankas che' (*Esenbeckia pentaphylla*, used for paralysis and the like), among others. Of these high-powered anodynes, only kambajau (*Dorstenia contrayerva*, an antidote) is a milpa weed.

Another 168 plants are used as ornamentals. Most are introduced, but many are native. Presumably the ancient Maya had their flower gardens, as flowers are prominent in their art. Some spectacular flowering trees, such as hok'ab (*Tabebuia rosea*), have spread from Mesoamerica to gardens around the world.

Logging is important, and 41 species are cut for sale. Sixty-two species are harvested for local timber use.

Minor uses may also be significant. Fourteen species are used for fiber and bast. All woody plants can be used for firewood; some thirteen species are sought out in particular, having superior burning qualities. Plants provide animal forage, wildlife food, basketry materials, nectar and pollen, tannin for hides, soil quality indicators, dyes, drugs, toys, soap, disinfectant, and ritual and symbolic values. Wild grapevines (*Vitis bourgaeana*) provide lifesaving water in the dry forest. There is even a plant whose sticky leaves are used to trap fleas.

So far, I have recorded 826 plant names, of which 460 have scientific identifications. Further research is continuing.

The Maya also recognize different sorts of vegetation, soil, and landscape. They are aware, for instance, of succession stages. In Chunchuhub, a regrowing milpa is first sak'al (weedy), then hubche' (young brush and trees), and finally kaanal k'aax (high forest)—at which time it is ready to cut again. Vegetation-landscape types include ak'alche' (low-lying damp areas) and other specialized formations. Soil terminology is complex and largely based on soil color (see Terán and Rasmussen 1994).

The Maya also find useful the Spanish custom of coining a plant community term by adding the suffix *-al* to the name of the commonest tree. Thus, *tintal* is used for forests of *tinto* (*Haematoxylon campechianum*, eek' in Maya), *zacatal* for tall grasslands, and so on. Modern Maya plant terminology has been enriched in many ways by Spanish influences, just as Yucatán Spanish has been enriched by countless borrowings from the Maya.

PLANT CLASSIFICATION

Yucatec Maya plant classification well exemplifies Berlin's general comments on ethnobiological nomenclature (Berlin 1992); this is not surprising because Berlin has worked largely with Mayan languages.

The concept of "plant" is expressed by the classifier *kul* (derived from *kul* "tree-trunk," but used to count any type of plant). Relevant also is the term *k'aax* "forest, wild vegetation." Within the plant category are life-form classes: *che'* "tree," *ak'* "vine, liana"; *xiiw* "herb"²; *su'uk* "grass"; and *k'uxun* "fungi," which are dubiously plants. Recently, this set has been enriched by borrowings from Spanish, now thoroughly Mayanized: *arbusto* "shrub" and *zacate* "large grass." (At least in Chunchuhub, large introduced grasses are truly seen as a separate life-form, not *su'uk*. *Zacate* is a Nahuatl word, assimilated into Maya via Spanish.) A large number of plants, including bromeliads (*ch'am*), reeds and reedlike plants (*halal*), cacti (each species or genus with its own name), sedges, and several other groups, fall very uncomfortably into these life-form classes, and are considered separate little worlds unto themselves. (This is a phenomenon widely reported for Mexican indigenous languages, as well as for other languages, including English, in which "reeds" and "cacti" are outside the normal life-form classes.)

Cross-cutting the life-form category, and conceptually separate from it, is the basic taxonomy. This, like other Native American taxonomies, is notably rich in generics and poor in higher-order and lower-order terms. Almost every

plant, or class of plants, has its own name—either monolexemic (elemuy, kambajau) or combined with a life-form term (*wako ak'*, *kaanser xiiw*).

Higher-order categories that would seem “obvious” to an Indo-European speaker, such as “squash” and “beans,” are not at all obvious concepts to the Maya. They see each squash species as a very separate and distinctive thing, and lumping beans under one term seems inconceivable to them because each species is so different! In some cases, Spanish has provided useful higher-order categories where none exists in Maya; all squashes, for example, are now lumped as calabazas in ordinary conversation. In fact, Yucatán Spanish has assimilated some Maya names. This is not due to a failure to see general similarities, but rather to a profound knowledge of the unique qualities of each species. In Spain, I learned that the Spanish language (as in Yucatán) separates each leguminous species.

Lower-order breakdowns do exist. Some folk generics are broken down into rather vague folk specifics. Thus, generally darker-looking acacias are box katsin “black acacia,” while generally paler-looking ones are sak katsin “white acacias.” Elemuy comes in three colors, black (box—the common form), white (sak) and red (chak); as far as I can tell, they are all just slightly different-looking individuals of *Malmea depressa*, but more research is needed here. Most other folk specifics are color terms too. Oranges, however, are either suuts' pak'al (“sour orange,” *Citrus aurantium*) or ch'ujuk pak'al (“sweet orange,” *C. sinensis*).

Major domestic plants have varieties, such as the common maize variety known as nalt'eel, “rooster maize.” (This term has been widely assimilated into English, interestingly, as “Nal-Tel.”) Lima beans (iib) have some delightfully named varieties: “tinamou egg” for one that is shiny and brown like a tinamou's egg, and “peccary's eyelashes” for one whose vivid stripes remind people of the long, thick vibrissae above the eyes of the peccary.

Life-form categories cross-cut, rather than include, these generics and specifics. Plants that can take either herb or tree form, such as cotton and pigeon peas, are well known. Still other cross-cutting distinctions exist, such as the distinctions between wild and tame plants, between domestic and weedy varieties of the same plant, and between tuberous plants (wiij “swollen root,” makal “tuber/corm”) and nontuberous relatives. (Makal is, however, also a specific term for *Xanthosoma yucatanense*, and ak'ij makal “vining makal” is a Colonial coinage for *Dioscorea* spp.) Hofling and Tesucún (1997) combine all these categories into one system, as if they were divisions within one taxonomy.

For the Yucatec, it is also clear that some plants are closely related to each other although they may be called by very different names. This can be deduced from the use of assimilated Spanish terms as folk familiars, as in the case of squash, or palms (Sp. *palmas* has no Maya equivalent). It can also be

deduced from routine generalization of native Maya names to cover entire categories. Bignoniaceous vines are routinely lumped (usually as sak ak' "pale vines" or the like), for instance, although several species actually have their own names.

One should be extremely conservative about inferring any perceived relationships beyond what is clear from the above usages. In fact, even a generalization of name is no proof of any relationship. Names such as k'an lool "yellow flower" or chak lool "red flower" are used too widely and vaguely to imply anything beyond the obvious. (K'an lool specifically means *Senna* spp., or similar plants, but is just as often used to mean literally any flower that is yellow. There is not even the juncture difference used in English to separate "black bird" from "blackbird.") Superficially similar plants can easily be confused by a careless speaker. Perceived relationships, beyond such unmistakable cases as squash and Bignoniaceous vines, are a very idiosyncratic thing—psychologically interesting, but not part of encoded Maya traditional knowledge.

MANAGING PLANTS

The Quintana Roo Maya are superb plant managers. They have an enormous and highly self-conscious knowledge of how to use plants, as well as how to use the environment to maximize the production of plants they use. When traveling in fields or forests, they are constantly performing small tasks, from clearing trails to repairing damaged wildlife habitats. The whole forest is constantly being influenced by thousands upon thousands of these tiny, almost subconscious acts. Even a brief catalogue of common management techniques would be far too long for this chapter. Though a few highlights will be mentioned.

In field agriculture, the Maya are expert at combination planting. The combination of maize (corn), beans, and squash has many advantages: maize serves as support for the beans and as shade and protection, beans fix nitrogen, and squash suppresses weeds and insects. The Maya know which species and varieties to combine to maximize these benefits, and which combinations do better on specific soil types.

When they cut forest for fields, they eliminate useless plants; they coppice trees that grow back fast and provide values such as holding the soil; and they carefully protect the most highly useful trees, such as thatch palms, wild fruit trees, and bee trees.

When Maya find a sapling of a useful tree species in the forest, they often cut a little firebreak around it. They are careful not to damage useful wild plants. When harvesting medicinal plants, they never take a whole stand; they leave some to reproduce and restore the stand. In fact, the whole Quintana Roo forest is managed like a farm. In a sense, it *is* a farm, because

every part of it has been repeatedly cut, burned, and shaped by selective management. It is no accident, for example, that 15 percent of the tree cover in mature forests around Chunchuhub is provided by chicozapote (*Achras sapota*=*Manilkara sapota*; this figure was kindly provided to me by the Plan Forestal office in Chetumal, and confirms my own observations). This tree provides fruit that is not only valuable for humans, but is also a staple food of game animals; a superior timber; and chicle, which is a commercial product. For thousands of years, Maya have been protecting these trees, which have come to dominate many forest areas.

Recently, reforestation with cedro (*Cedrela odorata*) and mahogany (*Swietenia macrophylla*) has become common. Also, the Plan Forestal, a government forestry plan, has worked successfully with several communities in Quintana Roo (Flachsenberg and Galletti 1998; Galletti 1998; Primack et al. 1998). The Plan Forestal uses traditional Maya management skills as well as modern forestry science. The results are much more successful than most tropical forest management schemes, and indeed the Plan Forestal has become something of a model. Traditional Maya plant management is thus, potentially, of world importance.

Maya forest management is maintained partly because of supernatural sanctions. The Lords of the Forest (yuumijk'aax or yuntsijloob) punish people who use the forest in a wasteful, inconsiderate manner. A man hit by a falling branch or tree, for instance, is often assumed to have done something that angered the yuumijk'aax, and stories of his thoughtless behavior are recollected to support this belief. The elves (alux, pl. aluxoob) are often put in charge of guarding a section of forest; both supernatural beings and humans can get them to do the work. The aluxoob scare away intruders by making a dreadful racket. These are part of a wider pattern of direct supernatural sanctioning of moral principles.

CONCLUSION

Recently, anthropologists have taken a thoughtful second look at traditional ecological knowledge. Particularly interesting has been a long dialogue between the Athapaskan peoples of Canada and a number of anthropologists (Cruikshank 2000; Goulet 1998; Ridington 1988; Sharp 1987; Smith 1998; see also Turner, Boelscher, and Ignace 2000 for a brief but model account of a neighboring group). The Athapaskans are among the few peoples who actually lived—and often still survive—largely by hunting large animals. Their knowledge system is very different from bioscience, but is consistent, well described for us, and above all brilliantly successful at keeping them alive in an incredibly harsh environment.

Scholars of Athapaskan knowledge are thus confronted with a system maximally different from their own, but clearly and formidably successful.

They naturally have become interested in contrasting the two, and understanding the Athapaskan “ways of knowing” (Goulet 1998).

Athapaskan knowledge is highly local, and is typically communicated either nonverbally (Goulet 1998) or through specific personal stories that have wide implications (Cruikshank 2000). Declarative, analytic, verbal explanation is seen as foreign and unsettling. They also attend to dreams, visions, subconscious perceptions, and indeed to the whole range of mental acts and processes. This is clearly related to their hunting activities (see Smith 1998). A hunter must attend to all possible cues, and integrate them at an intuitive or preconscious level; it is just not possible for the conscious mind to attend to all the cues that the “bush” presents. A hunter may dream that a moose is in a particular place, then actually go there and find it (Ridington 1988; Smith 1998). The dream serves to integrate the cues that the hunter has perceived while awake in the bush.

The Athapaskans prefer to teach by example. The young and naïve are expected to accompany their elders and to learn by watching and imitating. Later, tales and personal stories are used to convey more abstract messages.

Not surprisingly, the Maya also attend constantly to consciously and subconsciously perceived cues, and often understand nature through dreams and visions—although they do not (usually) dream the locations of game animals. The Maya, however, are more self-consciously pragmatic, systematic, and verification-oriented than the Athapaskans. They provide a useful intermediate case between Athapaskan and modern scientific “ways of knowing.”

It seems quite natural to me that people learn by observation, experience, story, and subconscious monitoring of the environment. How else, really, does one find animals in the field? Any veteran hunter or field naturalist experiences the field as a rich, complex, textured environment—far too complex to be monitored on the conscious level alone. Every field naturalist has his or her stories and personal experiences, and tends to remember knowledge in such concrete terms. Knowledge has its places, situations, and persons. Only in the classroom is it generalized and decontextualized.

Thus, there is a contrast between detached urban-academic ways and rural, contexted, experiential ways.

The Yucatec Maya are much more verbal than the Athapaskans and, indeed, love to explain things such as plant uses at enormous length. However, they also partake of the same rich ways of knowing as the Athapaskans. They, too, make their points by telling stories about specific events and places. They, too, prefer to teach and learn by example and observation than by verbal report. They, too, expect the aspiring student to come along in the field. Working with them has involved thousands of hours in the field, as well as much food preparation, medicinal plant selection and

use, and the like. I have spent hundreds of hours on remote forest trails and in isolated milpas. Without constant observation of how the Maya actually interact with plants in the field, the student cannot learn the details of Maya plant knowledge.

Some of the writers, notably Goulet (1998), have been led to see all knowledge as arbitrary. For them, knowledge is culturally defined and systematized. Each culture is a closed world, with its own ways of knowing. Thus, knowledge itself is not knowledge of some objective or external reality, but merely cultural lore. Goulet frequently reiterates that his friend's

accounts are immune to the arguments that might be made against them by an outsider to the interpretive community in which they are held to be true. In other words, in any interpretive community, reality is self-validating in that all aspects of it are mutually constitutive and, further, in that it reflexively preserves itself by stipulating in advance what is allowable as evidence" (Goulet 1998, 257–258).

Goulet makes it clear (here and in many other passages) that he does not believe in an objective reality or science; each culture has its system, self-validating and apparently self-created. Feedback from the outside world is irrelevant. Goulet believes this in part because the Dene Tha (the Athapaskan group with whom he lived) understand their world through dreams, visions, and prophecies as well as through direct interactive experience.

Smith has been led to exactly the opposite conclusion (Smith 1998). Experience with the Maya (and with many other traditional and nontraditional groups) shows that they have a superb grasp of objective reality, based on countless years of interacting with it. They use dreams and visions, as well as interaction and systematic learning, because dreams and visions work. They do not always provide accurate information, but neither does ordinary observation and interaction. Dreams and visions are often accurate when they integrate subconscious cues and long-buried, half-forgotten knowledge. Inaccuracies from visionary experiences are a small price to pay for the values of an intuitive system in a forest environment.

Goulet confuses factual knowledge with inferred explanations, meanings, and significances. Factual knowledge is verifiable and experiential—at least potentially—for the Athapaskans, the Maya, or anyone else. Thus, mint either helps stomach ache, or it does not. Inferred explanations are different in that they are typically hypothetical, in both Athapaskan and bioscientific circles. They are more or less indeterminate until overwhelming proofs are adduced. Meaning and significance, as well as religious belief, are in still a different cell; they are, typically, outside the realm of evidential proof altogether. If a moose is regarded as a sign from God, or seen as a visionary reminder of a

dead relative, no one can really prove or disprove that vision. The significance is an existential internal fact for the perceiver. (This is not to say that one cannot study visions scientifically—but that is a quite different question.)

Goulet usefully critiques interpretive anthropology for its indifference to direct experience. I agree, but I would add that Goulet's own theory is, basically, an interpretive theory, and thus subject to the same criticism. Goulet's own experiences, as recounted in his book, clearly play against his theory.

Goulet, like many anthropologists, sees knowledge as socially constructed, *and therefore arbitrary*. This is both a factual and a logical error. Of course, knowledge is socially constructed because it arises through human interaction. But humans interact with each other and with their environment, and thus are forced to learn—to make their knowledge ever more extensive and accurate. People cannot persist in the belief that strychnine is good food, nor socially construct such a belief as “knowledge.” Usually, the more socially constructed knowledge is, the more accurate it is. The obvious exceptions—racism, for instance—are clearly driven by perverse psychological mechanisms (Beck 1999). Anthropologists frequently assume that “socially constructed” means “irrational,” or even “wrong,” because they are used to dealing with religious, symbolic, and other nonscientific systems. Goulet looks at theories, and also at methods of teaching (stories vs. analytic lectures), and says knowledge systems (including “science”) are constructed out of whole cloth. I look at the actual data, and say that these systems are constructed, but on a basis of empirical truths—however many mistakes traditional people (and scientists) may make, due to limitations in the observations they can perform with the equipment at hand.

This matter is considered at some length because many anthropologists make similar mistakes, to the considerable cost not only of anthropology but also of the indigenous people in question—whose knowledge is, once again, peripheralized and trivialized. Traditional knowledge is *not* a mass of confused magical beliefs. It is a body of hard-headed empirical wisdom, integrated and held together by higher-order representations. These latter are often wrong and more often unprovable, and they may also lead to logical extensions that are incorrect. However, they are better seen as organizing heuristics than as defining theories. They play the same useful but often misleading role that paradigms play in western science (Anderson 1996).

The Maya are superb natural historians and folk scientists, and they are the better for their use of *all* methods of perceiving and integrating data. It is the academic biologist that is deprived—perhaps necessarily so, given the biologist's mission to verify every datum experimentally, but deprived nonetheless. Conversely, the Maya are deprived of the vast scholarly literature

available to the academic. Of course, most of the plant knowledge of both Maya and academic botanists comes from direct work with plants.

This is not to say the Maya are always right. I believe their knowledge of food, forage, timber, and craft plants is entirely accurate (except for a few details of medical belief about foods). Their plant cover management skills are consummate. Their medical knowledge is more controversial. Most of the medicinal herbs that I have tried actually work—some much better than drug-store remedies. However, many Maya herbal remedies seem to have few or no detectable pharmacological effects. Maya belief in their efficaciousness may be due to confusion, mistaken logic, wishful thinking, or simply to someone's use of an herb just before recovering naturally from a disease.

Finally, Maya knowledge of spirit beings in the forest seems to be based wholly on tradition and imagination rather than on believable evidence. But does this distinguish the Maya from the academic biologist? Academic biologists also believe in higher-order beings that do not verifiably exist: harmonious ecosystems, climax plant communities, group selection, etc. Academic economists also believe in the "invisible hand of the free market." The tendency of humans to see higher-order entities out there, controlling life, is irresistible.

Note that—contrary to Goulet's claim—both the Maya and outside visitors *can* evaluate the truth-value of many of these claims. For example, medicines can be tested in double-blind experiments. Other claims, however, are untestable. The Lords of the Forest, if they exist, are subtle beings, like other gods. They must remain matters of belief. The same is true of the virtues of the Free Market because a perfectly free market is inconceivable in the real world; thus, we will never observe how one would function.

In other words, beliefs may be true, false, or indeterminate. They may also be still under judgment, which means they are at present indeterminate but will not be so if they are examined; thus, many of the medicinal plants the Maya use are still not adequately tested by either Maya or biomedical curers, and are thus "hypothetical" as far as medical value is concerned (see Ankli, Sticher, and Heinrich 1999). In all these ways, Maya folk science is indeed a science, equivalent to academic biology in basic structure although not in sheer ability to generate factual knowledge quickly.

The Maya are constantly testing their views against experience. Mistaken beliefs do not usually last—if they are testable. New ideas are tested, and adopted if they are useful. Inherently untestable beliefs, such as religious beliefs, may persist indefinitely. In short, Maya traditional knowledge is scientific, in that it is based on systematic interaction with the world, and systematic testing of claims. It is not fully scientific, because it incorporates many beliefs that are called supernatural and that are not fully testable³. But neither is contemporary bioscience, for it too—in spite of its vast mass of

accurate knowledge and predictively-validated theory—depends to some extent on assumptions.

The idea that traditional cultural views are closed, self-maintaining systems is not confined to Goulet; it is common to many (perhaps most) anthropologists. Yet it is clearly wrong. Maya have incorporated not only Spanish plants, but also Spanish concepts, insofar as they find these useful. Of course, through the Spanish, they assimilated plants from all over the world. They are now assimilating words more widely too, as globalization brings English and other languages to their doors. Concepts also spread. In pre-Columbian times, the Maya incorporated concepts from central and east Mexican indigenous peoples. Today, they incorporate ideas about integrated pest management and sustainable development into Maya garden plots, thanks to such influences as the local agricultural college.

Similarly, the world is better for borrowing cacao (*Theobroma cacao*) and other plants from the Maya. The world would be still better off for borrowing plants such as chaya (*Cnidocolus chayamansa*; see Ross-Ibarra and Molina 2000) and mamey sapote (*Calocarpum mammosum*)—and also for assimilating concepts such as the Maya's active management of milpa regrowth. Views similar to those of Goulet ghettoize traditional knowledge, turning it into a mere curiosity.

There are also those who ghettoize traditional knowledge in the opposite way, by restricting the term “science” to modern western academic inquiry. Wolpert (1992), for instance, denies the name “science” not only to indigenous traditions but even to traditional Chinese inquiries into nature, although the latter were consciously experimental and theory-based. Inconsistently, Wolpert also calls the ancient Greek natural philosophers “scientists,” although their views resemble Chinese cosmologies more than modern scientists' views.

One could argue that the Maya do not have laboratories, or refereed journals, or case/control experiments, and thus cannot be said to possess truly systematic, accurate knowledge. This is clearly wrong; the Maya know the forest very well indeed—far better than any academic biologist. One could argue that the Maya live in a world of religion, magic, and dream, and thus cannot have accurate knowledge. This too is false; believing in the Lords of the Forest does not preclude knowing exactly when the sapotes will fruit, or what part of the elemuy tree is diuretic, or how to intercrop milpa. In fact, belief provides the moral and social grounding within which factual knowledge can be systematized and taught⁴.

The stakes in this seemingly arid debate are high. Insofar as all knowledge is merely an arbitrary social game, or insofar as all worthwhile knowledge is derived from laboratory science, Maya knowledge of the environment can be and should be ignored and rejected. Insofar as science is a

human endeavor in which indigenous forest-dwellers can generate useful knowledge and interesting theory, we cannot ignore Maya knowledge. For thousands of years, the Maya have been the only successful managers of the Yucatán Peninsula's fragile environment. Their knowledge has grown and evolved in the face of millennia of experience. We need to learn from them, and they have much to teach. To do this, we have to be properly respectful of the Maya and their wisdom.

In fact, more should be done. We have to be properly respectful of humanity. Our species has been wasteful and destructive, but has somehow kept the search for truth alive, and has used hard-won truths in successful management of harsh environments. We also have to be properly respectful of the other lives on this planet. That is perhaps the most important thing we can learn from the Maya.

NOTES

1. The name "Yucatec" is one of those words that delight a philologist. The people in question call themselves *maayaj*, source of the word "Maya" that now is generalized to all linguistic relatives. "Yucatán" was the name the Spanish applied to the peninsula when they first saw it. Stopping a canoe, they asked the startled paddlers about the name of the land now visible on the horizon. Evidently there was stunned silence, broken by some helpful soul who volunteered "He didn't understand what you said" (*ma' u yu'u'b' ka t'aan i*—or, as one Colonial Maya writer glossed it, *matan cub a than*, which would be *ma' t'aan ku yu'u'b' a t'aan i* in modern writing; Restall 1998, 122). The Spanish duly noted the accented syllables. Later, to compound confusion, they invented the word "Yucatec" by inflecting the name as if it were Nahuatl (-*tan* "place" being replaced by -*tek*- "person [of]").

Note: This paper uses the new standardized transcription system for Maya; however, the sources quoted normally use the old Spanish Colonial system. For example, Roys' *huhub* is *jujub* in the new system.

2. *Xiiw* is a Nahuatl borrowing (from *xiuitl*—probably via Spanish), but Itzaj has a native Maya word, *teek*, covering the same semantic space; Itzaj uses *xiiw* for certain medicinal herbs only (see Hofling and Tesucún 1997). I assume Yucatec once used *teek*, which is a term amusingly close to TEK.

3. On the other hand, individuals do report actually encountering the *yuumijk'aax* and other such entities. The outsider may cynically note that these encounters typically follow on the consumption of large amounts of *chakpool* (raw rum), but the Maya are not easily persuaded of the relevance of this fact. Witchcraft, too, can be validated by experience, as when my field assistant watched a curer taking a live scorpion out of the body of a girl. Having had the opportunity to observe the sleight-of-hand skills of the healer in question, I suspect there is no real proof of witchcraft in the observation. The point here, however, is that observation *does* give some support to traditional beliefs—*within the limits set by the testing situation*. The Maya do not have the luxury of million-dollar labs and case-control studies of thousands of volunteers. To this extent, Goulet is correct.

4. This is probably true everywhere, but especially in the western world. Would biology have developed without pre-Darwinian theories of change and organization? Would ecology have developed as it did without the Clementsian belief system?

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Chapter 30

The Tropical Forest Action Program: A Different Way to Handle the Management and Conservation of Natural Resources

Silvia del Amo Rodríguez
Veronique M. Rorive

INTRODUCTION

The new century has introduced a series of problems worldwide (e.g., eliminating poverty while maintaining biodiversity) that because of their nature require multidisciplinary and multi-institutional resolutions. More than two decades ago, the world realized the necessity of sustainability (see WCED 1987) without knowing how to reach this goal. Since then, there have been a few success stories when considering the enormous amounts of resources—be it economic, human, and scientific—expended upon sustainable projects worldwide.

The reason is simple. Sustainability is a conflict between “values” and “interests,” which, in this case, represents a conflict between poverty and environmental degradation, with “interests” (i.e., environmental degradation) winning during the last 30 years. In Mexico the impact of this conflict is enormous, especially when 75 million inhabitants out of a population of 100 million live in various degrees of poverty (Boltvinik and Hernández Laos 1999). This appalling situation is attributed to the poor distribution of resources and wealth that are the main obstacles in reaching sustainability, while sustainability, in itself, is the key to maintaining the equilibrium between humans and nature (Figure 30.1).

The establishment of sustainable development has not been carried out successfully because a major obstacle and real challenge of sustainability is

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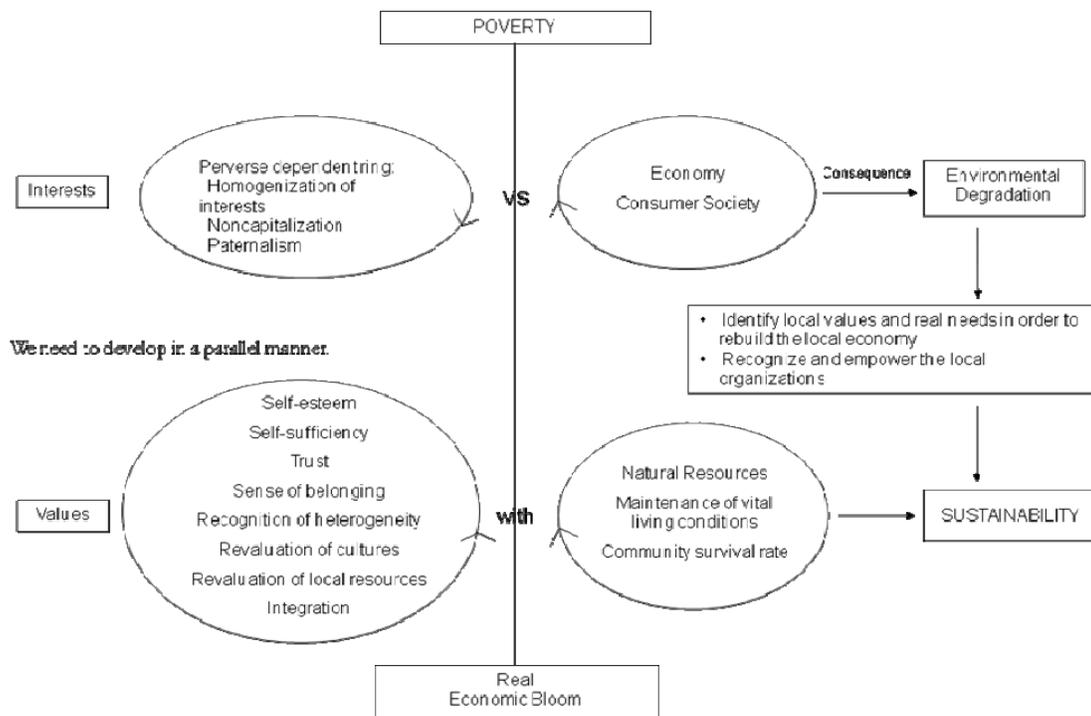


FIGURE 30.1. Today's economic model: Poverty seen in economic terms. To achieve a true sustainability, values and interests must be reconciled and considered within the economic model, recognizing the risk this may signify to the power of the state.

the global point of view. This represents the Pyrrhic struggle between values and interests.

Sustainability is born as an ethical and social imperative in which the human factor is the aggressor and transformer of nature. This function should be changed in a more productive and effective role by local populations in their own life, so that they are able to take a more active position in being reconstructed. Social sustainability is the minimum necessity that allows the permanence of people, societies, and resources with their heterogeneity of expressions. Other components of social sustainability include

- widening of the production base;
- promotion of the local internal market;
- applying common sense before rationality, and *not* applying homogeneity as a rule;
- recognition of local community successes and targets;
- management of natural resources in the long term;
- social investment; and

- joint action of the civil society (ranging from civil associations to universities to government through their development policies and agencies).

The most important error in the conceptualization of sustainability is in viewing it as a static goal. Sustainability is a dynamic process that cannot be measured by the number of things accomplished; rather, it is a learning social process for all of society (NRC 1999). To make this possible, new strategies need to be developed. These strategies will allow us to obtain new models of synergic local interventions, which comprise the reinforcement of local capacities and abilities in resources management (as well as social, administrative, and marketing tools) with the addition of some new and necessary techniques, produced by a mixture of scientific and local knowledge, to promote and provide feedback for the carried-out actions. The true transition to sustainability requires research and the pursuit of actions that let us detect successful social processes. This will be the reliable change factor.

Mexico is a country of contrasts: in the south lies a region that is underdeveloped in terms of education, nutrition, and marginalization (see INEGI 1995, 2000) and yet abundant in terms of the diversity of its natural resources. This contrast helps reflect the vicious trend that affects sustainability—that is, the loss of resources and poverty, which are two elements that are related intimately. In the last 30 years, this effect has become more significant due to the macroeconomic model adopted by Mexico. Ironically, the relationship between resources and populations should be fruitful, considering the rich biodiversity found in tropical regions. Nevertheless, time has shown that this relationship continues to deteriorate because these two elements are distinct phenomena: the management of natural resources and the state of well-being, which offer two different concepts of reality. Poverty is viewed in terms of “values,” whereby natural resources, due to their shortage, are viewed in terms of “interests.” Thus lies the importance of the problem as well as the need to overcome this conflict in order to achieve sustainability.

To alter the perverse relationship between values and interests in Mexico, we must transform the characteristics of the marginal population clusters. It is difficult to accept that the inhabitants of these regions who are richest in natural resources should also endure the poorest standard of living. Poverty needs to be measured not solely in economic terms but also by qualitative indicators such as self-esteem, a sense of belonging, social co-responsibility, proposals developed by the community members, and the recovery of traditional values and uses, among others (see Figure 30.1). A means of transforming these trends can be achieved through microcredit policies, compensations, and incentives that encourage conservation and production

alternatives, as well as leading eventually to a recovery of the local and internal national markets. Furthermore, the permanent and alternative management of resources will only be a reality if co-responsibility and partnership exists between nonprofit organizations and the communities they serve, with a special role from the universities performing research with the local population.

THE ROLE OF PROAFT A.C.

A little over ten years ago, the Programa de Acción Forestal Tropical, Asociación Civil (PROAFT A.C.) began to work with small and decentralized projects in southeastern Mexico with the objective to help others acquire the capacity to give local answers to social and technical aspects according to available natural and human resources. This is a new focus in community work—recognizing heterogeneity. The extant consumer society tends to homogenize values and interests, thereby seeing cultural diversity as an obstacle. Many different ways and diversity of expressions need to be found. PROAFT A.C.'s work is accomplished at a “micro” level. This means that work place in small communities, or along with a few community members, in an intervention (or interaction) model known as the tripartite alliances for the Conservation and Development of the Forest Patrimony (see Figure 30.2). Local human and natural resources are the key for the success of this strategy and must be recognized, promoted, and enriched (del Amo 2001).

Experience with community work has shown that the transition to sustainability can only be achieved through a social process of learning over medium- and long-term periods. In addition, the importance and need for all players to acknowledge and act upon the following concepts must be recognized:

- Globality (i.e., the global point of view) and the current economic focus applied to policies worldwide constitute a strong impediment to this transition.
- The sector living in extreme poverty is a result of the poor management of natural resources.
- Poverty contains qualitative aspects that have more to do with survival than with the homogeneous living standards that have been applied worldwide. The maintenance of biodiversity is strongly linked with heterogeneity. In other words, local and particular solutions should be applied to the problems and to the expectations of the local populations.

- During the last century, negative environmental effects have been considered an external fact of the dominant economic development model. Nothing is farther from sustainability.
- A large number of social conflicts in rural areas are directly related to environmental problems. Examples of this phenomenon can be found in two projects from Veracruz: (1) in Pajapan, vanilla producers have ceased to cultivate the crop due to extensive crop theft by other vanilla gatherers; and (2) in Laguna del Ostión, mangrove regeneration also has ceased because of the lack of respect by other communities who cut and then steal the lumber.

Another important lesson learned is that sustainability, in general, is possible as long as social sustainability is established before ecological sustainability.

An important component of working with these projects has been to identify, develop, and test viable production alternatives. As such, PROAFT A.C. is working with the following systems: agroecological agriculture; traditional management; agroecosystems (management of agrosilvopastoril systems, acahuales, and home gardens); vegetable cultivation; management of wildlife reproduction; native species reforestation; and ecotourism, among others. In the following section, two specific examples of PROAFT A.C.'s work and how they relate to the establishment of social sustainability and its transition to ecological sustainability will be presented.

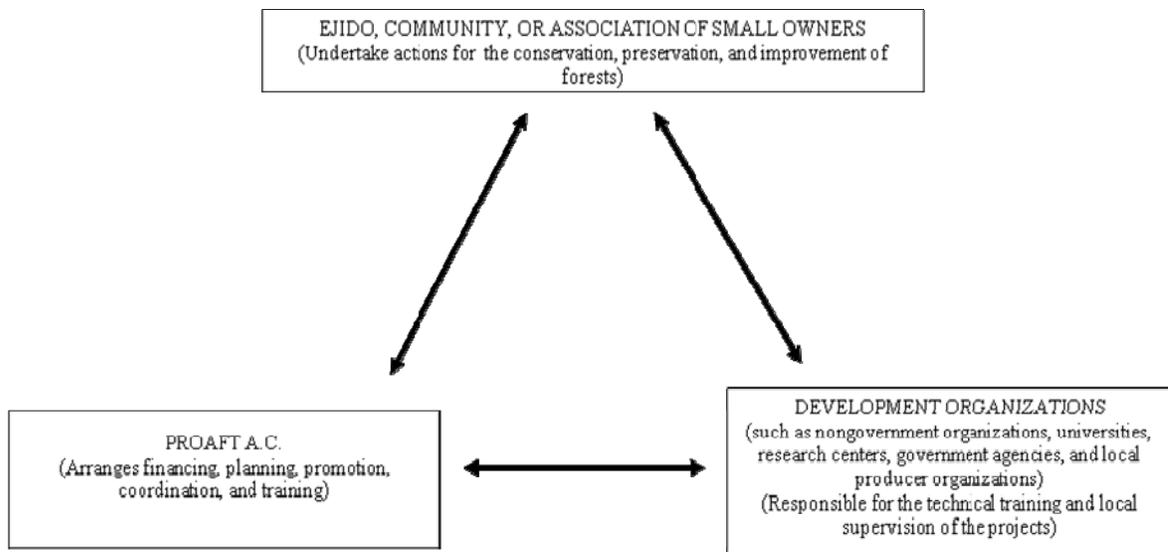


FIGURE 30.2. Tripartite alliances for the Conservation and development of the Forest Patrimony (Source: Modified from del Amo and Gómez-Pompa 1994).

Municipality of Las Margaritas, Chiapas

Work began in this region in 1992 with the participation of women from three ejidos (lands with communal ownership) in cultivating vegetables in their solares (home gardens). It is important to note here that the participants belonged to three different religions and ethnic groups. This component helps demonstrate how solidarity and tolerance of differences exist when experiencing and sharing similar problems, results, and successes.

From 1998 to 2001, a study for the disposition and usage of firewood, including the introduction of alternative wood-burning stoves was undertaken. The results show not only that the women have adopted these stoves, but also that they have adapted them particularly to suit their own needs, thereby demonstrating the flexibility and plurality required to address the needs of the local populations. These actions constitute one of the more important contributions obtained by PROAFT A.C. activities.

Currently, we are developing ecotourism modules within the three ejido communities. This alternative combines the reevaluation and conservation of forestry resources with that of generating employment alternatives and the improvement of the quality of life for the inhabitants. More importantly, it is a project developed and carried out by and for the locals that has proven to be highly productive as well.

Municipality of Calakmul, Campeche

Prior to the current collaboration with the Consejo Regional Indígena y Popular de X'pujil (CRIPX), a regional council composed of members from 23 *ejidos*, PROAFT A.C. began working in the Calakmul area in 1993 with a silvopastoral project in two communities. Since then, the diagnostics and projects undertaken in the region have varied greatly, ranging from the creation of an oven prototype for smoking peppers, to the management of wildlife, to the current goal of establishing experimental agroforestry plots in five communities.

As interests and needs arise within a community, a single organization often finds it difficult to provide the necessary framework and means to meet these needs competently and assure their continuity; thus, PROAFT A.C.'s role has expanded to include acting as a facilitator for communities. The agroforestry project currently in progress with CRIPX depicts the new role adopted by PROAFT A.C., which depends upon collaborating and coordinating activities, actions, and participation among various regional academic and research institutions and organizations (e.g., Departamento de Manejo y Conservación de Recursos Naturales en el Trópico [PROTROPICO], Universidad Autónoma de Yucatán, Universidad de Campeche, Escuela de Agricultura Ecológica, and AMEAP S.C.—Asociación

Mexicana de Apicultores, Sociedad Cooperativa). How does this work? As an example, one of the project's workshop series on the design of agroforestry parcels was organized and conducted by PROTROPICO researchers with years of experience with the theme and working in the region, thus assuring that the workshop theme covered local needs, resources and interests. The inclusion of two local graduates from the Escuela de Agricultura Ecológica as promoters and consultants of the project not only supplied a continuous presence and means to respond to concerns and/or problems in a timely manner as they arose within the community, but also provided a means to assist the graduates in their return and reestablishment within their respective community. Sponsoring the work of two undergraduate students to pursue their thesis studies in the communities helped broaden the scope and impact of the project and provided the students hands-on community project experience. The activities and projects undertaken in the Calakmul region reflect the interests and requests made by CRIPX and show the integral approach of PROAFT A.C.'s community work.

Figure 30.3 depicts in a condensed format PROAFT A.C.'s contributions towards a true sustainable development. Note that for each main step a serious set of rules must be established. First, a social process in which it is necessary to establish a diagnostic (step 1) that is intimately related with the future expectations of the local population (step 2). This has proven to be an adequate means for involving the local population in the project process from the beginning. Because a premise of the project is the organization and training of people as self-managing experts of sustainability, step 3 consists of the management and continuation of the projects by the local population. Finally, with strategic planning (step 4), different sectors collaborate as equals to establish values and set priorities for the future. Taken together, these four steps help provide constant feedback, in a continuous manner, of a process that ensures communities achieve true sustainable development.

CONCLUSION

Experience with PROAFT A.C. activities has shown that regional poverty is characterized by the absence of local opportunities, recognition of worth, and a decent quality of life, along with corresponding rights and responsibilities. Secondly, the unawareness of local communities' own riches, among others, leads to the inability of articulating demands, needs, rights, and responsibilities. A consequence of these factors, something that still is not wholly understood in Mexico, is the loss of the internal market, which implies the market economy as inoperable for the lack of consumers. Third, sustainability needs to be seen in terms of a prosperity that reflects the

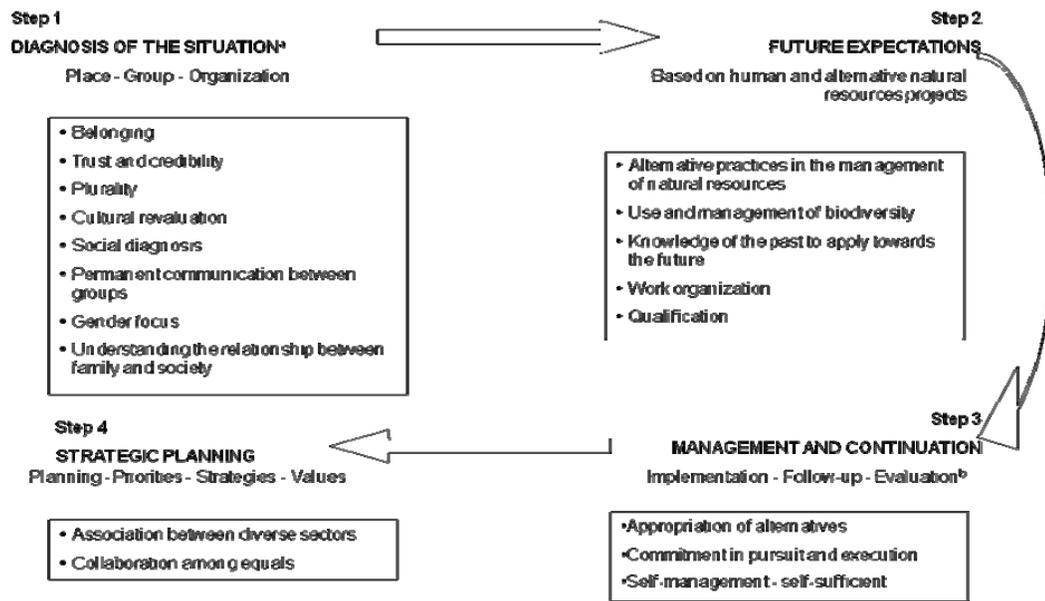


FIGURE 30.3. Contributions of PROAFT A.C. to the sustainable community process (Source: Modified from Aaker and Shumaker 1996).

^aVia workshops, site visits, and surveys

^bSimple instruments and classification scales must be differentiated.

opportunities expressed in terms of plurality, flexibility, diversity, and based upon available human and natural resources. Thus, trust, self-esteem, and a sense of permanence can be reestablished.

This view of sustainability has more of a social context than an economic context in that it is based more upon values than interests. Hence, sustainability takes on more of a qualitative than a quantitative approach; it is then subject to a medium- and long-term social learning process and requires the identification of both quantitative and qualitative indicators.

In today's dominant economic model of globalization, time is a factor against achieving development based upon values, which would be more just, fair, harmonious, and feasible of accomplishing. Plurality, heterogeneity, integrity, flexibility, and acceptance of empirical knowledge form the basic lines of work that permits PROAFT A.C. to make concrete community actions. This new focus of PROAFT A.C. inevitably leads to the reconstruction in an independent and self-manageable manner of not only the local economies, but also the rural societies as well. Although the benefits of this approach are obvious, the risks involved cannot be ignored as they directly challenge existing governmental power at the local, regional, state, and national levels.

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Chapter 31

The (Almost) Forgotten Plants of Yucatán

Robert W. Patch

INTRODUCTION

The lowland Maya people of today use the same plants for agricultural purposes that their ancestors did over three millennia ago. The most important plants, of course, are maize, beans, squash, tomatoes, and chili peppers. But between modern times and the ancient past, there was the period in time known as the colonial era (roughly 1517 to 1821); during those three hundred years, contact with the European, Asian, and African cultures took place and resulted in new plants being introduced. At the same time, old plants were used in ways that they no longer are used today. This paper will discuss the plants used by humans during the colonial period that are now largely forgotten, but which demonstrate the variety of human interactions with the environment.

INDIGENOUS PLANTS

Indigenous plants now in oblivion, but once quite important to the Maya and colonial societies will be reviewed first. First and foremost was cotton (Patch 1993:27–28, 81–93, 142, 161–165, 173, 179–181).

Cotton

The Maya cultivated cotton for thousands of years, and cotton cloth was virtually the only article of clothing for basic, rather than ceremonial, use. It was also the most important of the four major exports from Yucatán in the Post-Classic period (900–1500 A.D.) (the three others being salt, jade, and slaves). Indeed, Christopher Columbus himself, on his fourth and final voyage to America, ran into (and, of course, looted) a Maya trading vessel off the

coast of Honduras and provided a good description of the textiles being exported from Yucatán. His son Ferdinand remembered his father's encounter with the Maya as follows:

[I]t was his good fortune that there came at this time a canoe as great as a galley, eight feet wide, all of a single trunk . . . , which came loaded with merchandise from western parts, from the side of New Spain. Amidships it had a canopy of palm leaves, like that of godolas in Venice. . . . Under this canopy were the children, women, and all the baggage and merchandise. . . . [Columbus] then ordered that there should be taken from the canoe whatever appeared to be most attractive and valuable, such as cloths and sleeveless shirts of cotton that had been worked and dyed in different colors and designs, also pantaloons of the same workmanship with which they covered their private parts, also cloth in which the Indian women of the canoe were dressed, such as the Moorish women of Granada are accustomed to wear (cited in Sauer 1969:128).

Little is known about how the ancient Maya produced their cotton and cloth, but it can be surmised that the activity in place at the time of the conquest had been in place for centuries, and probably for millennia. Males carried out the harvesting of cotton, but it is not known if production was derived from plants growing wild all over the place, or from the systematic planting of seeds on cropland. Considering the quantities produced, it is likely that both methods were employed. More is known about the next phase of production. Women and girls removed the seeds, spun the thread, and wove the cloth in their houses using a back-strap loom. Cotton textile production, in short, was a cottage industry fundamentally similar to similar systems of production in China, India, the Middle East, Africa, and the central Andes before the Industrial Revolution.

The Spaniards found cotton textiles to be useful—not only for their intrinsic use value, but also for export. For that reason, as was true elsewhere in Mesoamerica and in the central Andes, the colonists created a tributary system in which the Maya would pay their taxes in kind, in the form of woven cotton mantles called mantas. These were so important in the lowland Maya area, and in Chiapas as well, that the Spaniards eventually used mantas as the measure of the indigenous population (that is, x number of mantas meant y number of people, production being on a per capita basis).

By the late sixteenth century, cotton production was becoming even more important in the lowland Maya area for two external reasons. First, disease hit the lowland Gulf Coast indigenous population of Mexico harder than the Yucatán area, and, as a result, cotton production decreased significantly in other parts of Mexico. Second, demand for the product was increasing

because of the Spanish colonization of northern Mexico as a result of the emergence of the mining economy following the discover of huge silver deposits in Guanajuato, Zacatecas, Durango, San Luis Potosí, Chihuahua, Coahuila, and Sonora. Because output of cotton and cotton textiles declined elsewhere, the lowland Maya were forced through a mechanism of colonialism called the *repartimiento* (a coercive putting-out system, requiring Indians to pay tribute debts in cloth) to produce more. This meant that Yucatán—far from being isolated from the world economy—was, in fact, an export platform, sending large quantities of cotton textiles to central and northern Mexico, which one of the most important places in the world economy at that time.

Yucatán's textile industry, therefore, was to a certain extent a backward linkage of mining. Moreover, when Maya production of raw cotton was insufficient to meet the demand, Spanish and mestizo landowners began to cultivate it on their farms and haciendas. Because the Maya did not pay tithes for their cotton production, the surviving tithe records for the 1780s give us an idea of the general areas of commercial cotton production by non-Maya people. These reveal that although the crop was grown throughout most of Yucatán, by far the most important areas of production were Valladolid and Tizimín [BCCA 1778–79, 1783–88, 1791–93; AAM Libros 19 (1791–94), 20 (1795–98)].

The viability and profitability of the lowland cotton industry declined significantly in the late colonial period. First, political and economic reforms designed to encourage competition, stimulate Spanish (especially Catalan) textile production, and diminish governmental corruption resulted in the elimination, in the 1780s, of the *repartimiento* system, which had boosted output beyond what was required as part of the tributary system. As a result, the Maya—now given a choice—continued to pay their tribute in cloth, but chose not to produce beyond what was necessary. Therefore, total output declined significantly.

Second, in the late colonial period the Industrial Revolution was taking place in England and Belgium (and eventually in the United States as well); this meant that European (and later, American) textiles that were both cheaper and better made would enter the Mexican economy and compete with those made in Yucatán using the old technology and structure of production. Because of the breakdown of political order in Spain and Mexico following Napoleon's invasion of the Iberian Peninsula, those cheaper textiles drove the lowland Maya producers out of business. In the 1840s, entrepreneurs in Yucatán attempted to take advantage of the local capacity to produce raw cotton by establishing a modern textile factory in Valladolid (a firm known as the "Aurora Yucateca"), but the expensive machinery imported from England was destroyed at the beginning of the Caste War (1847–1901) (Cline 1947). As a result, the cotton economy all but ceased to exist. This had few

deleterious effects on the Maya, however, for they had never received any of the benefits of production anyway—the profits having gone exclusively to the mercantile and governmental middlemen who controlled and marketed the final product.

Indigo

Another plant native to Yucatán, or at least to Mesoamerica, that became important in the colonial period, albeit briefly, was indigo (*añil*) (Patch 1993, 34–35, 145, 173, 178). This, of course, was used to produce the beautiful blue violet dye for textiles. It was valuable because it could be exported in return for hard cash. The lowland Maya area (as well as the region of Mesoamerica now known as El Salvador) was propitious for indigo production; as a result, in the sixteenth century Spanish entrepreneurs were producing the plant and the dye on their estates. Results were so good that the indigo mills (*ingenios de añil*) became the most valuable private estates in Yucatán. In 1577, at least 48 *ingenios de añil*, worth between 2,000 and 3,000 pesos, were in production.

But indigo production required a great deal of labor, and work in the mill itself—requiring laborers to wade into vats—was bad for the workers' health. Needless, to say, Spaniards did none of the labor. Rather, they forced the Maya to work for them; according to the Franciscans, labor in *ingenios de añil* was a major factor contributing to the Maya demographic decline of the second half of the sixteenth century. Under clerical pressure, in 1581 the government banned indigo altogether and successfully implemented the law, thereby effectively ending commercial indigo production in the lowland Maya area. Two centuries later some Spanish landowners in the Izamal area resumed production either in ignorance or defiance of the law, but output levels were so low that no one complained; in any case, no one made a great deal of money off of indigo. In effect, indigo was insignificant in Yucatán after 1581.

Honey and beeswax

Other all-but-forgotten indigenous products of the lowland Maya area are honey and beeswax (Patch 1993, 27, 28, 32, 81–92, 155–161, 189–190). Technically, of course, apiculture is not agriculture, but I have included it in this essay because of its indispensable link to plant life: bees acquire the necessary nectar from flora. It was because of the lowland area's flora that Yucatán, and not all of Mesoamerica, was a major apicultural producer.

As many scholars know, the lowland Maya area still exports honey. It has been produced in Yucatán and Campeche for millennia. Honey was the basis of *balché*, or mead; among the Maya, this was virtually the only alcoholic beverage known in ancient times. Consumption of *balché*, however,

was not widespread, for it was closely connected to religious ceremonies and was consumed only as part of Maya religious ritual. The indigenous people continued to produce mead after the Spanish conquest, but, because of its connection to a now illegal religion, consumers tended to keep information about balché a secret. The Spaniards, however, knew that it was produced and drunk, but knew little else.

The colonial regime found little use for honey, but quite a lot for beeswax, the other product of apiculture. Beeswax was used for candles; because of the Catholic Church's utilization of candles in religious expression, there was a strong demand for wax to make candles all over Mesoamerica. Beeswax, therefore, became Yucatán's second-most-important export (after cotton textiles). It was so important that the coercive repartimiento system that boosted textile production was also used to increase output of beeswax.

Little is known about the technical aspects of apicultural production. It is known that both Maya and Spaniard engaged in apiculture. Beehives regularly appeared in the inventories of landed estates, and sometimes accounted for up to ten percent of estate value. The Maya carried out apiculture around the home, but their repartimiento debts were so great that many people had to go into the forest in search of wild beehives to work. The trips in search of wax sometimes took days or weeks; as a result, the Catholic priests frequently denounced the repartimiento as an exploitative abuse that disrupted Maya family life.

The nature of beeswax varied throughout the lowland Maya area, presumably because of variation in flora. The best quality was what was called yellow wax, which tended to be produced in the western half of the Yucatán Peninsula. The lower quality black beeswax was produced in the eastern half of the peninsula. Exports derived from apiculture declined in the late eighteenth century, once again because of the reform program that eliminated the coercive and abusive repartimiento system.

NON-INDIGENOUS PLANTS

Orange, banana, and tamarind trees

Cotton textiles, indigo, and beeswax thus are indigenous products that the Spanish colonial regime found useful. At the same time, Spaniards also introduced new plants to produce the things of their homeland. Not all of these were of commercial significance and thus rarely made it into colonial records. For example, Spaniards planted orange, banana, and tamarind trees—none, of course, indigenous to the Iberian Peninsula—but the fruit was of too little commercial value to export. The first two were commercialized locally, however, and bananas became a high-status food for the Maya. In 1761, when

indigenous leaders believed that the return of the long-awaited Maya king—Jacinto Canek—was at hand, they sent bananas as presents to the man thought to be king.

Rice

A non-indigenous plant that acquired considerable commercial importance in colonial Yucatán was rice, a plant that Spaniards introduced into the lowland Maya area sometime in the early eighteenth century or earlier (Patch 1993:141, 145, 153, 175, 183, 206). Again, little is known about rice cultivation, other than that it was produced mostly in modern-day Campeche. The principal producing areas were in the parishes of Pich, Campeche City, and Calkiní; in Yucatán, producing areas included Maxcanú and Tekax. Small quantities were produced in Sahcabchén and Campeche Extramuros. The Maya never cultivated it at all (BCCA 1778-1779, 1783-1788, 1791-1793; AAM Libros 19 [1791-94], 20 [1795-98]).

Spaniards cultivated rice for several reasons. First, it was a common feature of the Spanish diet and thus was desirable as a European-like food. Second, in the eighteenth century there were growing food shortages in Yucatán, and rice began to be sold in the markets of Mérida at least as early as the 1720s. Finally, because of the burgeoning development of Cuba in the late eighteenth century, surplus production of rice could be exported.

The location of rice production was certainly due in part to geographical conditions, for the plant cannot be cultivated everywhere. Campeche thus became one of only three areas in all of colonial Latin America that have been identified as a rice-producing region (the other two being Guerrero in Mexico and the Sonsonate region of western El Salvador). In Yucatán, the plant probably could have been grown east of Campeche. It was not—except for small quantities grown near Tekax—probably because of competition with sugarcane. In effect, rice production was limited to an area lacking a large indigenous population that could be employed more profitably, as it was employed more profitably elsewhere, for the production of sugarcane.

Rice cultivation in the lowland Maya area was restricted not only in terms of geography but also in terms of the structure of production. The Maya never engaged in rice growing. Moreover, small non-Indian (mostly mestizo and mulatto) farmers also seem to have avoided rice. More than any product other than indigo, therefore, rice production was the exclusive realm of large landowners.

Sugarcane

The last plant of foreign origin that I shall discuss is also the one that had the most significant impact on the Maya: sugarcane (Cline 1948; Patch

1993:34, 142–48, 153, 166, 173, 175–78, 183, 190). This plant arrived early in Yucatán. The famous conquistador Adelantado Francisco de Montejo set up a sugar plantation around Champotón (coastal Campeche) as early as the 1530s. For laborers, he used the people of his *encomienda*, which by no coincidence was the village of Champotón. Shortly thereafter, however, Montejo was stripped of his *encomiendas* and lost access to labor; as a result, he abandoned sugar production. The labor shortage that plagued Yucatán from the second half of the sixteenth century to the late eighteenth century—the result of Maya population decline—then stymied sugarcane production until new demographic conditions emerged in the late colonial period.

Once Maya society had begun to expand rapidly (after 1730), and once it had recovered demographically (a condition achieved by the 1770s), sugarcane again became possible. Indeed, the late colonial period and three decades after Independence (the 1820s, 1830s, and 1840s), witnessed the continued expansion of cane production. This was not the commercialization of sugar. Rather, it was the commercialization of a sugar by-product, for practically all of the harvest was used in distilleries to make cane alcohol. The product, called *aguardiente* (“burning water”), hardly qualifies as rum or brandy. Rather, it was high-grade alcohol that served only one purpose: a cheap and effective way to get drunk.

And get drunk they did. By the late eighteenth century—that is, even before the great boom that followed Independence—consumption per capita of *aguardiente* has been estimated by one scholar at 118.1 liters (over 31 gallons) per adult Indian male per annum, or 108.6 liters (28.7 gallons) per adult male (Farriss 1984:197). If anything, per capita consumption must have kept up with (or even surpassed) the rapidly growing population of the early nineteenth century. At no time did Yucatán export sugar or *aguardiente*.

The emergence of significant sugarcane production seems to have occurred in three phases once the activity was resumed in the late eighteenth century. First, it was cultivated in small quantities by landowners in all but the western sections of Campeche, near the villages of Tekax and Peto in southern Yucatán, and just to the south of Valladolid. The second phase saw the expansion of sugarcane to the east of Tekax and Peto, into central Yucatán (Biblioteca Crescencio Carrillo y Ancona [Mérida], Manuscripts, 1778–79, 1783–88, 1791–93; Archivo del Ayuntamiento de Mérida, Diezmos, Libros 19 [1791–94], 20 [1795–98]). Finally, after Independence, the third phase of production spread further eastward from central Yucatán until it connected with the area south of Valladolid. At the same time, production also expanded southward in both Yucatán and Campeche. By the 1840s, sugarcane production had become the major crop of landed estates south of a line stretching from Valladolid to Sotuta to Tekax to Campeche City. It was this last spurt of development, into areas long free of Spanish incursion in the form

of land colonization, that helped contribute to the outbreak of the Caste War in 1847.

Sugarcane had a unique structure of production. First, it should be noted that the Maya never produced sugarcane. Nor did they grow rice or indigo. Maya agricultural conservatism, buttressed by religion and anti-colonial attitudes, thus preserved much of the lowland area for the traditional maize-beans-squash production complex.

Because sugarcane was therefore an exclusively non-Indian crop, it is no surprise to find that large landowners (i.e., Spaniards) were those most likely to engage in cane production. This was true even though sugar was not the final product, for distillation required machinery—which, in turn, required capital and which, in turn, restricted production to those with access to capital. But at the same time small producers (i.e., non-Indian farmers who probably did most of the planting and harvesting with their own hands) also took part. Their product, however, was usually low-quality sugar: syrup, *panela*, etc. As noted, this made up only a small part of total cane usage, thereby demonstrating that large landowners did indeed dominate sugarcane production.

Large-scale production of sugarcane, of course, requires labor, and development of the cane industry was intimately related to the development of labor systems in Yucatán. In fact, there was no labor market as such, for there were no proletariats ready to sell their labor in return for money to defray the costs of subsistence. Even efforts to import workers by bringing in African slaves failed, for slave traders found better markets for their goods elsewhere. Thus, an attempt by Campechano planters to purchase over 800 Africans came to naught. Landowners, therefore, had to use whatever labor was available in Yucatán itself.

As is to be expected, given the small number of non-Indians in Yucatán, those who wanted to expand sugarcane production turned to the Maya as their laborers. During the colonial era, the government helped planters by sanctioning labor drafts of Maya villagers. In other words, each village that found itself in the vicinity of a landed estate whose owner wanted to grow sugarcane was required to provide a certain number of workers every week during the planting and harvesting season. The draftees were supposed to be paid for their labor, but wages were either very low, or not paid to the workers themselves—instead going directly to the village leaders in return for their cooperation. Recipients of forced labor also were required to pay a small fee to the local royal official, thus providing him with income so that he would not need to resort to the illegal and exploitative *repartimiento* system to earn a living. This was the way in which the Spanish crown sought (and, to a certain extent, achieved) greater honesty in government. Forced labor was also justified as a necessary expedient to stimulate economic development, an

argument that justified continued forced labor drafts and peonage in Yucatán and Campeche throughout the entire nineteenth century and up to 1914.

CONCLUSION

It is not often known by archaeologists who study the distant Maya past (or social scientists and botanists who study the Maya present) that the lowland Maya area had a complex history of plant use and exploitation. Practically all the attention has been given to maize, and for good reason: maize was the food source that served as the basis of ancient and modern Maya civilization.

Nevertheless, the varied environment once made it possible and practical to raise cotton, indigo, rice, and sugarcane, while the flora allowed the development of apiculture. That none of these replaced maize in importance has as much to do with human history as it does with short-term environmental constraints. In the long term, however, it is unlikely that sugarcane could have continued its unchecked growth, for cane processing—like that of henequen—necessitated machinery requiring inputs of fuel in the form of firewood. The removal of the forest without the recycling of nutrients would eventually have led to soil exhaustion and economic decline. In a sense, then, the Caste War of Yucatán—by destroying sugarcane production—helped preserve much of the lowland area for more sustainable plant use in the present, as well as in the future.

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Chapter 32

From Milpero and Lunero to Henequenero: A Transition to Capitalism in Yucatán, Mexico

Piedad Peniche Rivero

INTRODUCTION

At the end of the nineteenth century, the cattle- and corn-producing haciendas in the northwest quadrant of the region centered on Mérida (capital of the state of Yucatán, Mexico) were transformed into large-scale henequen (*Agave fourcroydes* Lem.) plantations. This transformation was driven by commercial, technological, and financial forces operating outside the Yucatán Peninsula. The development of henequen production hinged on two technological processes: (1) the extraction of large quantities of fiber from henequen leaves, and (2) a mechanism whereby the twine made from these fibers could be used in a grain binder. In fact, the development of the rasper in 1856 (which could mechanically remove fibers from agave leaves) and the invention of the knotting device for Cyrus McCormick's grain binder in 1878 both contributed directly to the development of a U.S. market for Yucatecan henequen (Joseph [1982] 1988; Wells 1985; Joseph and Wells [1983] 1986). The input of North American capital, which helped finance the expensive process of converting haciendas from cattle and corn production to henequen production, was the third major ingredient in the development of capital-intensive, monopolistic agriculture in Yucatán (Wells and Joseph 1996).

Although these factors allowed growers to process an enormous amount of henequen, the cultivation of agave leaves proceeded at the same slow rate because there were no technological improvements in the principal energy source—man. Even if laborers used their instruments, it is astonishing that an 1880 inventory of hacienda Teya showed that their tools were valued at only 104.66 pesos, while the chapel itself was worth 477.06 pesos. In fact, the tool

collection of hacienda Ticimul (Teya's annex) consisted of two hammers, one pickaxe, two entire shoe liners, one half shoe liner, a mallet, and four zinc pails (AGEY Justicia, Uncatalogued 1880). Furthermore, because Maya peasants used migration as a way to resist exploitation, as they had done since Colonial times (see below), the need to control them became ever more necessary.

This paper explores henequen production in order to understand the impact of capitalistic and monetary expansion on a rural society consisting of haciendas, ranches, towns, and villages. This rural society of about 300,000 people was comprised of Maya peasants and laborers, petty merchants, and government officials. The elite of the hacienda owners did not live in the countryside, but resided in the city of Mérida, where they dominated politics and developed communications, banking, commerce, and some industry. The so-called "Gilded Age" they created was upset in 1915 by the Mexican Revolution (Wells 1985; Joseph [1982] 1988).

HENEQUEN PRODUCTION: SOCIAL AND NATURAL CONDITIONS

According to a former *hacendado* (planter; see García Cantón 1973), since 1857 haciendas had a double account—known by their Mayan names as *chichan cuenta* (small account) and *nohoch cuenta* (large account)—that kept the laborers (called "peons" or "servants") at the haciendas. The *chichan cuenta* came from the *tienda de raya* (hacienda general store) as small loans in goods (never more than 50 pesos), which henequeneros (peons) paid out of their weekly *jornales* (daily wages). The *nohoch cuenta*, however, was credit extended to grooms for the fulfillment of their traditional marriage obligations; these loans covered fees imposed by the Catholic Church to reproduce the symbolic kinship rites of weddings, baptisms, and funerals (García Cantón 1973), as well as other demands made by the patriarchy (Gill 1991). Thus, religion, kinship, and patriarchal ideologies were shared by Maya servants and masters alike.

In fact, haciendas put a premium on marriage. The *hacendados* actively participated in granting *nohoch cuenta* loans to bachelors, as well as to their eventual brides (Flores 1961). *Nohoch cuenta* loans granted *luneros* (senior henequeneros) the right to occupy milpa lands, a house to live in, medical care, a secure old age as a "*reservado*" (i.e., member of a reserve workforce) and full employment. In effect, *nohoch cuenta* loans served to finance rites of passage to legitimize kinship relations for hacienda peons—giving access to land and social security, as well as to the supernatural world, which included *compadrazgo* (or ritual kinship) between *henequeneros* and their masters.

Hacendado Augusto L. Peón was reputed to have hundreds of compadres (co-parents) and ahijados (godchildren) in his haciendas (Baerlein 1913).

The ecology of henequen cultivation

A henequen plant requires seven years to reach maturity and produce its first harvest; the cutting of the pencas (leaves) occurs three times a year. The harvest is the most labor-intensive element of the henequen ecosystem because it involves several operations and requires a large amount of energy. A young, strong, and disciplined workforce is essential. The cultivation tools were the same rudimentary ones that had been used for centuries—the knife and the coa (a curved iron blade, set on a wooden shaft about two feet long, that was used for weeding), which prolonged men’s hands. Engineer Rafael Portas portrayed the henequenero at harvest in the following words:

The overseer must put the cutters into battle line, assigning each one the cutting of one plant line, of which he won’t leave until arriving at the opposite end, in such a way he will watch the cutting better and will note each laborer’s labor difference, all of which will be of great help in regulating the labor team and a sluggish laborer’s pay, in the case he does not have a substitute. (Portas 1872)

Besides harvesting, the weeds that invade the planteles (field) throughout the year (and most intensively during the rainy season) must be cleared continuously from the time the agave leaves are in the nursery until they die twenty-five years later (Figure 32.1). At the machine house, the arriving bundles of leaves are raised by elevator to the second floor, where several men catch, untie, and spread out the leaves on a conveyor belt that carries the henequen into the rasper. The leaves are rasped, and their raw fibers extracted. The fibers are then dried in the sun; in one or two days they are ready to be pressed and sent to market. The waste (i.e., the leaf pulp, the juices, and the short fibers, which are approximately 95 percent of the leaf) flows into a collection wagon, which is first loaded onto a tram and then transported by mules to the refuse heap (Peniche 1994).

The organization of labor

Documents in the Archivo General del Estado de Yucatán (AGEY, or General Archives of the State of Yucatán) show that work in the henequen hacienda was organized according to sex, age, and civil status. For instance, hacienda Cozumal distinguished between luneros (a Colonial category of senior laborers), solteros (bachelors), and muchachos (boys). Also, there is



FIGURE 32.1. A henequen field (Source: Photo by H. Suaste.)

some evidence for the existence of a category of *reservados*—old men who were charged with cleaning the *hacienda casco* (precinct) and orchard. The *henequenero* was bound to tasks needing large amounts of energy such as harvesting, rasping, and weeding. Besides being residents of the *hacienda*, they still were due the *fajina*—that is, work performed without payment, which consisted of cleaning the *hacienda casco*. *Solteros* generally weeded, but they also harvested. *Muchachos* tended the fiber, cultivated the nurseries, and transported the leaf waste, but they never did any cutting (AGEY Justicia, Box 716 1909).

Women who were normally kept at home, far from the *planteles*, sometimes also worked beside their husbands as the latter cut the agave leaves (Gobierno del Estado 1914). This work was unpaid, as was the domestic work performed at the principal house, which usually involved tortilla making. Whenever women were required as laborers, they had to work. Payrolls confirm this social “specialization” that combined energy and civil status, but not technical skill, because the harvest operation paid less to young and inexperienced *solteros* than to more proficient and knowledgeable *luneros* (AGEY Justicia, Box 716 1909). Most of all, however, it demonstrates that producers were valued not so much for their individual production as for their reproduction. A pertinent example is the case of Emeterio Tun, who was dismissed from the *fajina* of *hacienda Tzuczalam* because she gave birth to twin sons (AGEY Justicia, Box 110 1875; Peniche 1999).

**DEMOGRAPHY AND SOCIAL ORGANIZATION
OF THE HENEQUEN HACIENDA**

The hacienda had to diversify its work force with non-resident, village henequeneros; indentured laborers from China and Korea; and Yaquis from Sonora, Mexico, who eventually intermarried with Maya servants. Nevertheless, labor scarcity was always a chronic problem in the henequen hacienda. Neither “loans,” nor the offer of exemption from military service (required by the State to protect southeastern border settlements from Indian attacks during the Caste War), enabled haciendas to maintain a permanent and sufficient resident workforce.

An interesting example can be found by examining the population at hacienda Dzibikak between 1879 and 1886. During that period, the 1886 population comprised as much as 53.4 percent of immigrants, with 39.2 percent residents and the remaining 7.4 percent newborn; among the 1879 residents, however, 54.5 percent had migrated, while only 29.8 percent were still there, and 6.9 percent were dead. The imbalance between the sexes in the 1879 population (less obvious in the 1886 population) confirms our suggestion that an important sector of migrants were marriageable men leaving the hacienda in order to avoid *nohoch cuenta* loans (AGEY Poder Ejecutivo, Box 103 1879; Box 66 [1886]; Peniche 1998).

The case of Genaro Uc, a lunero of hacienda Dzibikak, represents a successful investment because both he and his offspring remained attached to the hacienda. He was born in the village of Umán and moved on an unknown date to Dzibikak. In 1860, Genaro married Mauricia Uicab, who was born in the town of Hunucmá and resided at the nearby hacienda Texan [Archivo del Arzobispado del Estado de Yucatán (AAY), Libro 14 1859–1871]. In 1879, when Dzibikak had a population of 231 people (103 women and 128 men), Genaro and Mauricia had a twelve-year-old son, José Genaro. After Mauricia’s death, Genaro married a widow of Dzibikak named Florentina Poot. In 1886, the couple had two children. Meanwhile, in 1882, fifteen-year-old José Genaro married a woman who resided in hacienda Sacnité; unusually, he agreed to move to his wife’s hacienda, which was located in the same municipality of Umán and owned by the same *hacendado* as Dzibikak. In 1886, the couple had a daughter, Justa—Genaro Uc’s granddaughter—who was as young as his own children (AGEY Poder Ejecutivo Box 103 1879; Box 66 [1886]).

The combination of mobility and the high mortality rate in Yucatán enforced marriages between men and women of ascending generations, as well as marriages between a widow and a widower. For example, a man marrying the sister of his son’s wife, and becoming father-in-law and brother-in-law to his son’s wife, also became his son’s brother-in-law by marriage. In the hacienda, affinity relations were thus in constant movement and created a

new type of family, the “reconstituted family,” which is characterized by the changing status and double role that their members might assume (Kirk 1982; Peniche 1998).

FROM LUNERO TO HENEQUENERO

AGEY documents show that the decade of the 1870s was the period of transition to the capitalistic and monetary economy, which was also related to the expansion of the henequen international market (see Table 32.1). By “period of transition,” is a particular phase in the evolution of a society when internal and external difficulties prevent it from reproducing the social and economic relationships on which the society relies. At the same time, new social and economic relationships appear—some more or less quickly, others more or less violently—and go on to become the working conditions of a new society (Godelier 1987).

In the period from 1870 to 1880, landlords took measures to systematically reduce the land still held by the independent villages that cultivated maize with milpa techniques. In Umán parish during the 1780s, by comparison, only 44 percent of the peasants lived in the parish villages, while the rest were tenants of the 38 haciendas (Patch 1985). Almost 100 years later, an official 1872 document recognized that villages such as Umán in the northwestern Yucatán Peninsula didn’t have even fallow lands to complete

TABLE 32.1. Increase in henequen Exportation, 1860–1909

Years	Bales
1860–1864	8,545
1865–1869	40,840
1870–1874	112,034
1875–1879	124,715*
1880–1884	882,168
1885–1889	1,205,695
1890–1894	1,702,112
1895–1899	2,065,501
1900–1904	2,741,837
1905–1909	3,028,627

* 1878 and 1879 exportations are unknown (Askinasy 1936).

their “ejidos” (common lands), only some “land scraps,” because it was all private property. In the village of Samahil, peasants didn’t have even a quarter of the lands they were entitled to by law. Bolon was also in serious land default (AGEY Poder Ejecutivo, Box 180 1872). Restriction by private property was definitely a blow to milperos who needed five fallow plots for every one cultivated (Hernández 1985). Therefore, the peasant’s mobility, which had been a headache for the Spanish fiscal bureaucracy, needed to be controlled (Farriss 1978, 1983, 1984; Robinson 1981a, 1981b, 1987). Consequently, landowners turned to “debt” as a mechanism of social control. Over time, the lunero came to represent the passage from the milpero—a free, mobile, maize-producing peasant—to the henequenero bound to the haciendas by debt (Figures 32.2 and 32.3).

Lunero transition

Mercantile agriculture (but not capitalistic agriculture, which implies large-scale production) began by the 1780s with the increase in the internal demand for food (Patch 1985). The landowners, who before had simply ranched to maintain their families and their social status while receiving agricultural produce from their encomienda grants (i.e., rights over the labor



FIGURE 32.2. A “modern” milpero. (Source: Photo by H. Suaste.)



FIGURE 32.3. A "modern" henequenero. (Source: Photo by H. Suaste.)

and goods of Indian communities, granted by the Crown to Spanish conquerors), now invested in maize agriculture; as a result, haciendas attracted laborers and developed into population centers with mixed economies of ranching and agriculture. Two types of laborers existed: salaried laborers and tenants. Salaried laborers included senior and junior cowboys, overseers, and artisans. There were two kind of tenants repaying the landlord for the use of water and land: sharecroppers, who paid their rent in money (or kind), and luneros, who paid their rent in service—working one day a week, usually on Mondays (Cline 1950; Manual del Mayordomo 1860).

According to Cline, luneros had probably existed on cattle haciendas, then called estancias, since shortly after the Spanish Conquest (Cline 1950). García Bernal, relying on a 1739 Spanish document, states that the luneros were Maya migrants who moved to escape fiscal obligations in their communities. The haciendas welcomed their arrival—offering water and land for maize cultivation in return for service (García Bernal 1997).

In the eighteenth century, luneros came under official scrutiny when the Crown suppressed *encomienda* grants in 1786. After a search of legal precedents, Crown representatives came to the conclusion that luneros did not fit into any of the categories of Maya tributaries. In fact, they possessed qualities that defined several classes: resident salaried peons; tenants who rented private lands; and *vagos*, who had no known or fixed residence in recognized communities under a native chief (Cline 1950). To collect tribute payment in cash rather than in customary goods, local Bourbon officials asked

hacendados to advance the Treasury such sums as were due from Indian tributaries residing in their haciendas. The *hacendados* objected on the grounds that luneros were voluntary laborers who shifted from place to place, who earned no cash income, and to whom the landowner paid no money. Furthermore, as the *hacendados* merely extended the luneros a place in which to live, raise milpas, and pasture their animals, the only obligation these laborers recognized was the duty of working one day a week to repay the landlord for the use of water and land. In fact, most luneros exchanged their Monday dues for cultivating about an acre of maize (worth 8 reales, or 1 peso, during the 1870s) for their landlords. This maize was needed to pay salaried hacienda workers, and thus was not sold at market. Luneros also performed an unspecified amount of extra work known as *fatiga* (or, later on, *fagina*), as well as other tasks, including driving cattle, cutting firewood, and collecting wax, for which the *hacendado* paid no money but provided luneros a ration of maize in exchange (Cline 1950).

In 1787, settlement of litigation in favor of the local Bourbon bureaucracy forced landlords to pay 14 reales per lunero fiscal obligation. According to Cline, this payment crystallized in a labor-due increase for the luneros, because each lunero came to represent an annual investment of at least 14 reales. More importantly, settlement of this lawsuit resulted in a series of laws being passed to restrict lunero migration, including the 1839 law that forbid luneros from leaving the hacienda without clearing their debts (Cline 1950). Another law issued in the years following Independence was the Ley agrícola of 1843, which prohibited laborers from leaving haciendas while the agricultural year was in progress (Aznar 1850). This issue reflected the conflict of interests between the Crown and the proprietors over the conservation of peasants communities: the former favored its reproduction (and tribute) while the latter wanted their lands and people.

The lunero revolt

Throughout the 1870s, luneros began protesting because their rights as individuals (and the consent agreements they had been entitled to with their masters) were slowly being taken away. Before then, any unmade consent agreements were not binding and would simply go away if all debts were cleared; according to the law, luneros could be set free from their masters by obtaining and getting these *cartas-cuentas* (“*papers*”).

In 1873, for example, four luneros who were residents of hacienda Santa Cruz went to court and demanded the return of their *cartas-cuentas* on the grounds that they had not contracted to stay with the new owner of the hacienda under lunero conditions. They also stated that they gladly served their former master because of the good treatment he gave them (AGEY Justicia, Box 98 1873). For their part, luneros of hacienda Hotzuc proclaimed

their freedom when they proudly appeared in court to pay their debts after their master's death. They stated that they wanted to make themselves understood as "not having consented in recognizing the new owner" of the hacienda (AGEY Justicia, Box 105 1875). Similarly, six residents of the hacienda San Antonio Chum demanded their papers from the hacienda's executor by virtue of their master's death because they were "not under any kind of serfdom to pass under the rule or service of another [master] without the proceedings of a contract of our free and frank freedom" (AGEY Justicia, Box 87-A 1870).

In fact, since 1869 luneros complied with changes in the amount of service "against the hacienda customs" (AGEY Justicia, Box 87-A 1869). Juan Puc was very explicit in the Mérida Court of Justice when he demanded that his master hand over his papers. He complained about being forced to work four days a week cultivating a 20-mecates milpa, cutting 1,000 henequen leaves, and other services "that are not paid in their just value" (AGEY Justicia, Box 87-A 1869). Luneros of hacienda Eknacán went to court and demanded their papers for not accepting "more services than they were used to since immemorial times" (AGEY Justicia, Box 89 1871). Luneros of hacienda Teya complained about the same thing, but from another perspective. They said that their actual master was taking all their time, thereby preventing them from working in their "personal occupations," which they used to do freely with their former master (AGEY Justicia, Box 100 1874).

During the 1870s, a conflictive and violent henequen zone began: oppressive and rebellious violence went hand in hand. Luneros were beaten for contesting the escalating demand for their services, as well as its consequence—indebtedness. In fact, luneros of hacienda Eknacán testified in court to being lashed by the *mayordomo* (overseer) of their hacienda in order to force them to work more than ever before. Four residents of hacienda Tzuczalam testified that because their master was not discounting work from their accounts, they were "being indebted for life" (AGEY Justicia, Box 110 1875).

The 1870s also witnessed luneros inciting more violence than ever in the haciendas. Besides running away from their masters (AGEY Justicia, Box 90 1871), some luneros conspired to revolt against the *mayordomo* of hacienda Hoboyná (AGEY Justicia, Box 109 1875); others to beat and stone the *mayordomo* of hacienda Cholul (AGEY Justicia, Box 116-B 1877); and still others to kill an especially cruel master—Manuel Rodríguez Solís—of hacienda Kancabchen (AGEY Justicia, Box 98 1873).

In 1876, the complaint filed by four different luneros against their master, José Delgado Luján, lists the assorted tasks they were being forced to perform: two days *fajina* from sunrise to sunset, transfers to other haciendas lasting two or three months, sowing henequen and tobacco, and tak

merchandise to Mérida (AGEY Justicia, Box 111 1876). Delgado Luján justified his abuses on the grounds that luneros worked only three days a week (and sometimes only two days); the fact that they received medical attention, milpa land as needed, and money and goods to be paid with labor, shows how the lunero classification was gradually disappearing. Dues, which consisted of cultivating maize for their master in exchange for land and water, were eliminated; *fajina* and tasks paid by pieces were conserved; while haciendas were slowly being transformed into large-scale henequen plantations that continued enforcing *nohoch cuenta* loans.

It is not known how many luneros actually worked out their debts and obtained the papers setting them free. In fact, in spite of their actions and claims, those luneros who remained tied to the hacienda found themselves with spiraling debts. For example, in hacienda Yaxnic, the resident servants' average debt soared by 300 percent between 1876 and 1890 (Wells 1985).

During the 1880s, a rapidly increasing market for henequen proved the final blow to the lunero's old way of life: both he and his family were now completely under the hacienda's control. Although migration was still a possibility, the opportunities for moving grew ever more rare; haciendas increased their control through a 1880 law that gave mayordomos new legal powers to watch over and punish servants (Ancona 1880).

CONCLUSION

The transition from milpero to lunero and henequenero represented the development of both a mercantile local agriculture as well as large-scale henequen production and commercial exchanges. The management of the henequen ecosystem required the control of laborers—the Maya peasants who historically had resisted exploitation through migration. The transition not only involved violence, as laborers revolved against their increasing personal exploitation, but also the consent of those who shared their masters' religion, kinship, and patriarchal ideologies. Although this process did not create the proletariat, it did create a class of peons (or servants) who became increasingly bound to henequen haciendas by debt.

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PART VI:
THE FUTURE

Chapter 33

Restoration of Tropical Seasonal Forest in Quintana Roo

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INTRODUCTION

Seasonal tropical forest has been identified as one of the most endangered of native ecosystems (Gentry 1992). As little as 10 percent of the original forest remains in Central America, and less than 1 percent is in nature reserves (Janzen 1988). Seasonal tropical forest in Quintana Roo, Mexico, has undergone widespread historic land use and disturbance that is increasing in extent and intensity (Carranza et al. 1996). The forests have been cut for shifting cultivation and grazing. The resultant acahual has an increasing fire cycle that with time will cause a decline in biodiversity and conservation value of natural systems. The acahual is subject to invasion by *Pteridium caudatum*, and once this species dominates, the land has little utility either for conservation or the basic human needs of food, forage, fuel, and fiber. The acahual has become a fire hazard rather than a resource in some areas. Because so much has already been lost, restoration of existing areas is critical to maintain biodiversity, ecosystem functioning, and ecosystem services such as providing useful plant biomass. Restoration of diverse tropical vegetation is a difficult goal because of the many species involved, the slow successional process, and the rapid fire cycle. Restoration per se may be difficult to achieve, but we may be able to create "designer ecosystems" (MacMahon

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1998) that will initiate succession toward a diverse and sustainable forest. In addition, restoration projects must consider the influx of people into these forests and their needs.

The objectives of this synthesis are to examine restoration goals for this forest, describe the disturbance and successional processes as they relate to restoration goals, and conclude with a description of ongoing and recently initiated restoration projects. The work described is at the El Edén Ecological Reserve, located in the state of Quintana Roo within the Yucatán Peninsula. This is a region of *selva mediana*, based on its potential height growth, where mature forest is rare but there is considerable *acahual*. The processes at this site will be compared with another seasonal tropical forest on the Pacific Coast of Mexico—the Chamela Biological Station, where the seasonality of the forest is similar but the soils are loamy and deep rather than rocky. This difference in substrate creates very different processes between the two sites, and the unique characteristics of recovering vegetation of Quintana Roo and much of the lowland Yucatán Peninsula will be shown. A basic understanding of plant regeneration is critical to understanding restoration of these forests.

RESTORATION GOALS

There are many definitions of ecological restoration (e.g., Jackson et al. 1995), but they all have two main points in common. The first is that restoration requires human manipulation of the disturbed ecosystem, and does not rely strictly on natural successional processes. Restorationists may take advantage of processes such as dispersal, establishment, nitrogen fixation, competitive displacement and others, but they also attempt to enhance or manipulate these processes. The second point is that restoration has a goal of returning the system to resemble a previous ecosystem type, but exactly what this goal should be may be elusive (Aronson et al 1993, Pickett and Parker 1994, White and Walker 1997, MacMahon 1998). The goal may be a natural, semi-natural, or anthropogenic vegetation type, but it must be based on a model or reference area. If no reference area exists, setting and achieving goals are problematic. Historic records may be useful if they document the prior existence of species that are now absent. For instance, restoration of species and communities was based on biblical records in Israel (Naveh 1990). An analogous example could perhaps be found from historical Maya records, as they include useful plant species, including some that were purposefully introduced. These records could perhaps also be used to restore anthropogenic or cultural sites. However, the reintroduction of individual or even multiple species does not necessarily restore the ecosystem functioning

that sustains these species. Natural processes need to be reinstated as well, such as nutrient cycling in disturbed soils, or a normal fire regime where that has been disrupted. Once the processes and key species have been established, restoration may proceed by the self-organizing processes of ecosystems to attain a sustainable and desirable goal. It may not always be possible to predict this goal, because varying the initial conditions may vary the outcome (Allen 1988, Picket and Parker 1994).

There are less rigid goals than restoration of the original vegetation or ecosystem type, including reclamation and rehabilitation (NAS 1974). Reclamation means recreating a functioning ecosystem that may include species substitutions where certain original species are not available or will not perform as well in the new conditions, and typically includes a smaller number of species. Rehabilitation is the creation of an alternative ecosystem, such as a cultivated field where there was once forest. These goals may be advocated when “pure” restoration is too difficult to achieve, or does not achieve the intended purpose. A landscape that includes shifting agriculture and forest in different successional stages, as well as human dwellings, may be considered a cultural landscape, and constitutes another type of large-scale restoration goal (Naveh 1998). Restoration of “designer ecosystems” is advocated to serve a specific purpose for humans (MacMahon 1998). A site may be restored for a particular function or to conserve certain species. This may, for instance, include restoring the forest architecture without restoring all of the species. As explained in the following section, the architecture of the acahual in Quintana Roo promotes a rapid fire cycle, and at the same time diminishes the diversity of species. A return to mature forest structure using a designer approach may both break the fire cycle and promote biodiversity.

DISTURBANCE AND SUCCESSION IN SEASONAL TROPICAL FOREST

The vegetation of the Yucatán Peninsula is the result of a long history of disturbances by humans, fire, tree harvesting, and hurricanes. The Peninsula hosted the development of the Maya civilization during the last 2,000 years. Almost every area has been used in the recent or remote past and the vegetation composition prior to human use is unknown. The few sites where mature vegetation exists show signs of human intervention (Rico Gray and García Franco 1992; Gómez-Pompa 1998), and the Peninsula, as well as the broader Maya region, is almost entirely acahual, or secondary vegetation (Rico Gray 1991). The flora has developed under selection from repeated fires and felling, and the natural regeneration process by vegetative sprouting is a reflection of this selection. The forest also contains a high proportion of tree

species that are used for food, fiber, or medicinal purposes. These species were probably planted historically, and the present day vegetation is likely the result of colonizing plants from these historic plantings (Gómez-Pompa and Burley 1991).

Frequent fire has become a recent threat in the Yucatán Peninsula with the growing human population and increasing shifting cultivation that allows escaped fires. The latest fire in the El Edén region occurred in May 1999 and followed the path of a larger 1995 fire that burned thousands of hectares. The 1995 fire in part overlapped a still-larger 1989 fire (Carranza et al. 1996). Of these, only the 1989 fire followed a hurricane (Gilbert in 1988), and the more recent ones are the result of human activity. Historically large fires probably were driven by the cycle of hurricanes that downed timber and left large amounts of standing dead material during the subsequent dry seasons (Whigham et al. 1991, Whigham, this volume). The acahual that follows fire is highly flammable during every dry season, not just after hurricanes that leave downed wood. Increased flammability is likely related to the dense acahual vegetation that is formed by resprouting trees, as well as the shorter stature that may promote hotter, drier conditions than mature forest. The dense stands appear to form a stage of "arrested succession" (sensu Niering 1987) that persists for long time periods after fire. In selva mediana in the El Edén region, the resprouting trees have such a high stem density during the first 5 to 20 years following fire that they are impenetrable (Figure 33.1). For instance, 28 woody stems/m² in a five-year-old stand following fire were measured. The forest is called "selva mediana subperennifolia" in this region because the trees retain a high proportion of their leaves during the six month dry season in response to a high water table (4 m in culinary wells at the El Edén Ecological Reserve). However, the remaining leaves experience mid-day wilt and are probably quite low in moisture content. Their mid-day water potentials are regularly -3 to -5 Mpa (E. Allen unpubl. obs.). Areas that burn frequently also are subject to invasion by *Pteridium caudatum*, which is native to the area but is increasing in extent following fire. Bracken fern senesces above ground during the dry season, and has fronds almost 2 m tall that remain upright as dry tinder. This forms a dense, tall, fine fuel that promotes frequent fire. Once shifting cultivation is introduced into an area and the fire cycle is initiated, it may form a positive feedback of ever-increasing fire frequency as has been shown even in the moister climate of the Amazon forests (Cochrane et al. 1999). The spread of fire through previously burned areas invaded by flammable species is also a pattern in other seasonal forests, such as exotic grasses in Hawaii (Freifelder, Vitousek, and D'Antonio 1998).

Mature forest, by contrast, appears to be more resistant to fire. Mature forest in selva mediana is about 15 m tall in this area, and has a surprisingly open understory (Figure 33.1). The basal area of mature forest is not greater



FIGURE 33.1. (A) Mature forest, or *selva mediana*, at El Edén. The forest is approximately 15 m tall and has an open understory that may make it more resistant to fire than *acahual*. (B) Dense secondary forest approximately 20 years following a fire at El Edén. (C) Transplanted seedlings in tree protectors (September 1997) following an experimental burn in June 1997. The secondary growth was controlled using machedes. (D) Height differences between planted and control (resprouting) vegetation after three years (November 2000). Planted trees (left side) were 5 m tall after three years, while three-year-old densely resprouting vegetation (right side) was 3 m tall following a fire. Trees were planted at 2 m distances and resprouts were cleared, allowing rapid growth and maintaining an open understory that more closely resembles a mature forest.

than successional seasonal forest (Brown and Lugo 1990), indicating that the change is architectural with a decrease in stem density but an increase in diameter. The canopy is single-storied in much of the forest at El Edén, without a well developed shrub or small tree layer except patchy areas of palms (e.g., *Thrinax*). The major plants that impede movement across the forest floor are bromeliads. The observer has an open line-of-sight in the understory. The open architecture of this vegetation likely also increases its resistance to fire, except as explained above after a hurricane when downed branches increase flammability. Thus the few remaining areas of mature forest may escape fires from shifting cultivation, unlike the acahual. Surprisingly, acahual contains small patches measured in decameters that contain some quite large trees (e.g., 30 cm diameter at breast height) even within recently burned areas. The large size of the trees suggest the patches have escaped multiple fires. These areas have not been quantified either by size of patch, size of individual trees, or species composition, so the reasons for their persistence are at best speculative. However, their open architecture coupled with a low fuel load for fire suggests that few, large trees promote a negative feedback that makes this architecture resistant to persistent fire cycles. The open architecture of these patches, and of the remaining areas of mature forest in Quintana Roo, suggest a restoration strategy of thinning acahual to mimic mature forest. This strategy is part of our ongoing research, explained in more detail below.

Although resprouting is quite abundant after fire, natural succession to mature forest is apparently very slow. Even 100 years after disturbance, the Yucatán forests were still more similar in species composition to young forest than to mature forest (Rico-Gray and Garcia-Franco 1992). At El Edén many of the dominant species of acahual and mature forest are the same (Schultz, this book), but a group of mature forest species is missing from acahual. These include *Brosimum alicastrum*, *Talisia olivaeformis*, *Protium copal*, and *Sideroxylon foetidissimum* (Violi, unpublished observations). This indicates that natural successional processes will not return the diversity of many late successional species in frequently burned forest, and that enrichment planting is needed to return these species to the forest.

To understand the forest response to fire in Quintana Roo, it is important to compare it to other seasonal tropical forests. A unique feature of the Yucatán Peninsula that differentiates it from other seasonal forests is the rocky limestone bedrock that allows roots with belowground primordia to survive in fissures following fires. Permanent conversion to grassland occurs in 40 percent of logged tropical forest worldwide (Melillo et al. 1985). For instance, the lands surrounding the Chamela Biological Station have been converted to pasture, but these are deep decomposed granite soils that can sustain the fine roots of grasses (Allen et al. 1998). By contrast, planting pasture grass is not possible in much of the limestone substrate of the

Yucatán. These soils consist of bedrock that comes to the surface, with thin pockets of fertile, organic soils (Estrada 2000) that are suitable for growing sparse maize or vegetables, but not dense pastures. In fact, Rancho El Edén, adjacent to El Edén Ecological Reserve, was once a cattle ranch, but could not provide cattle forage without continual maintenance of the acahual in a very early successional stage. Planting pasture grass for forage, as is done in so many other seasonal tropical forests, is simply not an option over much of the region because there is little soil to maintain the fine roots of grass. Soil is such a limiting commodity that local landscapers and nurseries in Cancún must excavate it from occasional low-lying depositional areas and haul it at cost to housing construction areas.

RESTORATION EXPERIMENTS AT EL EDÉN

There has been considerable research on restoration of seasonal tropical forest restoration following conversion to exotic pasture, such as a recent special issue of *Restoration Ecology* (Aide 2000). These studies describe the slow rate of tree colonization into pastures, the lack of a native seedbank, the importance of nurse “trees” to attract animals that disperse seed, and other processes. The applicability of these studies to restoration of acahual in Quintana Roo is limited, as pastures occur only infrequently because of the rocky limestone soil. More applicable to the conditions at El Edén are the studies on tree thinning and enrichment planting in forests in Veracruz (Ramos and del Amo 1992).

The influence of mycorrhizal fungi on the restoration process in seasonal tropical forest has been studied. From studies at the Chamela Biological Station on the Pacific coast it is known that pastures have a depleted species richness and density of mycorrhizal spores compared to mature forest (Allen et al. 1998), and that early seral tree species have a smaller response to mycorrhizal fungi than late seral trees (Huante, Rincón and Allen 1993). More recently, 1,000 trees of ten species were planted at El Edén inoculated with mycorrhizal fungi from acahual and mature forest. The species composition of the early and late seral fungi is different, as the acahual soils have a low occurrence of spores in the Gigasporaceae (a family of mycorrhizal fungi) compared to mature forest (Allen et al. unpublished observation). Early results of growth in the field indicate that the ten species of trees all have greatest growth with early seral inoculum collected from two to three-year-old burn sites, and that late seral inoculum resulted in smaller plants. This result was consistent whether the trees were early (e.g., *Acacia pennatula*, *Guazuma ulmifolia*, *Leucaena leucocephala*) or late seral (*Brosimum alicastrum*, *Ceiba pentandra*, *Havardia albicans*). Of the latter, *Ceiba* and *Havardia* colonize disturbances but persist through later succession, while *Brosimum* is strictly a

species of mature forest (Ramos and del Amo 1992). However, growth rates of these different tree species is quite varied, with early seral trees growing faster than late seral (Figure 33.2). *Leucaena* was the fastest-growing species, but was matched by *Acacia* by October 2000, which both averaged 5 m. The tallest species at transplanting was *Brosimum* at about 30 cm, but it was also the slowest-growing with mean height less than 1 m by October 2000. *Brosimum* also suffered 90 percent mortality by the third year, mainly due to deer herbivory, and is known to be a shade-dependent tree (Ramos and del Amo 1992). *Guazuma* suffered 50 percent mortality, but had a slightly greater growth rate and was not as severely affected by herbivory. The other species had nearly 100 percent survival.

During the course of these experiments it was necessary to control secondary growth. The seedlings were transplanted from the nursery into an experimental burn, but within months after the burn, the vegetation began to resprout and quickly overtook the growing seedlings. Slow growing species such as *Brosimum* and *Guazuma* would have quickly been lost in the regrowth were it not for continual clearing of resprouts and weeds using a machete.

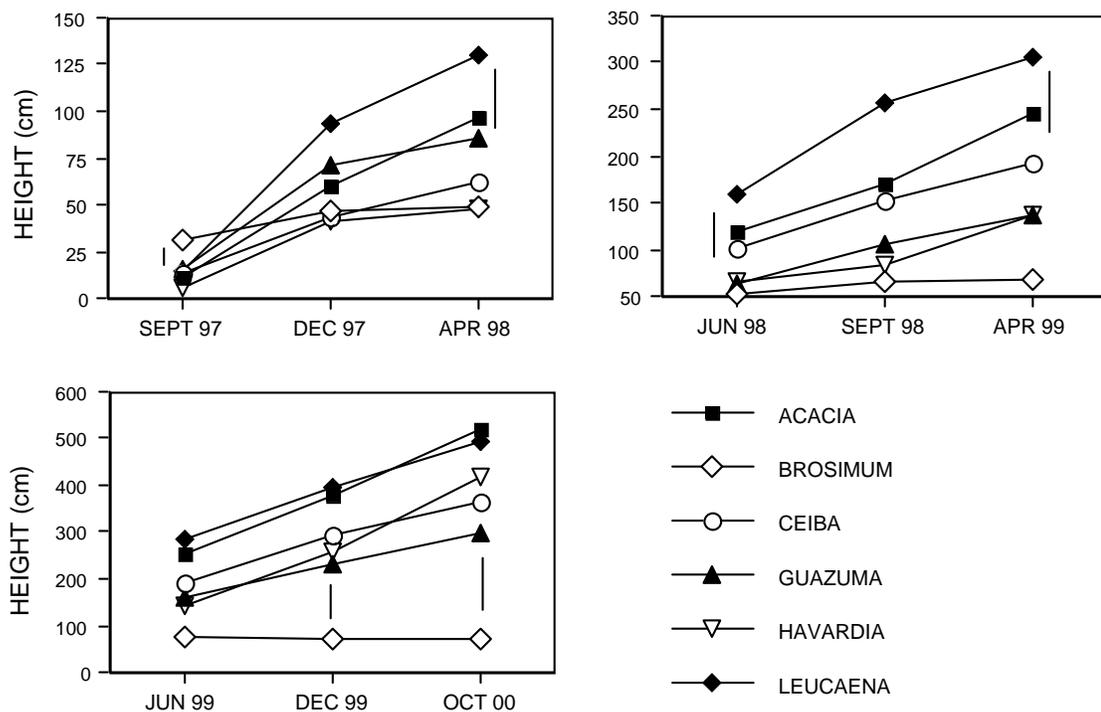


FIGURE 33.2. Growth rates of six tree species at El Edén. The trees were planted in September 1997 as two-month-old nursery transplants. The species are *Acacia pennatula*, *Brosimum alicastrum*, *Ceiba pentandra*, *Guazuma ulmifolia*, *Havardia albicans*, and *Leucaena leucocephala*.

One treatment of the experiment was an unweeded, unplanted control that was allowed to grow naturally. Four months following the burn the control plots had about 4 resprouting trees per m², and 21 plants total per m² (Table 33.1) with a total of 45 species (Table 32.2). Most of the trees and shrubs were resprouting, but the herbs and lianas originated from seed. Lianas were an especially large problem, with an average of two vines per seedling at each time they were removed. Liana and other regrowth removals occurred at 2-4 week intervals during the rainy season, June-December. By the second growing season, four of the tree species were quite large, and did not need continual weeding to enable survival. However, the labor involved in such an effort was considerable, as the plot size was about 2/3 hectare. Thus substitute all of the species in the plot with planted trees will not be a sustainable restoration practice. The labor is simply too intense to justify this kind of work except on an experimental basis.

The other noteworthy result of this experiment was how much taller the fastest-growing transplanted seedlings were (5 m for 3 year old *Acacia*) than the resprouts in the control plots (3 m; Figure 33.1). This occurred because of the extremely high density of competing stems in the control plots, that may be up to 20 to 28 woody stems per m² after 4-5 years. The nursery seedlings were planted 2 m apart, and probably suffered no competition at all during the first two years until the crowns of some of the species began to overlap (Figure 33.1). They were able to grow at the maximum rate that the soil and climate would permit. Thus while these experiments gave us insight into the growth rates of these species and the potential for enrichment planting of the different species, they did not solve the problem of larger scale restoration.

Restoration objectives and expectations have evolved for this site. First, the rapidly resprouting species that occur after fire must be used, rather than trying to remove and replace them. Second, the fire cycle must be broken. Third, species that will be of use to local people must be provided so they will take an interest in the project and participate in the restoration process. Finally, conservation goals need to be incorporated. The first and second

TABLE 33.1. Plant density [plants/m² (standard error)] following fire at El Edén. Data for the four-month burn were collected in October following the June 1997 experimental burn. Data for the four-year burn were collected in October 1999 following the June 1995 wildfire. Four years following the burn, 60 percent of trees were less than 1 cm dbh.

4 months Following Burn	4 Years Following Burn
4.2 (1.2) trees	20.5 (5.9) trees (60% < 1-cm dbh)
16.8 (2.2) herbs	

TABLE 33.2. Plant species composition four months after the June 1997 experimental fire at El Edén. Vegetation was measured in the control plots (Figure 33.1D) in 24 m² total of sampled area, same plots as described in Table 33.1. Trees and shrubs were resprouting, while lianas and herbs germinated from seed.

# Species	Life Form
13	trees
7	shrubs
15	lianas
10	herbs
45	Total

objectives may be accomplished in part by thinning the resprouting acahual. This will more rapidly create a forest that appears structurally like mature forest, and will reduce the fuel load to lessen the fire hazard. The current method of controlling fire is to make fire breaks, but these resprout rapidly and become a fire hazard again in a short time. Thinning is hopefully a better approach that will allow the remaining trees to increase in size. The third and fourth objectives may both require enrichment planting. The species chosen can be those that enhance the economic value of the forest for local inhabitants, similar to the species they currently plant in forest gardens (Bainbridge and Gomez-Pompa 1995). But these plantings can also include trees that are currently restricted to mature forest, and may be rare elsewhere.

The overall goal is to restore a forest that appears physiognomically like the mature forest, or in other words to create a designer forest that achieves the goals of reduced flammability and increased diversity. To achieve the four objectives, a second restoration experiment has begun using thinning to reduce tree density. For our first experiment in acahual thinning, a site was chosen in July 2000 that was last burned about 20 years ago, and removed all the stems that are < 2 cm dbh. A total 500 trees were marked, both in the removal and control plots, and will monitor these over time to determine the rate of height and diameter growth. During the next growing season, enrichment planting will be done with some of the species that are missing at this site, but present in mature forest. The remaining trees will be able to grow more quickly and will overtop the resprouts. Continued machete work will likely need to be done to control the resprouts, as well as treatment with herbicide, but this will not be as labor intensive as attempting to control all of the resprouts.

This area will be used as a demonstration plot to show local inhabitants that forest restoration is a worthwhile endeavor. Currently the acahual is a fire

hazard that people must flee during the dry season. Bainbridge and Gómez-Pompa (1995:408) wrote that we must practice forestry as if people mattered. If people are allowing the forests to reburn continually, this indicates they do not realize its value as a resource, but may also not know how to convert useless acahual into useful mature forest. Thinning acahual to improve growth of remaining trees will not only reduce the fire hazard, it will increase the utilitarian and conservation value of the forests.

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Chapter 34

The School of Ecological Agriculture: A Viable Liaison Between Campesinos and Researchers in the Yucatán Peninsula

J. J. Jiménez-Osornio

INTRODUCTION

The poor management of natural resources is a result of the type of development promoted worldwide. Mismanagement has generated problems such as contamination, biodiversity loss, erosion, and desertification, which, in turn, have increased social inequalities; contributed to poor nutrition; caused poverty; and encouraged migrations from rural to urban areas, as well as from underdeveloped to developing countries.

Although great achievements were made in terms of food production and other necessities during the twentieth century, the number of deaths worldwide caused by poor nutrition as a result of the meager distribution of resources remain high (del Amo and Ramos 1994). In some ways, the increase in production is a result of the extension of agricultural activities along marginal lands and forests. Given the constant increase in global population and the fact that the best agricultural lands are presently in use (or their potential already tapped), alternative agricultural practices are needed that not only meet nutritional needs, but also efficiently manage and protect natural resources. In other words, agriculture needs to balance social demands caused by widespread poverty with economic issues such as how increasing food production can strain limited environmental resources.

When the above issues are taken into consideration, the basic question to be answered is as follows: Are we capable of using present-day technologies to increase food production without contributing further to environmental and social degradation? Many attempts to modernize agricultural production consisted of introducing models or agricultural packages from other regions that were unsuitable to the environment being studied. These models failed to consider how the intensity or rhythm of production, along with local environmental characteristics, can be limiting factors for certain technologies.

It is unknown how long humankind can continue to cause environmental degradation and subsidize existing production systems without tapping out limited natural resources (Cox and Atkins 1979; Gliessman 1998). In essence, this question cannot be answered without recognizing the challenge posed by trying to conserve and maintain biodiversity while, at the same time, transforming the environment to satisfy the needs of both present-day and future generations.

The successful management and sustainable use of natural resources requires economic incentives, intensification of production systems, integrated use of resources, and self-management by the community. Additional social, political, and technical innovations may also be required (Jiménez-Osornio, Romero, and Mendoza 1998). Examples of such innovations include the following:

1. *Leadership roles:* Group leaders should be selected based upon their ability to work with different sectors such as universities; local communities; federal, state, and county governments; nongovernment organizations (NGOs); and research centers. Group collaboration should not only lead to the sharing of responsibilities and projects, but also reflect and influence trends in environmental politics, scientific research, and technological advances, as well as the formation of integrated human resources for sustainable development.
2. *Training methods:* New training methods should be introduced (or existing methods reinforced) that enhance the income of campesinos and ensure their nutritional and environmental security.
3. *Production methods:* Sustainable production methods should be created (or existing methods improved) that are based upon agroecological knowledge, accessible to current decision-making information, and flexible enough in design to adopt new alternatives.
4. *Use of natural resources:* The transition to sustainable development should be facilitated by adopting alternative production systems that have been proven to use local natural resources efficiently through various promotion and extension activities.

Campesinos should not be considered as objects of development, but rather as their own protagonists. A project that seeks to improve the quality of life in rural areas can only be successful if the campesinos remain in control of their own destiny. To maintain such autonomy, comprehensive training and learning opportunities are required to facilitate and hasten the development process. Faced with decreases in government contributions and subsidies, the lack of credit, and the urgent need to produce food, campesinos need “intellectual inputs” in their production process that are realistic and will counteract deficits in material inputs. By following this process, a greater

production level can be reached while economic and ecological costs are decreased (Gaitan and Lacki 1993).

A major constraint for sustainable development in rural communities has been the lack of feedback between the scientists who generate production technologies and the producers who use them. Most of the technologies developed in temperate regions differ greatly in terms of ecological and socioeconomic characteristics from those found in the tropics. These discrepancies not only lead to further losses (economic as well as natural resources), but also contribute to the increasing distrust of researchers and academics by farmers (FAO 1993).

Agriculture is a dynamic activity that considers variations in the production sector (ecologically and economically) along with the dynamics of the social sector. The generation and adoption of technologies should be adapted to these dynamisms in order to improve the conditions of the beneficiaries (i.e., the producers). Unquestionably, Mexico needs to (1) organize training methods that facilitate the sharing of obtained results; (2) propitiate training actions based on proven results in the region; (3) create accessible alternatives for comprehensive training, while ensuring its continuity; and (4) identify committed organizations and institutions that are interested in learning together—that is, producers, students, and professors/researchers of all disciplines.

Sustainable agricultural development in southern Mexico requires new decision-making attitudes towards production, consumption, and living together that are compatible with the needs of environmental protection. Such moves require new education methods and opportunities (both formal and informal), as well as new research methods and decision-making processes that facilitate the generation and adoption of those technologies. It is imperative for universities to institutionalize interdisciplinary teams that are academically solid and that include multisectorial participation (Castillo and Toledo 2000).

BACKGROUND

The initiative to establish the School of Ecological Agriculture (SEA), “*Uyits ka’an*” (Mayan for “Dew of the sky”), arose in 1992 from the “Pastoral of the Land” group—an organization within the Catholic Church of the Archdiocese of Yucatán State. In 1994, members of the “Pastoral of the Land” group, officials from the Department of Management and Conservation of Tropical Natural Resources of the Universidad Autónoma de Yucatán (PROTROPICO), and producers from distinct regions of the peninsula participated in a workshop course entitled “Ecologically Appropriate Agriculture.” One of the workshop activities required the identification and



FIGURE 34.1. Pyramid that depicts the hierarchical relation and interrelationships to activities required for the transformation of rural areas in the Yucatan Peninsula. (Source: modified from Neugebauer 1994.)

Prioritization of the hierarchical relations among the activities and interrelations needed to achieve sustainable community development (Figure 34.1).

To achieve sustainable community development, it is necessary to fulfill the needs of local inhabitants through proper management and conservation of the environment. Sustainable management of natural resources is a long-term process that requires the formation of new professionals. Campesinos act as promoters of alternative technologies and generation of new technologies that encourages increases in production without being dependent on high-cost inputs. The pyramid components (Figure 34.1) thus form the basic elements of the SEA philosophy.

The design, establishment, and development of the SEA is a result of a combined effort among members of the “Pastoral of the Land” group; PROTROPICO; the nongovernment organization, Popular Association for Social Integration (APIS A.C.); and the Regional University Center of the Yucatán Peninsula–Autonomous University of Chapingo, which joined the initiative in 1995. The goal of the SEA is the:

. . . formación de alumnos en el uso integral de los recursos naturales con que cuentan en el medio rural, para satisfacer sus necesidades básicas de alimentación e incrementar sus satisfactores económicos y

sociales, dentro de un programa de formación integral que incluye aspectos tecnológicos, culturales, humanos y espirituales.

[. . . formation of students in a comprehensive use of natural resources found in the rural areas to satisfy their basic nutrition needs and to increase their economic and social living standards, within a comprehensive education program comprised of technological, cultural, and spiritual elements.]

The structure of the SEA programs is theoretical and applied. The subjects are varied and consist of courses such as horticulture, composting, plant propagation, animal production (e.g., chicken, sheep, pigs, goats, and native bees), agroforestry systems, social organizations, rural development, communication, sanitation services, comprehensive nutrition, Maya culture and traditions, and spirituality (see Table 34.1). Each subject matter has work projects during which a large portion of the training is carried out.

The students of the SEA are campesinos. They are selected by their communities to be taught in the management and conservation of the environment, as well as its logic and cycles. An annual call is issued, sponsors nominate candidates, and SEA Advisory Board members complete the admission process by interviewing the applicants. When the yearlong program is completed, the sponsors expect that the students will return to their respective communities to apply what they have learned and to partake actively in the community's development.

Students stay at the SEA (located 2 km from Mani, Yucatán) from Tuesday afternoon through Friday. In February 1997, women were enrolled for the first time into the SEA program, where they participated in a workshop series that offered classes during weekends (Friday through Sunday). In 1999, after further evaluation, the Board decided to establish only one common curriculum for men and women.

ORGANIZATION OF THE SEA

The SEA has an Advisory Board that includes representatives of collaborating institutions, students, alumni, promoters, and the SEA Director. Any problems and needs are presented and resolved at the monthly meetings. A general evaluation of the SEA is conducted annually, and modifications are defined for the following school year. The SEA director is responsible for discipline, planning of activities, and coordination of the 22 professors that participate in the courses: ten from the Universidad Autónoma de Yucatán, seven from Universidad Autónoma Chapingo, two from APIS A.C., two from the Catholic Church, and one as a traditional herbalist. In 1999,

TABLE 34.1. Subject areas and courses offered at the School of Ecological Agriculture (*Uyits ka'an*)

Ecological Agriculture	Organization	Health and Nutrition	Human Development
Ecological basis	Production units	Herbalists	Maya culture and traditions
Horticulture	Social organizations	Sanitation services	Spirituality
Composting	Development of proposals	Comprehensive nutrition	Theology of liberation
Corn production	Participatory methods		Entertainment
Plant propagation	Rural development		
Animal production: chicken, sheep, pigs, goats, native bees, apiculture	Communication		
Agroforestry systems			
Postharvest management			

trusteeship began—a group of individuals who manage the fund-raising activities of the SEA.

To date, five generations have graduated from the SEA—a total of 138 students from the 161 initially enrolled. Most of them are from Yucatán State, but there have been students from Campeche and Quintana Roo as well (Figure 34.2). Mani, the community nearest to the SEA, is the only community that has supplied students in all five generations.

The diploma earned in ecological agriculture serves as recognition of a campesino-driven rural development, based upon their own knowledge and capabilities. Table 34.2 presents a summary of the number of communities where the alumni from the SEA are working, as well as the support groups (i.e., sponsors) that interact with them. Major support groups for students include the local Catholic churches and the National Institute for the Indigenous (INI); there have also been NGO and research groups that support students who go to the SEA.

Indicators of the interest and motivation by past SEA students are the funds generated by the SEA alumni from proposals submitted and funded by INI and PNUD-PPS (United Nations Development Program—Small Subsidies

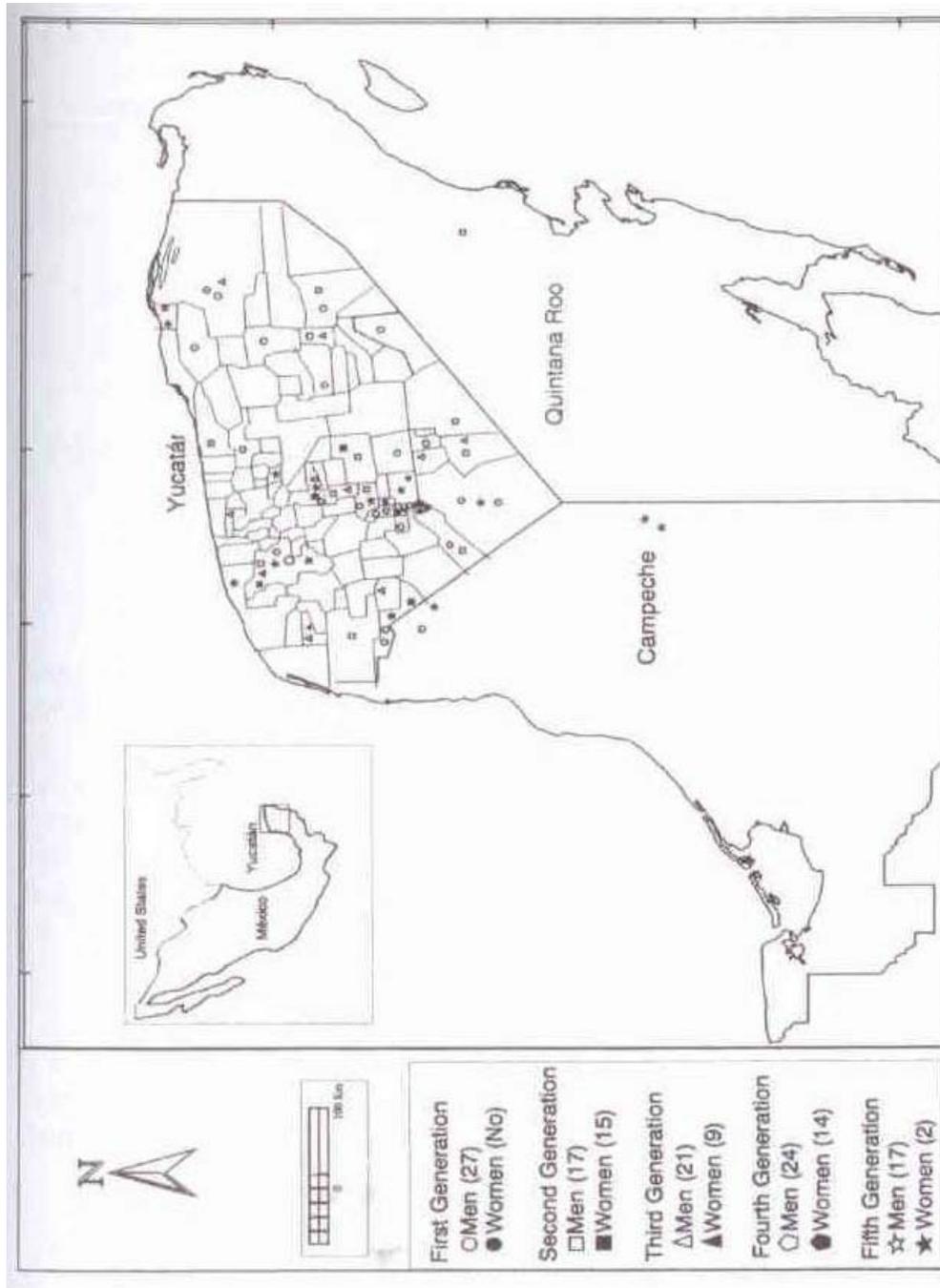


FIGURE 34.2. The origin and location of alumni graduated from the School of Ecological Agriculture (*Uyits ka'an*).

TABLE 34.2. Students, communities, and their support groups that have participated in the School of Ecological Agriculture (*Uyits ka'an*).

Generation	Female	Male	No. of communities represented	Sponsors
1996	---	27	18	2
1997	16	18	21	11
1998	8	12	13	8
1999	12	24	18	2
2000	2	19	15	5
TOTAL	38	100	63*	14*

*The total in each column has been reduced to account for common communities and sponsors.

Program). These funds are managed by the alumni and used to promote continuing ecological agriculture activities after graduation.

In a recent study of the SEA alumni, it was found that a total of 89 alumni are promoting ecological agriculture in 65 different communities (Table 34.3). Campesinos are as eager as anybody to learn and accept techniques that will improve their quality of life. Alumni from the SEA are starting to combine technical knowledge and traditional knowledge to develop alternative agricultural practices compatible not only with technological and environmental factors, but also with sociocultural dimensions and economic reality.

HIGHLIGHTS AND LESSONS LEARNED

The experience shared by students of the SEA has been, and continues to be part of, a dynamic learning process. Key elements guide the formation of the SEA, such as

- an alternative education system that emphasizes hands-on learning approaches and encourages graduates to see themselves as agents of change, with the means to make and evaluate decisions;
- the instruction and promotion of alternatives to adopt production methods respectful of their culture, resources, and the natural environment;
- the possibility to motivate the creativity and ingenuity of the campesinos with the creation and promotion of new technologies;

- the inclusion of women in SEA programs, as well as a reevaluation of their role in the communities' development; and
- the creation of a campesino-promoter network that shares a common philosophy and provides vocational training that can help contribute to the consolidation of local development processes.

An analysis of the alliances created through the SEA identifies certain elements that favor(ed) the development of this project:

- A common goal is known and shared by all participants, which does not imply agreement in world views, values, or backgrounds.
- Opportunities exist to analyze and respond to diverse situations. The open communication as practiced by the SEA Advisory Board is fundamental for decision-making as well as follow-up on any actions taken.
- A true spirit of collaboration is present among members. Participants act on their own initiatives, which prove helpful with making decisions, and renew annually their commitment to the program.
- Flexibility and tolerance are practiced among participants, especially in terms of understanding and resolving the needs and problems faced by all students. Mutual respect is strongly promoted.

A review of the experiences shared by participating academics recognizes the lessons learned by both students and faculty. The SEA offers an opportunity for training not only campesinos, but also new professionals and researchers. Certain lessons learned are worth mentioning, including the following:

- The importance of managing a common language among the producers and faculty, both in oral and written forms, cannot be overstated. It has been difficult to find a writing style for the training materials that reflects the spoken style.
- It is necessary to have experience with the rural areas as well as practical know-how in teaching campesinos the applied element of the theory. As some producers have stated, "Campesinos learn by seeing."
- Didactic tools are needed for informal teaching methods.
- The importance of well-founded modes of communication is recognized, as well as the need for continuous evaluations of the SEA programs and infrastructure.
- The use of available resources must be optimized, in order to eliminate unproductive and unnecessary activities.

- The training sessions of academic students (undergraduate and graduate) can be combined with those of the campesinos as long as it is recognized that each group has different goals. Campesinos will not apply scientific methods to their experiments, while researchers may be unable to apply all of the production activities.
- Campesinos and faculty need to manage the same concepts, principles, and mechanisms; in turn, much can be learned from the campesinos as they give examples and apply what they learn. This requires a recognition by all involved of the value and importance of empirical knowledge gained by years of experience, and, in some cases, experiences passed along from one generation to the next.

In the Yucatán Peninsula, the SEA represents a distinctive alternative, dependent upon the participation of multiple players and with the focus upon the campesino producer. For all of those involved (instructors, students, promoters, and directors), this process has been an adventure and a constant source of discovery, with its own particular set of challenges and opportunities. A spirit of collaboration and learning is the vision that best describes “*Uyits ka’an.*”

In order to achieve successful and self-sustained grass-roots development, activities must be arranged that consider the inherent social organization of the community (e.g., authorities, leaders, etc.). For a sustainable community development, collaboration among the players (NGOs, government agencies, educational institutions, and donors) is imperative. Collaboration here is understood not only as joining efforts and resources towards a “common” goal, but as a synergistic process where the results exceed the sum of the parts. The interactive training of campesinos and new

TABLE 34.3. SEA alumni promoting ecological agriculture.

Generation	Female	Male	No. of communities represented	Sponsors
1996	---	15	13	3
1997	12	10	18	5
1998	5	8	9	6
1999	5	19	15	6
2000	2	13	10	5
TOTAL	24	65	65	22*

* The total in this column has been reduced to account for common sponsors

professionals that takes place at the SEA is a viable alternative in the Yucatán, which will allow both development and improvement of the environment.

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Chapter 35

HabitatNet: Conducting Biodiversity Research with Secondary-School Science Classes

Daniel J. Bisaccio

INTRODUCTION

A simple directive begins both my Temperate and Tropical Ecology courses: I ask my students to sketch an insect. Whether it is a graduate school tropical terrestrial ecology class—or one of my high school classes that includes Advanced Biology, Nature and Literature Seminar, or Tropical Ecology—my introduction to those classes begins with my request for the students to apply their notion of what an insect is. It is a simple directive, but much more telling than asking my students to define an insect.

Without doubt, most students who first take my courses (in graduate school or high school) should be able to respond to my question by saying that an insect has “three body segments and three pairs of legs.” What I find most interesting, however, is that the majority of these students have no idea where

Projects such as this achieve success through the vision and active participation of many individuals as well as organizations committed to research, education, and global conservation. I thank Dr. Arturo Gómez-Pompa and Biologist Marco Lazcano Barrero for their expertise, support, and belief that secondary school students are capable researchers. My colleagues at Souhegan High School, Melissa Chapman and Kathy White, have provided invaluable ongoing pedagogical and technical support.

In addition, the Administrative Team of Souhegan High School has given this project their unconditional endorsement. Gillian Schultz and Juan Costillo have unselfishly given their time and expertise to our project by assisting us with the identification of tropical plant species.

Chris Ros at the Smithsonian Institution believed from the beginning that HabitatNet would become a reality and not just remain a dream. Initial funding for this project came from the NSTA/Toyota Tapestry Grants Program. Without that funding, HabitatNet may never have been fully developed. Finally, a special note of thanks to the hundreds of student researchers, known affectionately as our SHS BioSwat Teams, who have demonstrated global stewardship and offer proof positive hope for our future.

to place the three pairs of legs on their drawings. Often, they do not realize this practical knowledge is missing until they try to sketch an actual insect; after several false starts, they invariably have to ask for assistance. (It is important to realize that many of these students are intelligent honors students who have achieved academic success by mastering content without application.)

Recent research and recommendations from prestigious national science education reform committees strongly indicate a need for “application” of scientific concepts and skills (AAAS 1989:4–8; NSTA 1992:I:134–135) instead of simply memorizing information. Additionally, I might also suggest that if science educators hope to develop a society that is both scientifically and environmentally literate, then they also need to develop a curriculum that teaches science as it is practiced in the field.

This concept is not new. Certainly one may trace back to Pliny and Socrates the importance of observation and critical discussion to the learning process. More recently, Comstock’s classic *Handbook of Nature Study* begins the chapter on “What Nature Study Is” with the following quote: “Therefore, the object of the nature-study teacher should be to cultivate in children powers of accurate observation and to build up within them understanding” (Comstock 1911:1).

Perhaps what we need to observe as educators in this new millennium is not how we “teach students,” but instead how we may enable students “to learn.” If we want our students to have enduring knowledge and skills in which they are mindful of the natural world, then we need to involve our students in the process of science. Individual choices and decisions regarding the environment are not restricted to those students who pursue a career in the sciences. Clearly, this must become an imperative for those of us who “teach science,” regardless of the level we teach. Since 1995, all students in my high school science classes (both advanced and general) have been involved in an authentic biological diversity research project I developed with funding and support from the National Science Teachers Association’s (NSTA’s) Environmental Tapestry Grant Program. The project is called “HabitatNet: A Global Biodiversity Research Project” (Bisaccio 1996). HabitatNet utilizes the Smithsonian Institution’s Man and Biosphere international assessment of biodiversity (SI/MAB 1992) protocols, which are taught as biological field skills to the students.

High school students at Souhegan High School, located in Amherst, New Hampshire (NH), have conducted primary biological diversity research at two sites. One site is located on Amherst Town Conservation Lands, which is adjacent to our school, while a second site is located at the El Edén Ecological Reserve in Quintana Roo, Mexico.

Student work begins with taxonomic biological diversity surveys that include plant community analysis with regard to terrestrial succession, as well

as possible natural or anthropogenic disturbance indicators. After the initial research is completed, student-generated questions regarding functional biological diversity hypothesis are investigated. Student questions are variable and reflect the diversity of the student population. All students, however, are required to develop a scientific hypothesis regarding functional biological diversity dynamics and conduct a research project investigating their hypothesis. Student work is then presented, via a poster session, at the conclusion of the curriculum unit.

METHODS

The pedagogical focus on content includes a vast array of typical topics covered in biology courses. Topics include taxonomy, ecology, genetics, and evolution. Moreover, students are required to apply their knowledge in each of these areas to develop a presentation that includes three key components: (1) a terrestrial succession report that discusses past, present, and future predictions based on observed and calculated plant community status (this may include both natural and anthropogenic disturbances); (2) status reports on species found within the biodiversity plot, with notes regarding “special or unusual” species; and (3) status reports of migratory bird species found in both the Amherst and El Edén Ecological Reserve biodiversity plots.

Further work includes developing a conservation management plan for a “featured creature” located in that biodiversity plot. This must be a native or endemic species in need of a management plan that is supported by their research.

STUDY AREAS

The Amherst, NH, site is located on public conservation lands adjacent to Souhegan High School. The site is a secondary growth white pine (*Pinus strobus*)–mixed oak (*Quercus* sp.) forest that was logged 40 years ago. The soil substrate is primarily a xeric glacial outwash sand with parts of the tract including a hydric flood plain of the Souhegan River. The location of the biodiversity plot is lat. 42° 50' 06" N, long. 71° 35' 10" W.

The second site is at the El Edén Ecological Reserve located in the Mexican State of Quintana Roo. It is a semideciduous tropical dry forest that historically has been utilized for “chicle” (*Manilkara sapota*) and lumber in near recent years, as well as historically by the Maya. Past and present natural disturbance regimes include episodic hurricanes and fires. The coordinates for this site are lat. 21° 12' 57" N, long. 87° 11' 51" W.

Both sites, as prescribed by SI/MAB, are one hectare (ha.) in size. Each one-hectare site is divided into 25 quadrats, measuring 20 m x 20 m, and

numbered sequentially. The baseline of the hectare biodiversity plot (and subsequent quadrats) is numbered “one” with a clockwise numbering of each of the four border boundaries. As such, lines one (1) and three (3) for each site represent East-West, while lines two (2) and four (4) represent North-South.

Trees in each quadrat are numbered (referencing the quadrat and individual tree) and measurements for individual trees are taken. Measurements include species identification, diameter at breast height (1.3 m), tree height, and status (i.e., live standing, alive leaning, dead standing, or dead leaning). Basal area/dominance, species density, and species frequencies are then calculated by quadrat and for the biodiversity plot (see Table 35.1) overall. In addition, canopy density is calculated for each quadrat.

Students use this data along with supplemental information regarding climate, disturbance indicators, and historical references to construct a terrestrial succession history for the biodiversity plot. Once this is completed, students then generate a list of questions for further investigation. These questions are rich in student experience gleaned from their now prior fieldwork within their quadrats.

RESULTS

Scientific Data

Thus far, three one-hectare biodiversity plots have been completed at the Amherst site. The one-hectare site in the El Edén Ecological Reserve is 100 percent complete.

Annual field reports are written and submitted to the Smithsonian Institution, the Amherst Conservation Committee, and the El Edén Ecological Reserve. Additionally, field reports for the El Edén Ecological Reserve are published online at the HabitatNet Web site (Souhegan High School 2000) and at the University of California/Riverside Web site (University of California/Riverside 2000).

Pedagogical Data (Ongoing)

Since 1995, 530 secondary school students have participated in this project (see Table 35.2). Many of the student “HabitatNet Alumni” are currently in undergraduate or graduate school programs. Informal

TABLE 35.1. Cumulative quadrat tree data for the HabitatNet/SI-MAB Data Plot, El Edén Ecological Reserve, Quintana Roo, Mexico, semideciduous tropical dry forest.

Species	August 1999		Quadrat Tree Data		Tree Diameter \geq .1 meter		
	Number of Trees	Number of Stems	Average DBH/ Stem	Basal Area	Relative Density	Relative Dominance	Relative Frequency
<i>Metopium brownei</i>	69	70	.201	2.428	14.94	18.07	8.13
<i>Ficus yucatenensis</i>	60	60	.180	2.224	12.99	16.56	5.63
<i>Manilkara sapota</i>	37	39	.217	1.775	8.01	13.21	5.00
"Sak piich" Mayan	28	28	.188	.934	6.06	6.95	5.00
<i>Bursera simaruba</i>	45	46	.155	.934	9.74	6.95	5.00
<i>Lysiloma latisilquum</i>	16	16	.236	.822	3.46	6.12	6.25
AAA BBB (Dead)	32	34	.145	.644	6.93	4.79	6.25
<i>Vitex gaumeri</i>	20	21	.151	.427	4.33	3.18	5.00
Sabal yapa	33	33	.121	.386	7.14	2.87	5.63
<i>Caesalpinia gaumeri</i>	15	15	.158	.325	3.25	2.42	3.75
<i>Guettarda gaumeri</i>	7	8	.198	.314	1.52	2.34	1.88
<i>Loncho- carpus</i> sp2	15	15	.142	.261	3.25	1.94	3.13
<i>Gymnopo- dium floribundum</i>	8	11	.149	.213	1.73	1.59	3.13
<i>Ficus</i> sp1	7	7	.169	.196	1.52	1.46	2.50
Leg UNK	12	12	.125	.151	2.60	1.13	3.75
<i>Loncho- carpus</i> sp1	7	8	.149	.150	1.52	1.12	2.50
Chak te	3	3	.237	.135	.65	1.01	1.25
<i>Thouinia paucidentata</i>	5	5	.175	.134	1.08	1.00	1.88
<i>Brosimum alicastrum</i>	3	3	.208	.124	.65	.93	1.25

TABLE 35.1 (continued)

Species	August 1999		Quadrat Tree Data		Tree Diameter \geq .1 meter		
	Number of Trees	Number of Stems	Average DBH/ Stem	Basal Area	Relative Density	Relative Dominance	Relative Frequency
<i>Coccoloba</i> sp1	2	2	.250	.114	.43	.85	1.25
<i>Lonchocarpus rugosus</i>	4	4	.165	.102	.87	.76	1.88
Fia UNK	3	3	.193	.099	.65	.74	1.25
<i>Lonchocarpus castilloi</i>	3	3	.172	.083	.65	.62	1.88
<i>Lonchocarpus xuul</i>	5	5	.138	.076	1.08	.57	1.25
<i>Hippocratea celastroides</i>	2	2	.210	.075	.43	.56	.63
<i>Coccoteinax reade</i>	3	3	.165	.066	.65	.49	.63
<i>Croton</i> sp1	4	4	.133	.059	.87	.44	1.88
<i>Nees</i> sp1	2	2	.157	.041	.43	.31	.63
<i>Gueberda gaumeri</i>	2	2	.130	.028	.43	.21	1.25
<i>Thouinia paucidentata</i>	1	1	.150	.018	.22	.13	.63
<i>Hampea trilobata</i>	2	2	.100	.016	.43	.12	1.25
<i>Bauhinia divaricata</i>	1	1	.130	.013	.22	.10	.63
Rub UNK	1	1	.130	.013	.22	.10	.63
<i>Sapini gaumeri</i>	1	1	.130	.013	.22	.10	.63
<i>Coccoloba spicata</i>	1	1	.110	.010	.22	.07	.63
<i>Jatropha gaumeri</i>	1	1	.110	.010	.22	.07	.63
Myr UNK	1	1	.110	.010	.22	.07	.63
Lau UNK	1	1	.010	.010	.22	.06	.63
TOTAL: 38 species	462	474	.160	13.433	100.00	100.00	100.00

TABLE 35.2. HabitatNet student and teacher participant numbers since 1995 with projected biological and pedagogical goals for the program

Year	High School Students	Graduate Students	Teachers	Total
1995-1996	101	19	12	132
1996-1997	117	19	14	150
1997-1998	110	18	13	141
1998-1999	105	18	6	129
1999-2000	97	18	0	115
TOTAL	530	92	45	667

Next Phase of HabitatNet: Year 2000-2001

1. Continue Biodiversity Research at
 - a. Amherst Town Conservation Lands
 - b. El Edén Ecological Reserve, Mexico
 - c. Blue Mountains, Jamaica W.I.
2. Develop "Concurrent" Biodiversity Projects/Analysis:
 - a. Initiate Specific Flora/Fauna Surveys
 - b. Generate Statistics from Data Sets (five years)
3. Interview "HabitatNet Student Alumni" with regard to
 - a. Impact of "Hands-On" Science in Developing Scientific Literacy
 - b. Impact of "Hands-On" Science in Developing Environmental Literacy

correspondence (letters and e-mail), as well as direct conversations with past students (Bisaccio 2000), indicate the importance of participation in this project to their ongoing studies or interest in the environment.

The informal response of anecdotal comments by past student participants has prompted the need to conduct a more formal survey. Two typical comments include the following: (1) "It changed my life. HabitatNet was the best opportunity I had in high school and showed me how great life could be as a field scientist or teacher.", and (2) "The best aspect of the fieldwork was to have the chance to ask my own question and then engage in a scientific investigation to answer it!" (Bisaccio, personal communication).

As such, a survey instrument was developed and sent to HabitatNet Alumni in December 2000. The intent of the survey was to examine more closely the relationship between field experience and learning. Results and discussion will be posted on the HabitatNet Web site.

DISCUSSION

In Aldo Leopold's salient essay, "Good Oak," he writes: "There are two spiritual dangers in not owning a farm. One is the danger of supposing breakfast comes from the grocery, and the other that heat comes from the furnace" (Leopold 1949:6).

As we look ahead to the future of conservation biology, priority must be given to answering Leopold's challenge. More and more often I find that students not only have difficulty with locating where they need to place appendages on insects, but also where all that sustains us as humans comes from. It has become an abstraction for all too many of my students.

As such, science educators and researchers have a poignant moment to merge their respective efforts with regard toward global conservation and educational change. One conservation issue is the immediate need to collect long-term biological diversity data to more fully understand the complexity of functional biodiversity as well as basic taxonomic biodiversity in the face of funding scarcity. The educational challenge of developing curriculum that provides science content and skills to foster scientific literacy (and I add "environmental literacy") has the potential to address the conservation biology need by developing student researchers. Students learn science by doing science while conducting biological research. Developing scientific habits of mind as well as scientific literacy means that students are not "taught" science but experience science through actual scientific investigations that are meaningful not only to them, but also to a wider audience.

Collaborations between science educators and researchers allow educators an opportunity to directly address the National Research Council's position statement: "Inquiry into authentic questions generated from student experiences is the central strategy for teaching science" (NRC 1996, 31). Additionally, *The National Science Education Standards*, as stated in Content Standard A—Science As Inquiry, states that students need to be able to have "abilities necessary to do scientific inquiry" as well as "understandings about scientific inquiries." Content Standard C—Life Science, discusses the need for students to understand "biological evolution," "interdependence of organisms," and "matter, energy, and the organization in living systems" (NRC 1996:173).

What do initial findings from "HabitatNet: A Global Biodiversity Project" suggest? Merging scientific research with educational projects may not only serve the needs of researchers and educators, but also allow students to develop scientific and environmental literacy that is personally enriching as well as enduring.

Students become more than just data collectors if allowed to engage intellectually with the data they collect. Their first-hand experience in

collecting this valued data must then nurture their curiosity in following through with a scientific inquiry. As Leopold observed:

The last word in ignorance is the man who says of an animal or plant: "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering. (Leopold 1953:146–147)

Developing collaborations between research and education benefits educators and researchers immediately as well as fosters a more environmentally literate society to safeguard the future.

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***PART VII:
SUMMARY
OF RECOMMENDATIONS***

Chapter 36

The Maya Lowlands: A Case Study for the Future? Conclusions

Michael F. Allen
Arturo Gómez-Pompa
Scott L. Fedick
Juan J. Jiménez-Osornio

INTRODUCTION

Pulling together an overview for such a broad topic as this one is challenging under the best of circumstances. Organizing the conclusions for a topic that has been so extensively researched by many of the world's leading archeologists, agronomists, biodiversity scientists and ecologists, is daunting. However, there are several major advances and new directions in this book that are exciting-both in the context of understanding the Maya and their extraordinary culture and environment, and for creating a case study of how humans might begin to address the crucial challenges of the future of the globe.

There are two potential approaches to analyzing the continuing global environmental challenges and identifying the causal factors behind them. The first approach is to attempt to describe or predict the overall changes in the human and "natural" world over some undefined time period. This approach has been utilized in major works by eminent authors such as Erlich (1968) and Diamond (1997). It is also the general approach taken by social and environmental groups (e.g., Worldwatch Institute, World Wildlife Fund, United Nations, World Bank). These have lead to several assessments of the "world situation", as can be found in many publications (Brown, Flavin, and French 2001).

Within this approach, there are quantitative assessments of human and environmental conditions that can be based on countries or other

organizational entities. For example, Wang et al. (2001) developed a sustainability indicator based on social, economic and environmental parameters. Interestingly, for countries that include the Maya area, Belize, and Mexico rank average or above average with an increasing sustainability index whereas Guatemala, El Salvador, and Nicaragua rank below average with a decreasing sustainability index. The large disparity in values, even within a cultural region, suggests that these approaches have clear limitations when the focal unit is on a political entity.

Although this approaches provided considerable understanding of how we got where we are, few solutions to current environmental dilemmas are apparent. Nor do we understand how responses have been formulated because most human groups, when faced with these challenges, have usually migrated, been subsumed, or died.

A second approach is to develop case studies of individual cultural/geographic systems that have persisted, despite being subjected to the perturbations of the environment resulting from both “natural” and “cultural” impacts. Gómez-Pompa (this book) outlined several challenges, not the least of which was to justify a focus exclusively on one culture-the Maya.

The Maya fit this second approach. They have remained in a region for over three millennia. Their “accomplishments” and “failures” are spectacular and chronicled in both written and archeological records. Finally, they remain a viable and vigorous population retaining many of their original cultural traditions, while simultaneously incorporating new and useful ideas into their technologies, lifeways and belief systems. Because of this, understanding how the Maya survived past perturbations, how they live today, and how they perceive the future makes these studies important to the future of our world. In the last chapter these challenges will be addressed as defined by the participants in the 21st symposium of Plant Biology and the contributors to this book.

MOSAICS

A major contribution of this symposium was to expand the view of the Maya lowlands as a highly variable region in both space and time (see also Fedick 1996b.c). This mosaic of variability emerges at various scales in both environmental and cultural characteristics.

When viewed at the macroscale, the Maya lowlands appears to be a rather homogenous region. As a geological unit, the Maya Block is a single fragment with little topography, until very recently, it was largely marine in the geological time-scale. Thus, there is little space or history for geographic separation in which speciation generally occurs. While a general gradient in environmental characteristics exists from south to north, the entire region

shares common species of most plants and animals. As a culture entity, the Maya also shares a rather astonishing sameness over thousands of years and thousands of square kilometers (Pyburn 1996:240-241).

However, as Pyburn has noted (1996), behind this “vener” of cultural continuity is a system composed of an interconnected yet highly varied system of local behaviors. As the landscape comes into focus at increasingly detailed scales, the mosaic of diversity is revealed (Fedick 1996a). Local variations in geology, topography and hydrology emerge, which, in turn, influence soil development and the structure of biotic communities. Dunning Beach, Farrell et al. (1998) recently defined 27 distinctive adaptive regions of the Maya lowlands. Each of these units is heterogeneous, but as a repeating pattern of ecosystem types that define a distinctive landscape (see Forman and Godron 1986). It is at this level of disturbance that Maya land use over at least the last three millennium shaped the pattern of biodiversity and ecosystem structure.

The pattern of land use by the Maya, both in the present and in the past, is a clear case of shifting mosaic structure at a range of scales. The persistence of biota in the region may well be attributed to the dynamic structure of Maya land use.

At the local scale of homesteads and villages, the seeds of regional biotic diversity are literally contained and preserved within the homegarden (see Herera et al.1993); a common component of Maya agriculture, both modern and ancient, that has until recently been little-recognized by researchers (see Flores 1993; Goñi 1993; Herrera Castro 1994; Ortega et al. 1993; Stuart 1993). The outfields that surround the village represent an array of cultivation and management technologies (Toledo Maya Cultural Council and Toledo Alcaldes Association 1997). Slash-and-burn cultivation, practiced in combination with selective cutting and replanting, results in the creation of “forest gardens” as an end product of managed succession (Gómez-Pompa, Flores, and Sosa 1987; Gómez-Pompa and Kaus 1990). Within particular landscapes, hillsides might be terraced, and the variety of wetland ecosystems modified or transformed for cultivation (Beach et al., this book; Beach and Dunning 1995; Fedick 1997; Fedick, this book; Fedick et al. 2000; Jiménez-Osorio and Rorive 1999). Dispersed within these managed landscapes, and surrounding larger units of land use, is the wilderness, or wildland forest. The interface of wild forest and various forms of cultivation is essential to deer, peccary, turkeys, and other animals heavily utilized by the Maya. In addition, while the “forest wilds” were feared by the Maya as places of danger (Taube, this book), they also served for protection from one’s neighbors and as refuges for many species of large animals persisting today.

At a larger social scale, archeological and historical evidence clearly demonstrates that at no time did any one city or political unit dominate the entire region simultaneously. City-states of varying size and power, ruled by

royal lineages, competed for prestige and control of lands through alliances, arranged marriages, and warfare (Dahlin 2000; Demarest et al. 1997; Martin and Grube 1995, 2000). The success or failure of such campaigns likely corresponded with major shifts in population levels. Thus, while forest resources would be severely depleted in one area, they might recover at another in a shifting pattern dependent on the particular status of various kingdoms (Dunning, Beach, and Rue 1997; Johnson, Breckenridge, and Hansen 2001). This shifting mosaic model is absolutely essential to the preservation of biodiversity and forest resources and is a tenet of conservation biology theory.

BIODIVERSITY

Due to the extraordinarily high human population pressures for such a long time, we would postulate that biodiversity should be very low. Indeed, some argued that the diversity is low for a tropical region compared with expectations. However, the survey information presented in this book strongly suggests that the biodiversity is not really low. It may be structured differently due to the geological context of the region. Diversity of any one location is high. And, as one moves across the landscape, there is continued turnover, but few real breaks in community types. Although endemism is high in the Yucatán Peninsula, those organisms are widely found across the region. Schultz (this book) reported that on an area basis, a small reserve like El Edén has plant species richness per unit area approaching better-known biodiversity hot spots (e.g., the Chamela Reserve in Jalisco) in both endemics and total species per unit area. However, no plant species are endemic to the El Edén Ecological Reserve or to the larger Yalahau region. They are largely the same list as the one for the peninsula as a whole.

Research on many other groups, including algae, fungi, slime molds, protozoa, and the many others reported here, clearly indicate that we have only scratched the surface of the total biodiversity of the Yucatán Peninsula. Symbiosis (such as mycorrhizae and dinitrogen fixation) predominate, and the functioning of the regional ecosystems is dependent on a myriad of unknown organisms and relationships.

This suggests is that biodiversity was not overwhelmed by the large human population density and broad land use. Species, even endemics, are widely spaced across the region. If they decline at one point, they can persist in another. This allows for continual recolonization events. Many types of vegetation resprout after natural disturbance such as hurricanes and fires, or following agricultural practice such as slash-and-burn cultivation, which help make these plant species highly resilient. Bases on the evidence presented here, the persistence of biodiversity is largely due to the mosaic management

strategies practiced by the Maya themselves, coupled with the regional-scale mosaic nature of the rise and fall of the individual city-states.

CLIMATE

Climate also provides a dynamic rather than static background, directly influencing human culture and settlement patterns as well as biodiversity. Climate also changes at local scales in response to human activities. Isotopic evidence from Brenner and colleagues (this book) points to the Classic Period as being unusually dry in the longer climatological history. Further, they provide clear evidence of a severe prolonged drought coinciding with the end of the Classic Period (see also Gill 2000; Hodell, Curtis, and Brenner 1995). It is also important to note (M. Allen and Rincon, this book; see also Sage and Cowling 1999) that the “natural” atmospheric CO₂ level was approximately one-third lower than today (i.e., less than 250 parts per million [ppm] during the rise and fall of Maya civilization to over 370 ppm today). Thus, water-use efficiency was dramatically lower for C₃ (cool-season) plants making any drought much harsher than would be found today. (this would affect all vegetable and tree species, excepting only C₄ [warmseason] grasses such as maize.)

However, it is still unclear if the spatial pattern of the Terminal Classic collapse is important. Archaeological and epigraphic evidence demonstrate that the major cultural collapse primarily affected the central-southern lowlands. This may be related to the orographic (i.e., mountainous) precipitation of the inland region, which, in part, is derived from the transpiration of upwind vegetation. Alternatively, the precipitation of the northern regions is dependent on moisture derived from ocean evaporation, including hurricanes. If deforestation were widespread, then the precipitation in the inland, higher-elevation sites could have been affected but not necessarily the northern lowlands. (M. Allen and Rincon, this book).

The northern lowlands also appear to have a greater number of hurricanes than the southern inland regions (Boose et al., this book). These can cause extensive damage to croplands and make the forest more susceptible to fires (Whigham and Olmsted, this book). In his original description of Maya life, Landa ([1566]1978) described the terrible effects of hurricane damage on crops, disease and structure of Maya villages (see also Konrad 1985). Humans have little impact on hurricanes, but the presence of La Niña can increase hurricane intensity while El Niño can reduce it. The climate change reported by Brenner and his colleagues (this book) presents evidence for a severe drought in the northern Yucatán Peninsula, but cautions that the data related to drought in the inland central-southern lowlands is

ambiguous. It is not known if the drought period seen in the north is tied to hurricane activity or general precipitation.

COLLAPSE

As agriculture expanded with the increasing population base, the area devoted to forest resources declined while those reserved for urbanization increased—a situation not different from today. The forests became less productive as they shrank, and the resource base within an area controllable by a landed nobility declined. Importantly, there was not a single “collapse” of ancient Maya society. The Classic Period of the Maya was characterized by a large number of city-states vying among each other for hegemony. The Terminal Classic Collapse really consists of the fall of a number of these cities-states and interruption of construction of ceremonial centers. Numerous political and demographic collapses in the Maya lowlands occurred in various areas, and at various times, both before and after the well-known Terminal Classic collapse. The fact that this was not a singular event may be critical for understanding the past as well as for making predictions for the future.

POPULATION DENSITY

Up to the early 1970s, the Maya were still perceived as a collection of dispersed slash-and-burn farmers peacefully co-existing within their tropical forest environment (see Hammond 1978; Turner 1978). A decade ago, there was still some debate as to the human population density and structure in ancient times and whether the population densities were high into the present (Culbert and Rice 1990). Current archeological evidence clearly points to extraordinarily high population densities across the Maya lowlands (see Turner, Kepleis, and Schneider, this book). The cities were large, requiring enormous amounts of land for agriculture, which, in turn, resulted in extensive land erosion. As sites can be found in almost every region as early as the Preclassic Period, this implies that the entire region was occupied. The major Classic sites, however, were concentrated in the central-southern lowlands at slightly higher elevations. Cities were especially large; the population density was very high—possibly even higher than today, and the various city-states probably covered most of the region with developed lands. Just as important, at the end of the Classic Period, the collapse in the population was largely focused in the Petén and other inland areas with a simultaneous emergence of new cities in the lower elevation, flatter regions of northern Yucatán. There was a second major regional demographic collapse in the sixteenth century with the introduction of new diseases by the Europeans. The population has

continued to rebound through today with expected explosive growth from the present into the near future. These observations support the notion that there are patterns of initiation and collapse that have an environmental and cultural basis.

FOOD

How was food procured during periods of high population densities? A lot has been learned about the food and fiber plants used by the ancient Maya—that is, which ones were domesticated, as well as how they were cultivated (see Fedick 1996c; White 1999). The Maya not only domesticated or adapted those plants that we know today such as chocolate (*Theobroma cacao*) and henequen (*Agave fourcroydes* Lem), as well as the traditional maize, beans, squash, and chilies, but they also used many forest and wetland plants. Just as importantly, forest and wetland animals such as deer, ocellated turkey, curassow, and apple snails were heavily utilized and probably managed (Carr 1996; Emery 1999; Shaw 1999).

The use of these resources constitutes an extremely important advancement and likely also sowed the seeds of Terminal Classic Collapse. The Maya mode of life depended on mosaics of land use. Mosaics of forest gardens and milpas, within a forest matrix, comprised the landscape of each population unit, whether village or city-state. Algal mats and wetland muck may have been a staple mechanism for improving soil fertility, as investigated by a group of collaborating researchers working at the El Edén Ecological Reserve (see chapters in this book by Fedick; Morrison and Cózatl Manzano; Novelo and Tavera, and Palacios-Mayorga et al.). Interestingly, despite many generalizations on the “impoverished” tropical forests, work in the Maya lowlands has consistently shown that soil nutrients are actually quite high in much, if not most, of the region. Growth studies in both agricultural and restoration sites (see E. Allen et al., this book; M. Allen and Rincón, this book) show excellent plant growth if water is available. Even Landa ([1566]1978) commented on the fertility and excellent plant growth in the cracks between the rocks.

Importantly, both ancient writings and symbols and modern practices clearly demonstrate the crucial role of wildland forest as places with resources, but also show these areas as the home of magic beings (e.g., animals such as jaguars) and as scary regions to penetrate (see Taube, this book). These myths and reverence together make for careful use and facilitate the maintenance of wildland mosaics within the regional spatial structure of even developed city-states (Anderson, this book).

The careful use of resources and innovative development of crops was clearly coupled with innovative governmental cooperatives, leading to greater

organization and separation of activity. These innovations allowed populations to expand around villages, then city-states. The resulting division of labor allowed for the incredible scientific and architectural achievements so clearly articulated during the Classic Period. They also created disturbances at ever-larger scales, changing mosaics to large, developed matrices.

PERSISTENCE, RECOVERY AND SUSTAINABILITY

Although the Maya populations collapsed at least twice during this period, they never disappeared. On numerous occasions their populations declined in one area, and recovered in another, either by reproduction or through immigration. The areas from which they declined sometimes recovered, sometimes not.

One reason may lie in the concept of carrying capacity as outlined so eloquently by Turner and his colleagues in this book. They postulate that the population exceeded the carrying capacity leading to a “back-bite” and ultimately population loss. However, as previously described, the environment is not a static backdrop. In ecological theory, the carrying capacity, or k value, is only a theoretical limit for the limiting resource. In the case of the Maya, the population collapse may have been due to a loss in food production because of excess land degradation. However, this means that k had dropped due to soil loss- not necessarily that some number had been exceeded. Further, because of the drought, production may have been virtually halted as it was limited by the amount of water available. If k can decline, it can also recover and grow, and it can also vary spatially.

Thus, the collapse of the Classic Maya may not have been due simply to the excess utilization of resources, but a caused by a combination of a temporally and spatially reduction in the major limiting resource (water?), which regulates k . The fact that k could recover allowed the Postclassic population recovery to occur. By the time of the Spanish occupation, the Maya population was likely still rebounding from an earlier high.

The population collapse following the Spanish occupation was largely caused by the introduction of exotic disease from Europe. These diseases do not spread except in relatively high population densities. There is little indication that the Maya were overutilizing their resource base at that time.

The Maya knew when they had taxed their resources to a level beyond their institutions. Just as they had ceremonies for creating new kingships, they had an elaborate ceremony to decommission a temple, and kingdom. At Cerros, for example, when the kingship failed, the Maya undertook a “termination ritual” and went back to the fisher and farmer lifestyle (Schele and Freidel 1990). This could be associated with a political collapse, or a loss due to a dramatic environmental change affecting available resources (reduced

k). When this happened, they changed their resource allocations (a higher proportion of the population engaged in food acquisition versus elite activities such as science and architecture), or moved to another region.

Nevertheless, the critical elements of their culture survived. Chontal Maya appears to have persisted as a written language despite the cultural challenges from the Yucatecan Maya and Spanish. Was this persistence supported by small groups of knowledgeable scribe/scientists that were dispersed around the region, and even shifting through time? Perhaps this occurred in a manner similar to the retention of Latin as in modern science and religion? If this written language survived, what pockets of wisdom still remain uncovered by modern anthropologists and biologists? The local extirpation of both human and wildland resources as a function of hurricanes or other natural disasters and re-establishment by regarding the region as a continually fluctuating mosaic bears further careful examination. These elements are complex, but probably hold the keys to their long-term survival as a culture, and to the maintenance of natural biodiversity of a heavily populated region.

SYNTHESIS

If anything is to be learned from the changing Maya world, it is that understanding space and time is absolutely critical to human persistence. There is no absolute *k* value to which we, or any culture, can strive. The *k* value is variable. Humans must allow for fluctuations in both wildland and agricultural use of lands. This must incorporate patchy land use, in both short-term and long-term utilization. This solution resides at the landscape scale of occupation and has been eloquently described by Naveh (1998) as homeorhesis—that is, the shifting landscape patches that cycle in different stages of succession and human use.

Another solution resides in the creation of corridors at a regional scale for sustainability of populations and the migration of plants and animals. The Sian Ka'an an-Calakmul corridor project (World Bank 2000) is one example of such an effort. Another is the effort of the El Edén Ecological Reserve to establish linkages stretching across the wetlands from Yum Balam to Sian Ka'an. It is only in this context that we can understand the Maya world, and develop models for global human survival.

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