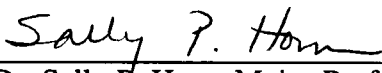


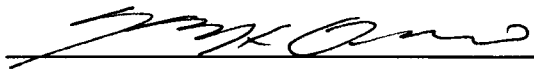
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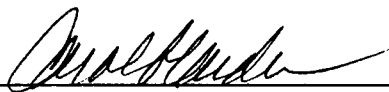
I am submitting herewith a thesis written by Lisa Marie Kennedy entitled "Prehistoric Agriculture, Fires, and Droughts at the La Selva Biological Station, Costa Rica: Paleoecological Evidence from the Cantarrana Swamp." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geography.



Dr. Sally P. Horn, Major Professor

We have read this thesis
and recommend its acceptance.





Accepted for the Council:



Associate Vice Chancellor
and Dean of The Graduate School

PREHISTORIC AGRICULTURE, FIRES, AND DROUGHTS AT THE LA SELVA
BIOLOGICAL STATION, COSTA RICA: PALEOECOLOGICAL EVIDENCE
FROM THE CANTARRANA SWAMP

A Thesis
Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville

Lisa Marie Kennedy

May 1998

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ABSTRACT

The La Selva Biological Station in the Atlantic lowlands of Costa Rica is a key site for research on neotropical rain forest environments and biota. While the modern ecology of the station is well studied, researchers are just beginning to consider its long-term history and the degree to which that history might influence modern ecological patterns and processes. Until recently, much of La Selva's forest was considered to be "virgin", i.e., undisturbed by people. That view has been abandoned with the recent discovery of preColumbian ceramics, and charcoal fragments that may reflect human-set fires on plots cleared for agriculture.

While it now seems clear that forests at La Selva have been subjected to a long history of human disturbance, questions remain about the chronology and nature of past human activity and the role of natural disturbance in shaping modern forests. This thesis presents a 3200 year record of environmental history from paleoecological evidence preserved in a 5.9 m sediment core from the Cantarrana Swamp. Pollen, fern spore, and charcoal profiles, along with characteristics of the sediment, support the emerging conception of tropical rain forest as a highly dynamic ecosystem influenced by natural and human disturbances such as treefalls, droughts, fires, and agricultural clearing.

Pollen grains of maize (*Zea mays*) are present in the upper half of the core (100 - 312 cm), in sediments that appear to represent approximately 300 to 1100 cal. yr BP. These maize pollen grains provide the first direct botanical evidence of prehistoric crop cultivation at La Selva. The period of maize cultivation at the Cantarrana Swamp falls within the La Cabaña regional archaeological period, which is otherwise almost unrecorded at La Selva. Large La Cabaña village sites have been found within 20 km of La Selva, but human populations within the reserve itself may have been relatively small at this time.

Dramatic fluctuations in pollen percentages of *Cecropia* and other secondary forest taxa indicate episodic forest disturbance around the site. Macroscopic charcoal fragments ($> 500 \mu\text{m}$) are present in half of the samples examined ($n = 25$), indicating fires very near to, or within, the swamp basin. The lowest macroscopic charcoal, a large fragment near the base of the core, produced an AMS date of around 3200 cal. yr BP. Microscopic charcoal, though present throughout most of the record, is most abundant in sediments older than about 700 yr BP. This pattern may indicate higher human populations during the earlier part of the sediment record, a conclusion supported by archaeological work. Much of the charcoal is probably related to human activities, but some may signal wildfires that spread into intact forest during exceptionally dry periods. Lightning may also have ignited some fires.

Other aspects of the Cantarrana sediment record also may indicate late Holocene droughts, as have been documented in other parts of Central America, southern Mexico, and the Caribbean. I interpret high percentages of indeterminate (degraded and mechanically damaged) pollen grains to result from oxidation during periods of enhanced seasonal drying of the swamp surface. Matches between indeterminate pollen peaks and peaks in fern spores and charcoal support this interpretation.

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CHAPTER 1

INTRODUCTION

PreColumbian forests of tropical America have been conceptualized by some researchers as "virgin" or "pristine," i.e., undisturbed by people. Others have argued, often without direct fossil evidence, that aboriginal dramatically influenced vegetation patterns. That humans have had some degree of influence on most tropical forests is becoming increasingly clear, but in what ways and to what extent forests have been altered is not yet fully understood. Disturbances not associated with human activity, such as treefalls, floods, and droughts, and in some cases, lightning-set fires, also shape tropical forests. And tropical climates, once thought to have been stable throughout the Holocene, are now known to have undergone significant fluctuations in many areas of the neotropics. Such climatic shifts would have had direct ecological impacts and would likely have influenced human activity and thus human impacts on forests.

Paleoecological records derived from the study of pollen grains, spores, charcoal fragments, and other microfossils, and the sediment matrix in which they are preserved, can provide evidence of human disturbances such as forest clearance, agriculture, and fires, as well as evidence of climate change and other types of environmental change. However, such records are sparse in the neotropics. Consequently, the history of human alteration of forests and long-term patterns of disturbance remain largely unknown for most sites.

The La Selva Biological Station in the central Atlantic lowlands of Costa Rica (10°26' N, 83°59'W) is a key site for research on rain forest environments and biota (McDade *et al.* 1994), especially trees (Hartshorn & Hammel 1994). More than thirty years of study are represented in the recently published compendium, *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (McDade *et al.* 1994). While the modern

ecology of the station is well-studied, researchers have only begun to consider its long-term history, and the degree to which this history might influence present ecological patterns and processes.

Mature forests of the La Selva Biological Reserve were once thought to be undisturbed by humans (Frankie *et al.* 1974, Hartshorn 1983). But discoveries of preColumbian pottery and worked stones along the rivers (Quintanilla 1990, Sol 1998) have shattered the myth of undisturbed forest at La Selva. Archaeological research is revealing a long history of human activity at La Selva, but the ecological implications of this activity will require much further study and clarification.

Understanding the present ecology and successional status of La Selva forests requires a knowledge of past environmental conditions and human activities in the reserve. Some recent and ongoing research at La Selva is addressing that need. Archaeological studies to date have produced evidence of prehistoric occupation of the reserve by at least the La Montaña (3000-2300 yr BP; Quintanilla 1990, Sol 1998). Horn and Sanford (1992 and in preparation) and Harrell (in progress) have found abundant charcoal in La Selva soils. Some of this charcoal, which dates to the late Holocene, may reflect human-set fires related to agricultural activities, cooking, or other intentional burning; other charcoal may reflect wildfires that burned intact forest during exceptionally dry years (Horn and Sanford 1992). A recent landscape-scale analysis of palm distributions implicates later (historical) human populations as agents of forest disturbance, in this case through harvesting activities (Clark *et al.* 1995).

While it now seems clear that forests at La Selva have been subjected to a long history of human disturbance, questions remain about the chronology and nature of past human activity and the degree to which this disturbance has altered the physical and biotic

environment. The disturbance history of La Selva's forests may also include natural disturbances such as treefalls, flooding and other hydrologic change, climatic events and change, and lightning fires. Some of this history can be inferred from studies of modern soil, geology, climate and vegetation, but direct evidence of such changes and events in the past is lacking.

This thesis investigates evidence of human and other disturbances and climatic variability preserved in a 5.9 m sediment core recovered from a La Selva swamp. This core from the Cantarrana ("singing frog") Swamp yielded the first paleoecological record for La Selva and is one of only a few that have been completed in the humid lowlands of Central America. The results of this project add a needed data point to ongoing efforts to reconstruct regional environmental histories for Costa Rica (Horn and others, in progress) and complement the growing compendium of archaeological and ecological knowledge at La Selva.

In this work, I have addressed the following questions. Is there evidence of human and natural disturbance in the Cantarrana sediment record, and if so, how does it compare with other paleoecological and archeological research in Costa Rica and the larger region? What is the record of fire history as indicated by micro- and macroscopic charcoal in the sediments, and how does it compare to records from other neotropical sites? Are climatic shifts or hydrological changes in the swamp indicated and do these fit with climate history as documented elsewhere in the circum-Caribbean region? And finally, is it possible to disentangle the effects of human disturbance from those of natural disturbances, based on evidence in the sediment record?

This thesis is divided into five chapters. Chapter 2 is an overview of the environmental setting of the La Selva Biological Station. The first section discusses some

of the important physical and biotic characteristics of the reserve and the second considers its human history. Chapter 3 describes the Cantarrana core site and explains my research methodology. Chapter 4 details the results, first with respect to the stratigraphy and chronology of the core, and then in terms of the pollen, spore and charcoal analyses. This chapter also includes the pollen diagrams. In Chapter 5, I discuss the results and in Chapter 6, draw general conclusions on the environmental history of the site.

CHAPTER 2

ENVIRONMENTAL SETTING

THE PHYSICAL ENVIRONMENT AND VEGETATION

The La Selva Biological Station is located at the confluence of the Sarapiquí and Puerto Viejo rivers, in the cantón of Sarapiquí, province of Heredia, Costa Rica (10° 26' N, 83° 59' W; Figure 2.1). The 1,536 ha La Selva reserve encompasses an area of physiographic and ecotonal transition between the steep foothills of the central volcanic mountain chain and the extensive Atlantic coastal plain. Elevations range from about 35 m along the rivers on the northern edge of the reserve to 137 m in the steep hills that dominate the southern portion of La Selva.

Soils at La Selva are highly variable with parent material and age accounting for most of the differences in soil types (Sollins *et al.* 1994). All parent materials in La Selva derive from volcanic activity; lava flows have descended the Cordilleran volcanoes periodically over the last two million years, covering most of the land surfaces within the reserve (Sollins *et al.* 1994). Lahars are evident in the general area but are only of minor importance to the geomorphology of La Selva proper. No evidence of ashfall has been detected (Sollins *et al.* 1994). Topographic position is important locally, especially in the development of the distinctive Tropaequept soil complexes found in swampy depressions of the reserve. Both forested and open swamps occur in depressions where drainage is impeded by bedrock (Pringle and Triska 1991). In swampy areas of the reserve, three Tropaequept soil types, Histic, Lithic and Typic, occur in complex interwoven patterns that are apparently unrelated to parent material and soil age (Sollins *et al.* 1994). Histic Tropaequepts form where there is standing water and large amounts of organic material,

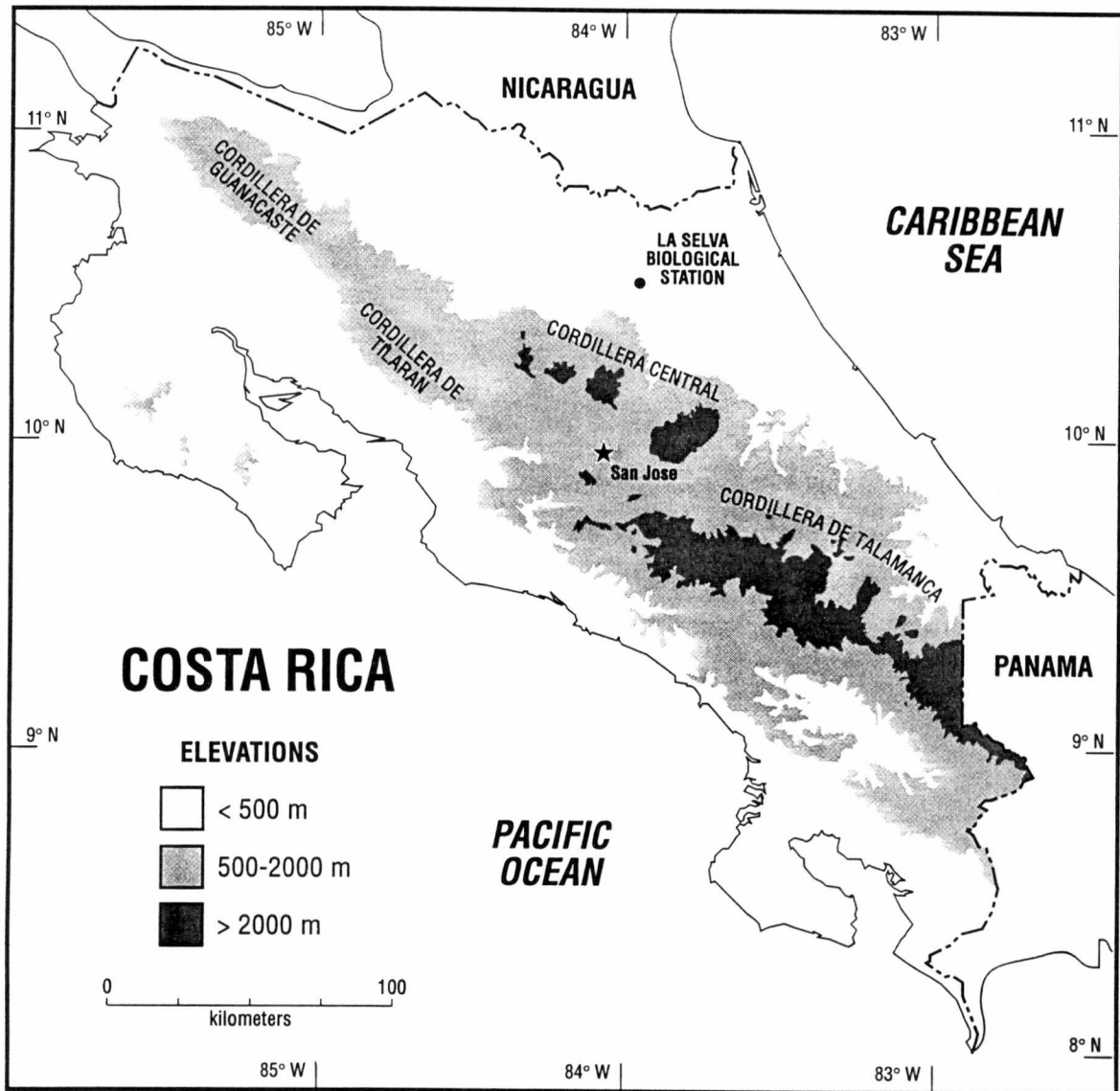


Figure 2.1 Location of La Selva Biological Station, Costa Rica.

Typic in areas with a lower water table, and Lithic where streams have cut down to the bedrock (Sollins *et al.* 1994).

In the climate classification of Herrera (1985), La Selva's climate falls into the $G_{2(a)}$ group, described as very humid, very hot and without a water deficit. A water balance diagram for La Selva (Herrera 1985) shows precipitation values far in excess of potential evapotranspiration in all months except February and March, when they are about equal. The average daily temperature at La Selva is 26.2°C and approximately 4 m of rain falls annually. Precipitation is bimodal with peaks in July and December and the driest period occurring between February and April. A second short and less intense dry season (locally called "veranillo") may occur in September or October, but its regularity and severity are not well documented (Sanford *et al.* 1994, Newstrom *et al.* 1994).

Between 1963 and 1991, average annual precipitation ranged from a low of 2605 mm (1983) to a high of 5,659 mm (1970) (Sanford *et al.* 1994). Moisture-laden trade winds and cold air drainage down the slopes of the adjacent volcanoes contribute to canopy condensation and drip during most nights, providing even more humid conditions than would be expected from precipitation data (Hartshorn and Hammel 1994). Monthly rainfall totals almost always exceed 100 mm, even during the dry season. Nevertheless, soil moisture can be significantly reduced during the dry season (Sanford *et al.* 1994).

The long-term average period between rainfall events (defined as amounts >5 mm, see below) during March and April is about 12 days (Sanford *et al.* 1994). Sanford *et al.* (1994) use a value of 5 mm as a threshold for significant rainfall events because most lighter precipitation is intercepted by the canopy and does not contribute significantly to soil moisture. The most extreme drought on record occurred in April 1983, when thirty days

passed with daily rainfall totals ≤ 5 mm and the monthly total fell below 10 mm (8.8 mm). The monthly mean precipitation for April (1963-1991) is 202.4 mm. Extreme events such as the one in April 1983 may be important to ecosystem function and structuring of communities (Sanford *et al.* 1994, Bawa and McDade 1994). The April 1983 drought occurred during an El Niño year, but not all El Niño years lead to dry conditions in the Atlantic lowland region (Quesada 1992).

A detailed forest typing study (Hartshorn and Peralta 1988) placed the entire La Selva reserve within the tropical wet forest life zone of the Holdridge bioclimatic classification (Holdridge 1967). The reserve contains classic rain forest vegetation: a species-rich, multi-layered community with diverse and abundant trees, lianas, epiphytes, and broad-leaved monocots. As of 1988, 1678 naturally occurring vascular plants had been identified in the reserve, of which approximately 323 were tree species (Hartshorn and Hammel 1994). While much of the flora of La Selva has already been documented (Hammel and Grayum 1982, Wilbur and collaborators 1994), only trees, the focus of a large number of studies, are thought to be completely known. Lianas, the growth-form most difficult to collect, are the least well known. About 220 weedy exotic species flourish in disturbed areas of the reserve; among these, grasses (Poaceae) and composites (Asteraceae) are particularly speciose (greater than 70 species combined). The overall flora is estimated at nearly 2000 species (Hartshorn and Hammel 1994).

Vegetation patterns at La Selva are influenced by topographic and edaphic complexity as well as by historical land uses (Clark *et al.* 1995, Bawa and McDade 1994, Hartshorn and Hammel 1994). Ridgetops contain the highest numbers of species, while species richness and vegetation density is reduced on less well-drained sites (Lieberman *et al.* 1985). Swamp forests in the reserve are noted for their lack of upland species and a disproportionate abundance of species, such as *Carapa guianensis*, *Pterocarpus officinalis*,

and *Astrocaryum alatum*, that are tolerant of waterlogged soils (Hartshorn and Hammel 1994).

Before 1968, some of La Selva's forests were selectively logged while others were converted to plantations of laurel (*Cordia alliodora*), cacao (*Theobroma cacao*), pejibaye (*Bactris gasipaes*), and banana (*Musa paradisiaca*), or to cattle pastures (Pierce 1992). These recent land uses have resulted in a mosaic of vegetation types that includes intact, mature forest (about 55%), moderately high-graded forests, secondary forests, early successional forests, and abandoned plantations, as well as managed habitats associated with the biological station (see Figure 2 in McDade and Hartshorn 1994). Prehistoric people also have used the forests of La Selva, particularly its alluvial soils (see next section). However, some areas of the reserve, such as the Reserva Ecológica Rafael Chavarría in which my research site is located, are thought to have been undisturbed for "extended periods" (McDade and Hartshorn 1994).

La Selva's forests are unique among tropical rain forests because of the abundance of one tree species, *Pentaclethra macroloba*. This leguminous canopy tree is so common that tree diversity is often masked at the local scale. Importance values for *Pentaclethra* range from about 18%-20% in primary forest on all three major types of terrain at La Selva: rolling uplands, old terraces, and swamps (Hartshorn and Hammel 1994). No other species has importance values more than half as high. As in many other neotropical forests, leguminous trees are species-rich at La Selva: the family accounts for 13% of the total number of tree species. La Selva is also noted for its unusually high diversity of epiphytes (mostly pteridophytes and monocots), which account for 23% of all vascular plant species (Hartshorn and Hammel 1994). Like most tropical rain forests, La Selva has a high incidence of plant species that occur in low numbers. Detailed descriptions of vegetation types and patterns are included within chapters of the recently published

compendium, *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (McDade *et al.* 1994).

Pteridophytes contribute more species to La Selva's floristic richness than any other group. A recent inventory (Grayum and Churchill 1987) documented 173 species in 45 genera, a higher species richness than for biological reserves of Barro Colorado Island, Panama and Manaus, Brazil--sites that are often compared to La Selva (Hartshorn and Hammel 1994). Almost three quarters of La Selva's fern species belong to the Polypodiaceae, the largest vascular plant family in the reserve (Grayum and Churchill 1987). No La Selva pteridophyte species are known to be endemic to Costa Rica, probably due to efficient wind-dispersal of fern spores (Grayum and Churchill 1987). While ferns are regular components of the understory in most La Selva habitats, they are also often temporary colonists in disturbed or weedy sites in primary or secondary forest, and along the landslide-prone banks of the Ríos Puerto Viejo and Sarapiquí (Grayum and Churchill 1987).

HUMAN HISTORY

The earliest evidence of human presence in Costa Rica comes from fluted projectile points, scrapers and other lithic artifacts found in a paleo-Indian quarry near Turrialba on the eastern slopes of the Cordillera Central (Snarskis 1984). These artifacts, believed to date to around 10,000 yr BP, are thought to have been left by nomadic hunter /fisher /gatherers. Archaeological evidence of human activity over the next several millennia is sparse. Sedentism and ceramic production are not documented in the central Atlantic watershed until about 3000 yr BP.

The La Montaña regional archaeological period (about 3000-2300 yr BP) is characterized by flat raised-rimmed griddles that are identical to ones found in South

American sites (Brazil, Venezuela, and Colombia) where they were used to process manioc (*Manihot esculenta*) (Snarskis 1984). Both crop types and agricultural techniques used in the preColumbian Atlantic lowlands during this and later periods appear to have had strong South American influences (Hall 1985). Tubers such as manioc and tiquisque (*Xanthosoma violaceum*), and the cultivation of pejobaye (peach palm, *Bactris gasipaes*) and cacao (*Theobroma cacao*), were apparently introduced from South America (Snarskis 1984).

The small size and widely dispersed nature of La Montaña sites in Costa Rica may signify that large tracts of land were needed for subsistence during this period. Quintanilla (1990) characterized people of this period as incipient agriculturalists subsisting on cultivated tubers and fruits harvested from the surrounding forests. Snarskis (1984) however, postulated that La Montaña-phase people were more experienced farmers, and the last to depend primarily on root and tree crops; later populations would begin to depend more on maize (*Zea mays* L.) cultivation. The presence of maize pollen in sediments of Laguna Bonillita in the Reventazón Valley reveals maize cultivation as early as about 2500 ¹⁴C yr BP in the Central Atlantic watershed (Northrop and Horn 1996).

Sites from the next archaeological period, El Bosque (2300-1500 yr BP), are larger and vastly more numerous than sites from earlier periods. Snarskis (1984) has inferred from the archaeological record that this was a time of explosive population growth in the Atlantic lowlands of Costa Rica. Stone (1956) envisioned the El Bosque period people as a purely root- and tree-crop subsistence culture with maize relegated to a minor, possibly even ceremonial role. However, Snarskis (1984) interpreted more recent archaeological data, especially the high frequency of unrimmed metates (millstones used for grinding grain, especially maize) and loaf-shaped manos (instrument used for crushing of grain on the metate) in El Bosque sites, as evidence for a maize-centered agriculture. The pollen

evidence from Laguna Bonillita (Northrop and Horn 1996) and macrobotanical evidence of maize and other cultigens from other El Bosque sites (Blanco and Mora 1994, and references therein) support this interpretation. Snarskis (1984) attributed population growth during the El Bosque period to the adoption of full-scale maize agriculture, possibly with improved varieties, and the rapid colonization of fertile alluvial soils.

The next archaeological period in the Central Atlantic region of Costa Rica is the La Selva period (the name is unrelated to the name of the biological station). Lasting from about 1500-1000 yr BP, this archaeological phase is marked primarily by the introduction of gold metallurgy and drastic changes in material culture including stylistics of ceramics and possibly house types (Snarskis 1984). Carbonized maize remains from one La Selva-period site were identified by Galinat as a slender, moisture-resistant race of popcorn similar to races from Peru and Colombia (Snarskis 1984). While some may consider this type of maize primitive, Snarskis (1984) considered it to be highly developed and interpreted it as further evidence that maize agriculture was well established even before this period.

The final preColumbian archaeological period identified for the Central Atlantic watershed is the La Cabaña period (1000-450 yr BP), a time of the nucleation of settlements into ceremonial centers (Snarskis 1984, Quintanilla 1990). Highly organized caciques, or chieftains, ruled eastern Costa Rica from about one thousand years ago until the arrival of the Spaniards in the 16th century. Settlement patterns, which had earlier been associated with proximity to biotic resources and fertile alluvial soils, appear to have been more random during the La Cabaña period (Snarskis 1984). Snarskis (1984) argued that the apparent change in settlement patterns indicates the predominance of sociopolitical boundaries and defense over agricultural considerations. Subsistence systems were probably similar to those described for earlier periods; Spanish explorers commonly

reported polycropping of maize and various root and tree crops (Snarskis 1984).

Cubujuquí, a site dating to the La Cabaña period, is located only about 20 km from the La Selva Biological Reserve in Horquetas. Analyses of ceramics indicate a short but intense occupation of the site beginning around 1000 yr BP and ending with site abandonment around 650 yr BP, 200 years prior to the Spanish Conquest (Gutierrez and Mora 1988).

Archaeological research in the La Selva reserve has revealed that sedentary agricultural groups had settled the alluvial terraces at least by the La Montaña period (3000-2300 yr BP; Quintanilla 1990, Sol 1998). Most of the archaeological evidence presently available from La Selva, as well as that for surrounding areas of the cantón of Sarapiquí (Quintanilla 1990), is associated with the El Bosque (2300-1500 yr BP) and La Selva (1500-1000 yr BP) periods. Although the later La Cabaña period is represented at Cubujuquí and other sites near La Selva (Gutierrez and Mora 1988, Quintanilla 1990), very little archaeological evidence from this period has been found at La Selva. The first archaeological study of the area found no La Cabaña artifacts (Quintanilla 1990). In a preliminary report on more recent archaeological work at La Selva, Sol (1998) reported that human occupation of the Atajo site along the Río Sarapiquí, seems to have extended into the earliest part of the La Cabaña period. However, the ceramic evidence upon which Sol based this suggestion is still under study.

Prior to recent archaeological work and studies of soil charcoal and tree distributions, mature forests of La Selva were generally described as "virgin" or undisturbed by people (Frankie *et al.* 1974, Hartshorn 1983). Small amounts of charcoal have been found in soils in many areas of La Selva (Horn and Sanford 1992; Sol 1998; S. Horn and R. Sanford, unpublished data; Harrell, in progress). The patterns of charcoal distribution suggest that prehistoric people burned forests even far away from likely habitation sites on alluvial terraces (Kennedy and Horn 1997). Radiocarbon dating of

charcoal in soil cores collected outside of known archaeological sites indicates fires at about 2400 yr BP that may have been accidentally or intentionally ignited by people or by lightning (Horn and Sanford 1992, and in preparation). Charcoal dating to around 2400 BP was also found within one of the archaeological sites identified by Quintanilla (1990; site 8 in Horn and Sanford 1992).

In a recent study of the distribution of palms, spatial patterns of *Iriartea deltoidea*, a species favored by indigenous people and early settlers, revealed another type of “footprint” of human activity in the forest (Clark *et al.* 1995). Clark *et al.* found *Iriartea* to be conspicuously absent on alluvial soils near sites of recent (historical) human habitation while present on other alluvial soils in the reserve. They attributed the unusual distribution of *Iriartea* to a protracted time of intense harvesting, probably before the station was protected in the early 1980s. Although in this instance the human disturbance was probably modern or historical, it is conceivable that similar activities in prehistoric times have also left imprints on La Selva's modern landscape.

Butterfield (1994) has reviewed the recent history of the region encompassing the La Selva Biological Station. Throughout postColumbian times, up until the 1970s, population densities in the Atlantic lowlands were low, with intensive land use restricted to the richer alluvial soils along the main rivers. During the 1970s however, improved access (roads, bridges and telephone lines) opened up the agricultural frontier in Sarapiquí. Colonization projects begun in the 1960s allowed people to claim land that they cleared of forest; settlers maintained their claims and kept their land clear by grazing cattle. Over the next twenty years pastures expanded while forest shrank in conjunction with increasing populations in the region. The agricultural frontier closed in the 1980s, as unclaimed forested land finally disappeared. Presently, over 50% of the cantón of Sarapiquí belongs to large farms (mostly cattle ranches) with absentee owners, with the rest in small farms

owned by locals. Little forest remains in the Sarapiquí except in reserves such as the La Selva Biological Station.

Dr. Leslie Holdridge, a conservation-minded tropical forester, acquired the core of the La Selva reserve (587 ha) in 1953 to experiment with tree crops that could be incorporated into native forests. To test his early ideas about sustainable, nondestructive uses of rain forest, Holdridge planted economically useful native species such as laurel (*Cordia alliodora*), pejibaye (*Bactris gasipaes*), cocoa (*Theobroma cacao*), and robusta coffee (*Coffea canephora*). Most of his plantings were on previously disturbed alluvial soils and consequently his work left much of the mature forest intact. The Organization for Tropical Studies (OTS), then a fledgling consortium of U.S. universities interested in tropical research, bought La Selva from Holdridge in 1968. OTS has tripled the size of the reserve and made vast improvements in its infrastructure including an extensive trail network (about 50 km). La Selva is now a major tropical field station with average use exceeding 45 persons/day (McDade and Hartshorn 1994).

A detailed survey of the reserve in 1991 resulted in a 50 x 100 m grid system covering the entire property with permanent monuments at all grid points. These data, along with elevation and other geographically referenced data (e.g., soils) are stored in a computer-based Geographic Information System at the station.

CHAPTER 3

CORE SITE AND METHODS

CORE SITE

Between 1991 and 1994, Sally Horn and others collected sediment cores from four swamps at La Selva for paleoecological analysis. I participated in the February 1994 coring of the Research Swamp, and made observations on vegetation and water levels in all four swamps in August 1994 (Cablak *et al.* 1994). All of the sites are on terraces of the Río Puerto Viejo (Figure 3.1). The Suampo site is a forested swamp dominated by *Pentaclethra macroloba*. The other three swamps (Cantarrana, Research Swamp, and Machita (unofficial name)) have open canopies. Some open swamps within areas of the reserve that were formerly pasture are thought to have resulted from forest conversion. However, the Cantarrana, Research, and Machita swamps, like most in the reserve, are considered to be natural (Hartshorn and Hammel 1994).

This thesis reports on the analysis of pollen grains, fern spores, and charcoal preserved in a 5.9 m sediment core recovered from the Cantarrana Swamp in 1992. I selected this core for analysis because it is the longest and most complete (i.e., with fewest gaps) of the sediment cores from La Selva, and because initial laboratory work showed good to very good pollen preservation. I also chose this core because the Cantarrana site appears not to be affected by subsurface inflows of geothermal groundwater, which can contaminate sediments with isotopically dead carbon of volcanic origin, and hence interfere with the use of radiocarbon analyses for core dating. While not all the core sites have been studied, it appears that geothermal waters may influence the Suampo site (Pringle and Triska 1991; S. Horn, unpublished data).

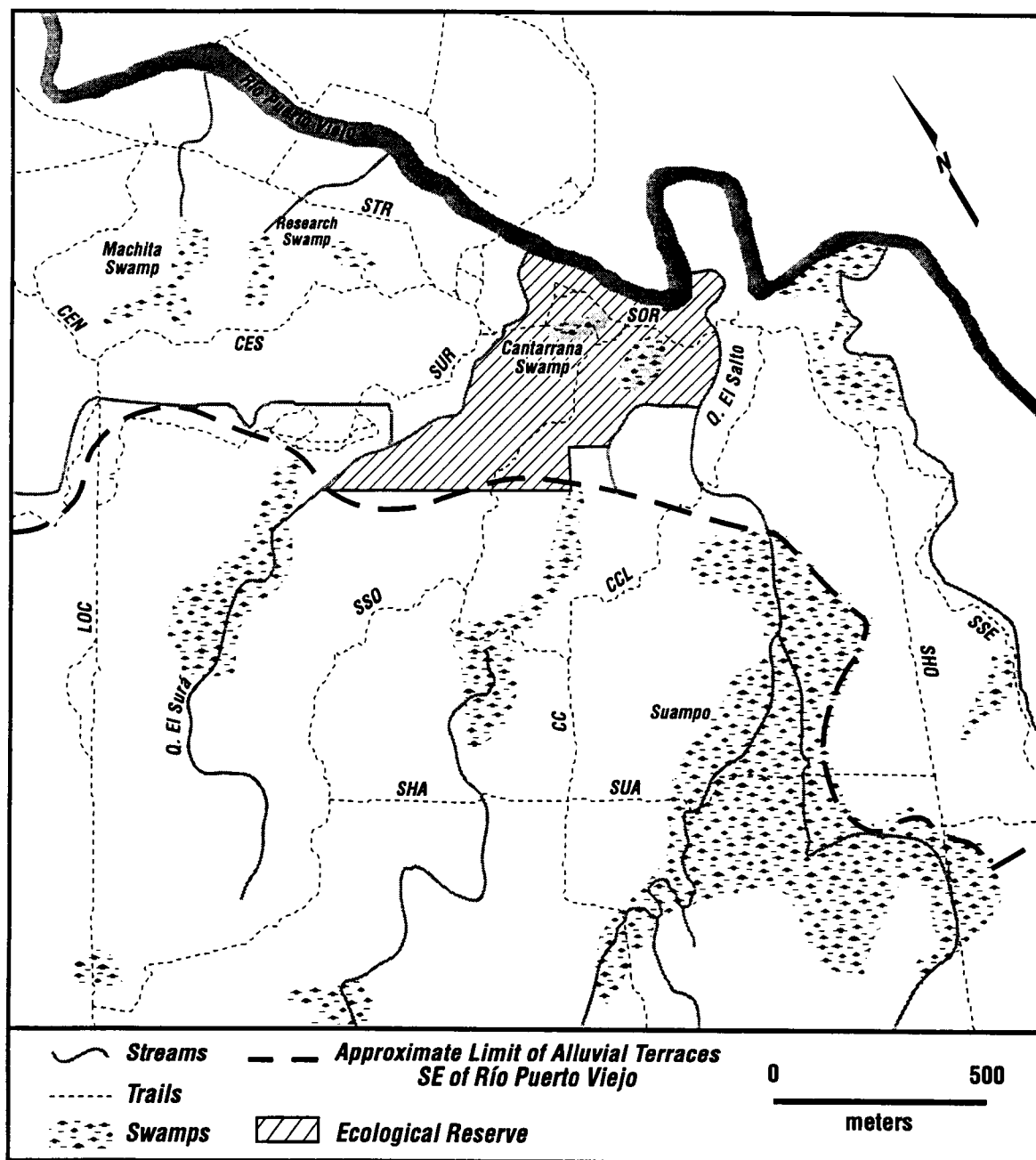


Figure 3.1 Swamps within the northern section of "Old La Selva." Sediment cores for paleoecological analysis have been recovered from the Machita, Research, Cantarrana, and Suampo sites. After La Selva GIS and maps in McDade *et al.* (1994). Río Puerto Viejo flows toward the northwest.

The 0.5 ha Cantarrana Swamp (Figure 3.2) is located on a lower terrace (elevation about 36 m) of the Río Puerto Viejo (Sollins *et al.* 1994) within the Reserva Ecológica Rafael Chavarría. This area has been designated an "absolute preserve" that is not available for research without special permission. Walking through the swamp is not permitted, but an elevated walkway across the swamp provides access. The sediment core from this site was taken near the walkway while standing on wood planks laid down on the surface of the swamp. Special permission for coring was granted by the La Selva Advisory Committee in recognition of the potentially unique value of the study.

The vegetation of the Cantarrana Swamp is dominated by low perennial herbs, with one aroid, *Spathiphyllum friedrichsthali*, particularly abundant. Scattered shrubs and trees, especially *Pentaclethra macroloba*, are also present but the persistence of standing water appears to impede woody colonization/survival. Appendix A is a provisional species list for the swamp and adjoining forest compiled by station naturalist Orlando Vargas.

METHODS

Sally Horn, Robert L. Sanford, Jr., and assistants from the University of Tennessee and University of Denver raised a 588 cm sediment core from the Cantarrana Swamp in 1992 using a square-rod piston corer (Wright *et al.* 1984). The core sections were extruded and wrapped in plastic and foil in the field, and sealed in protective plastic tubes for transport to the University of Tennessee, where they were X-rayed and then stored at 8° C. I recorded the stratigraphy of the core by noting changes in color and texture. Sediment samples (0.25 cm³) taken at approximately 8 cm intervals were processed for pollen analysis using standard procedures (Appendix B; HCl, HF, KOH, acetolysis, safranin stain; Berglund 1986). *Lycopodium* spores were added to determine pollen concentrations and influx values (Stockmarr 1971). Duplicate samples were dried

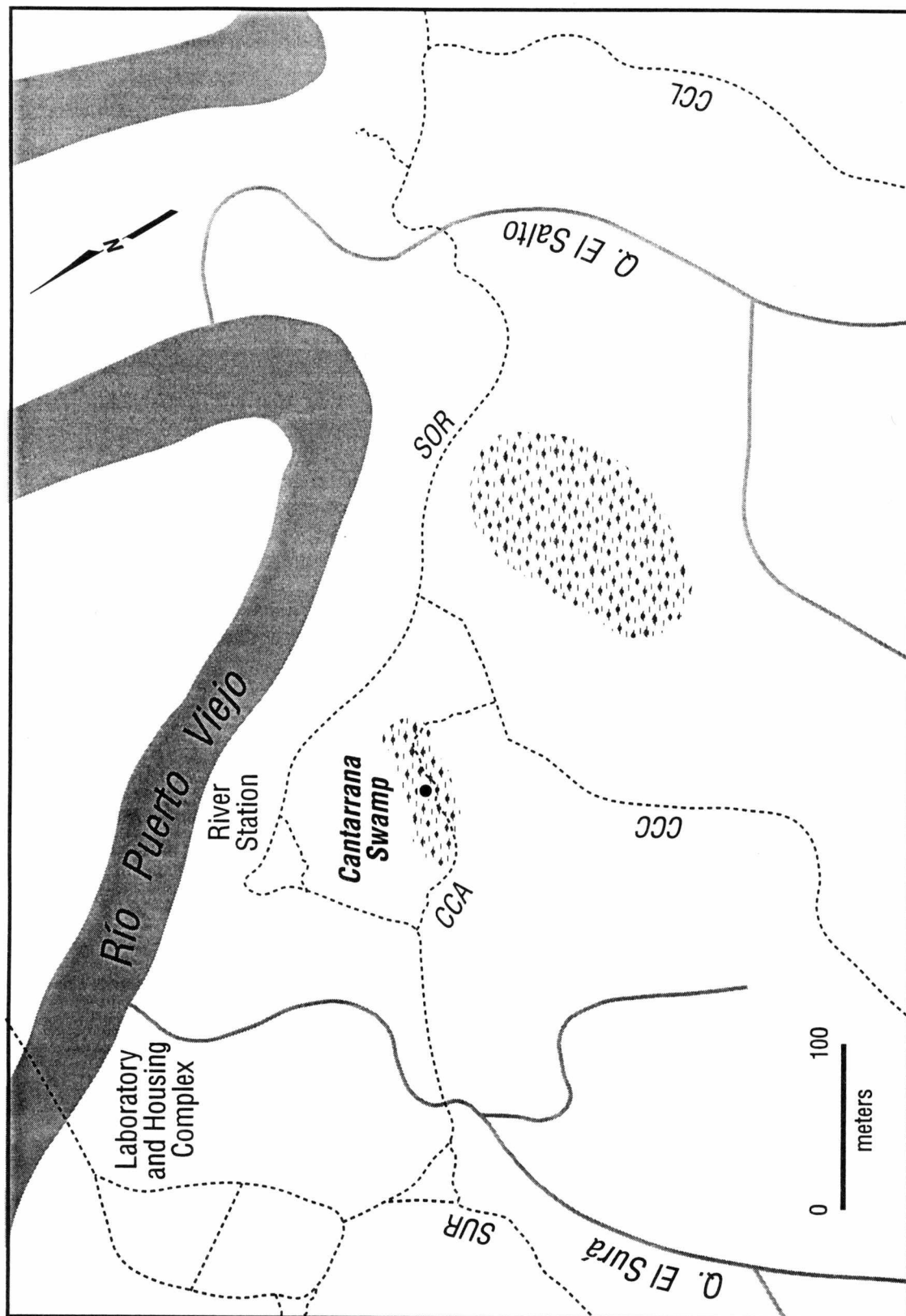


Figure 3.2 Location of Cantarrana Swamp and core site (•). After La Selva GIS and maps in McDade *et al.* (1994).

at 100° C overnight and ignited for 1 hour at 550° and 1000° C (Dean 1974) to measure water content, organic matter and carbonate content. Five samples of organic material were submitted for radiocarbon dating: three to Beta Analytic and two to the National Ocean Sciences AMS facility. Two of the dated samples were large wood fragments (one charred); the others were *Pentaclethra* leaflets and macroscopic charcoal sieved from the sediments.

The Cantarrana sediment core was recovered using successive one meter drives with the piston corer. Recovery was 80-97% in all but the first meter, which upon extrusion was only 48 cm long. Later experimentation in the Research Swamp using the same piston corer produced similar results in the near-surface section of that swamp. (Our special permission to core the Cantarrana Swamp did not allow for additional coring of that site). I interpreted the abbreviated length of the first core section to be caused by compaction. I adjusted sampling depths as if the compaction had occurred consistently over the 48 cm core, using a factor of 2.08. If the short length of the first section of core is actually due to a gap rather than compaction, depths on the pollen diagram would change but the interpretation would not be materially affected.

Residues from the chemical processing were mounted on microscope slides in silicone oil. I counted pollen grains, fern spores and charcoal fragments at a magnification of 400x to a minimum sum of 300 pollen grains, exclusive of indeterminates and spores. Complete counts were made from 24 levels in the core spaced 8-24 cm apart. I scanned slides from additional levels for maize pollen (see below). The pollen, spore, and charcoal data were plotted with a modified version of CalPalyn (Bauer *et al.* 1991).

I identified pollen types by comparison to a pollen reference collection prepared from vouchered plant specimens collected at the La Selva Biological Station and in other

areas of Costa Rica and the Latin American tropics. I also used published keys and descriptions of neotropical pollen types (especially Heusser 1971, Bartlett and Barghoorn 1973, Hoogheimstra 1984, Horn 1986, and Roubik and Moreno 1991). Pollen identification was greatly aided by the excellent photomicrographs and morphological descriptions of the pollen and spores of Barro Colorado Island, Panama in Roubik and Moreno (1991).

I identified pollen to the lowest possible taxonomic level, but the pollen richness of the sediments was so great that in many cases rare types were grouped together for the purpose of data analysis and display. For example, I recognized a few pollen grains from certain genera of the Rubiaceae (e.g. *Warszewiczia* and *Sabicea*) but for the pollen diagrams these were grouped together as Rubiaceae. Taxonomy and nomenclature follows Wilbur *et al.* (1994) except that alternate family names are used for Gramineae (Poaceae), Palmae (Arecaceae), Leguminosae (Fabaceae), Guttiferae (Clusiaceae), and Compositae (Asteraceae). For taxa not covered in Wilbur *et al.* (1994), taxonomy follows the Flora Costaricensis series (Burger 1977-1995), or if not covered there, Standley (1937-1938).

Pollen grains representing the Urticales order, which includes a large number of genera in the Moraceae, Urticaceae, Ulmaceae and Cecropiaceae families, are abundant in the Cantarrana core. The order is well represented in Costa Rica and includes trees, shrubs, vines and herbs that grow in mature and successional forests and more open areas in both the lowlands and the mountains (Burger 1977a, 1977b, 1977c). Many Urticales pollen types are small, psilate or scabrate grains that are often dispersed by wind, except in the case of *Ficus* which is insect pollinated (Ramirez 1969). There is a great deal of overlap in the morphologies of pollen grains from the Urticales and only a few genera can be readily distinguished (Byrne and Horn 1989, Roubik and Moreno 1991). I differentiated *Cecropia*, *Ficus*, *Trema*-type and *Celtis*-type. *Trema* and *Celtis* were

considered “types” because while their pollen appears to be distinctive, a study of reference samples from Costa Rican species showed some overlap in morphology with other genera (J. Rodgers III, unpublished data). *Ficus* counts in this study include only oblate (lozenge-shaped) grains (Horn and Ramirez 1990). *Ulmus* and *Dorstenia* are also distinctive types in the Urticales order, but no pollen grains of these genera were observed. Other Urticales pollen grains were classified by pore number: diporate, triporate, 4-porate and polyporate. Pollen grains that were identifiable as Urticales but for which pore number could not be determined (most common in the case of damaged pollen grains) were classified as “undifferentiated Urticales”. Some of the genera possibly represented by these pollen morphotypes are listed in Appendix C.

Indeterminate pollen grains are those that cannot be identified due to postdepositional chemical, biochemical, and/or mechanical damage that obscures the key characteristics of the grain. I classified indeterminate grains with reference to the major factors contributing to their indeterminate status (corrosion, degradation, mechanical damage or concealment by detritus; Delcourt and Delcourt 1980). Rather than using the combined categories of Delcourt and Delcourt (1980) (e.g., degraded and corroded, degraded and mechanical damage), I classified each indeterminate grain by the type of deterioration that I thought most contributed to its indeterminate status. I did, however, take note of levels in which there were many grains that were both mechanically damaged and degraded, the only common case of combined factors that I encountered.

For unknown pollen grains, I assigned each morphotype a number, described and roughly sketched its morphology, and recorded the coordinates of examples on the microscope slides to facilitate reexamination. The identification of one morphological class of pollen grains, the tricolporate reticulate grains, is especially problematic (Horn 1986, Roubik and Moreno 1991). Taken through the pollen key for Barro Colorado Island

(Roubik and Moreno 1991), these characters can lead to as many as a dozen possible families. Horn (1985) and Horn and Rodgers (1996) have referred to this class of pollen grains as the "ERA" group, after three families that produce this type of pollen in Costa Rica (Euphorbiaceae, Rutaceae, Anacardiaceae). Other speciose and abundant families that produce this type of pollen in the Atlantic lowlands of Costa Rica include Fabaceae (Papilionoideae), Flacourtiaceae, and Rubiaceae.

Because of the tremendous diversity of pteridophytes in tropical wet forests, overlapping spore morphologies, and commonly poor preservation of important surface characters, it was infeasible or impossible (using light microscopy) to assign generic or family names to most of the fossil spores contained in the Cantarrana sediments. I classified fern spores by morphology (shape and surface characteristics) except in a few cases of distinctive genera such as *Danaea*, *Cyathea* and *Pteris*. Altogether, I had 18 categories (3 genera and 15 morphological types) of fern spores.

Charcoal particles were tallied on the standard pollen count transects in two size classes (5-25 μm and >25 μm in maximum dimension). I counted as charcoal only black, completely opaque, angular fragments to ensure origin by fire. Some samples contained many particles that appeared to be partially burned plant fragments (black, opaque and angular with orange from the safranin stain still visible), but I took a conservative approach and did not include these in the counts. I used *Lycopodium* control spore counts and water content data to convert the charcoal counts to dry weight concentrations (fragments g^{-1} dry sediment).

To check for the presence of macroscopic charcoal, I sieved sediment samples from all of the counted levels of the core. I cut 2 cm disks (5 cm core diameter) from around the sample level (e.g. for level 272 cm, I cut 271-273 cm) and removed half of the disk to

sieve, retaining half for archival purposes. In a few levels (100 cm, 416 cm, 464 cm and 588 cm), I removed only half of a 1 cm disk in order to preserve more of the core for possible radiocarbon dating or for other uses. Each sample was approximately 20 cc of sediment, or 10 cc in the case of the half disks. In removing sections from the uppermost meter of the core I did not take core compaction into consideration; thus the reported intervals are wider than for other levels. I washed the samples through nested 500 μm and 250 μm sieves. Examination of the material caught on the sieves confirmed the presence/absence of charcoal; I recorded these data for each sieve size and preserved samples of the charcoal on microscope slides, or in vials or plastic cases in silicone oil.

To obtain more detailed information on agricultural history, I prepared from 1 to 6 slides from each of 67 levels to scan at 100x magnification to detect the presence of maize pollen and microscopic charcoal. Because the concentration of maize pollen grains was so low in most levels, I examined a minimum of 3 slides to determine whether maize was present. I separated *Zea* pollen from other grass pollen by grain and pore size and exine character. The *Zea* grains in the Cantarrana core were 63-87 μm in diameter, with pores 10-14 μm in diameter and tectate exines. These dimensions are within the size ranges of modern and archaeological samples of maize pollen from Mexico and Central America (Ludlow-Wiechers *et al.* 1983).

CHAPTER 4

RESULTS

SEDIMENT STRATIGRAPHY AND RADIOCARBON ANALYSES

Core Description

The Cantarrana sediment core is composed primarily of clay and silt with variable organic content (8% - 37%). Wood fragments, charcoal, *Pentaclethra* leaflets, and seeds and other plant fragments are abundant in many levels. The most organic sections of the core are black, very dark brown, or very dark grayish brown (Munsell 10YR 2/1, 2/2, 3/2). Less organic layers are mostly between dark brown and dark gray (Munsell 10YR 3/3 and 4/2, 7.5YR 3/2, 3/0). Near the bottom (at 540 cm), the sediment becomes a mottled mixture of dark brown clay (10YR 3/1) and yellowish brown (10YR 4/4) silty to sandy clay. Color changes are reflected in a general way by the curve for organic content, with darker sediments correlating with higher organic levels. At the fine scale, however, X-rays revealed more subtle and complex patterns in sediment character.

The base of the Cantarrana core (575-588 cm) is alluvium composed of a variety of differentially weathered and mechanically fragmented rock debris (G. Michael Clark, pers. comm., March, 1997). The mostly sand-sized particles are primarily volcanic, but also include sedimentary and metamorphic rocks. The alluvial material at the base of the core indicates that the Cantarrana Swamp was probably part of a stream channel around 3000 years ago. The stream flowing through it may have been the Río Puerto Viejo (the swamp is located on its lowest terrace; Sollins *et al.* 1994), or alternatively the nearby Quebradas Surá or Salto (Figure 3.1). The terrace that includes the Cantarrana Swamp has flooded occasionally in recent history (Sollins *et al.* 1994) and may have done so throughout the record of this sediment core.

Radiocarbon Chronology

The first four radiocarbon determinations, a standard date on wood (β -54281) and three Accelerator Mass Spectrometry (AMS) dates on organic macrofossils (OS-3545, OS-4410, OS-4411) indicated a normal stratigraphic sequence (Table 4.1). However, sedimentation rates appeared to be much lower in the lowest meter of the core. Sediment in the upper 465 cm of the core accumulated at approximately 0.3-0.45 cm/yr, while the lowest meter or so of the record apparently accumulated at only 0.06 cm/yr. If sediments are missing from the top meter of the core (rather than compacted) as discussed in the "Methods" section of Chapter 3, sedimentation rates would have been lower in that part of the core (around 0.23 cm/yr.).

To better understand the sedimentation of the lower part of the core, an additional AMS date was obtained on *Pentaclethra* leaflets from the 504-506 cm interval. As shown in Table 4.1, the date for that sample is younger than that for two samples from the fourth meter of the core (412-417.5 cm and 464-466 cm).

The most likely explanation is that this younger date is the result of contamination during or prior to the coring. When extracting macrofossils from the Cantarrana core for dating, every attempt was made to avoid material near the edges of the core, which could have adhered to the core barrel and have been carried downward during the coring. But it is nevertheless possible that the dispersed *Pentaclethra* leaflets extracted from the 504-506 cm sample included some much younger leaflets carried down from higher levels of the core, or from the modern surface, where such leaflets are abundant.

It is also possible that contamination could have resulted from human activity within the swamp. During times more recent than that represented by the 504-506 cm level, people could have dug holes or ditches in the swamp that might have caused younger

Table 4.1 Radiocarbon Determinations on Organic Material from Cantarrana Swamp

Lab Number	Depth (cm)	Material Dated	$\delta^{13}\text{C}$	Uncalibrated ^{14}C Age (^{14}C yr BP)	Calibrated Age Range (cal. yr BP) $\pm 1 \sigma$	Calibrated Age Range (cal. yr BP) $\pm 2 \sigma$
OS-4410	222-224	CWF	28.47	805 $\pm$ 35	729 (701) 671 ¹	771-664 ¹
β -54281	412-417.5	WF		1570 $\pm$ 70	1531 (1415) 1354 ¹	1605-1308 ¹
OS-3546	464-466	PL	29.27	1620 $\pm$ 30	1536 (1523) 1503 ¹	1556-1410 ¹
β -95592	504-506	PL	30.20	1250 $\pm$ 40	1240 (1171) 1089 ¹	1276-1064 ¹
OS-4411	561-562.5	CF	28.21	3030 $\pm$ 30	3320 (3214) 3167 ²	3338-3086 ²

Analyses were performed by National Ocean Sciences AMS facility (OS numbers) and Beta Analytic Laboratory (β numbers). Errors represent 68% probability.

CWF = charred wood fragment, WF = wood fragments, PL = *Pentaclethra* leaflets, CF = charcoal fragments.

¹ Stuiver and Pearson 1993

² Pearson and Stuiver 1993

sediment (and material preserved therein) to be buried beneath older sediments. Regarding the original issue of the sedimentation rate in the lowest meter of the core, it is possible that the apparently lower rate of sediment accumulation reflects post-depositional losses of sediment. It may be that some time slices between about 3200 and 1500 yr BP are missing from the record. Loss of sediments could have occurred due to droughts that might simultaneously decrease organic matter production and increase organic matter decomposition within the swamp, or fire which could destroy organic material. Ongoing analyses of sediment cores from the Machita Swamp at La Selva (Horn and Kennedy, in progress) may shed further light on this possibility.

POLLEN, SPORE AND CHARCOAL ANALYSES

A summary pollen diagram showing curves for selected individual taxa and composite groups (described below), indeterminate pollen, fern spores, and charcoal is presented in Figure 4.1. Figure 4.2 shows curves for fern spores, unknown pollen, individual classes of indeterminate pollen, pollen concentrations, organic content, charcoal and maize pollen. Individual taxonomic and morphological groups that belong to the order Urticales are presented in Figure 4.3. Figures 4.4 and 4.5 show curves for selected lowland tropical forest taxa (primarily arboreal). Arboreal taxa represented by less than five pollen grains in the entire record are not plotted, but are included in Appendix C. Curves for pollen types representing primarily nonarboreal taxa (grasses, sedges, forbs, small shrubs and epiphytes) are presented in Figure 4.6 and those for members of the Premontane and Montane group are shown in Figure 4.7.

Curves for all pollen types other than indeterminates are based on total pollen counts excluding fern spores and indeterminates. Fern spores are expressed as percentages of the total counts of pollen (excluding indeterminates) plus fern spores. Indeterminate pollen counts are expressed as percentages of the total pollen count including indeterminates. Charcoal concentrations are expressed as fragments per gram dry sediment in two size classes. Figure 4.1 graphs all charcoal together, while Figure 4.2 plots data separately for fragments 5-25 μm and >25 μm in maximum dimension.

Pollen Preservation and Concentrations

Pollen preservation varied substantially throughout the core. Overall, 17% of all the pollen grains counted (9434) were classified as indeterminates. For this report, indeterminate pollen grains that are damaged beyond taxonomic recognition by mechanical processes, or by degradation or corrosion, are shown both individually and grouped

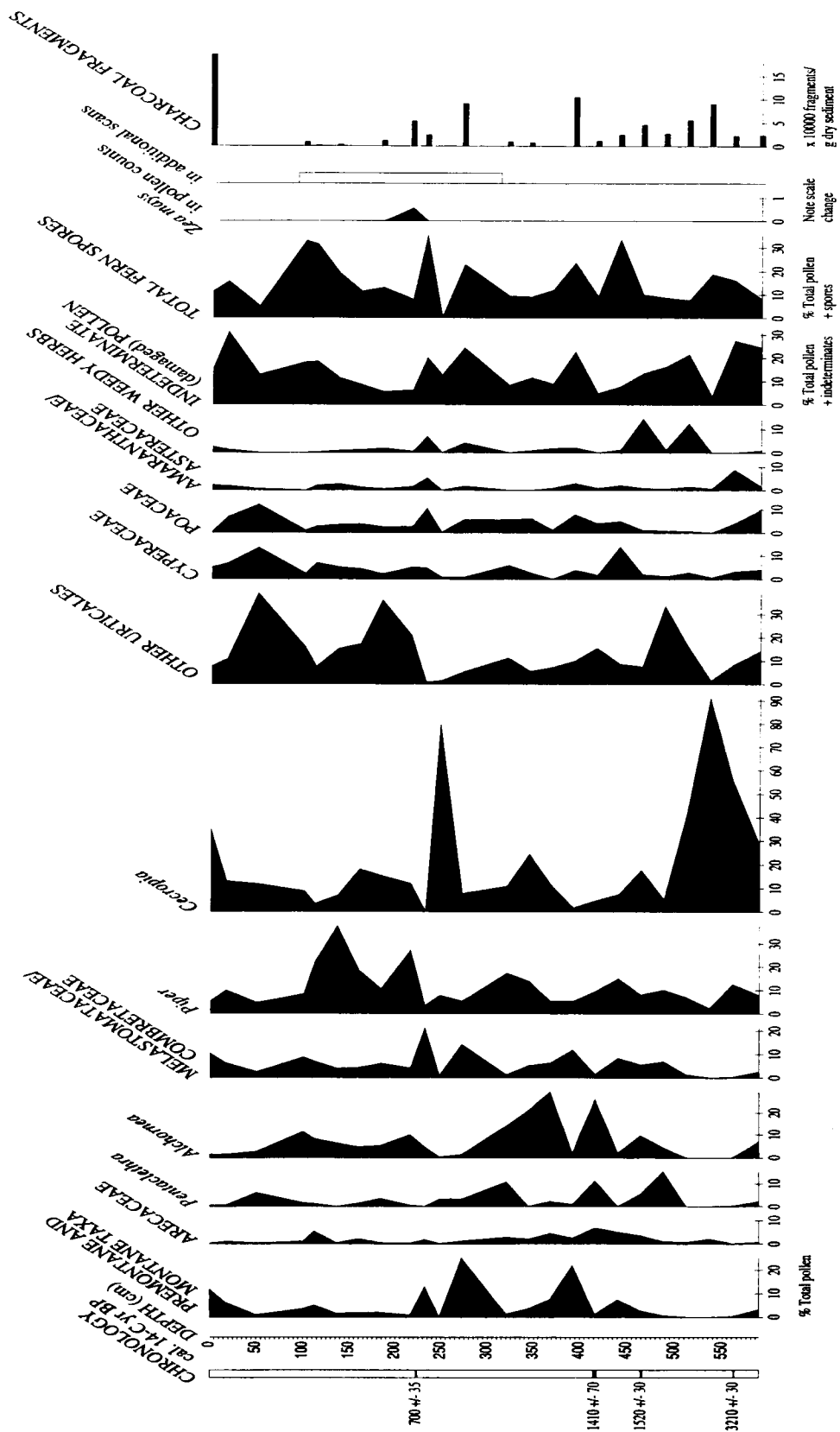


Figure 4.1 Cantarrana Swamp: Summary Pollen Diagram

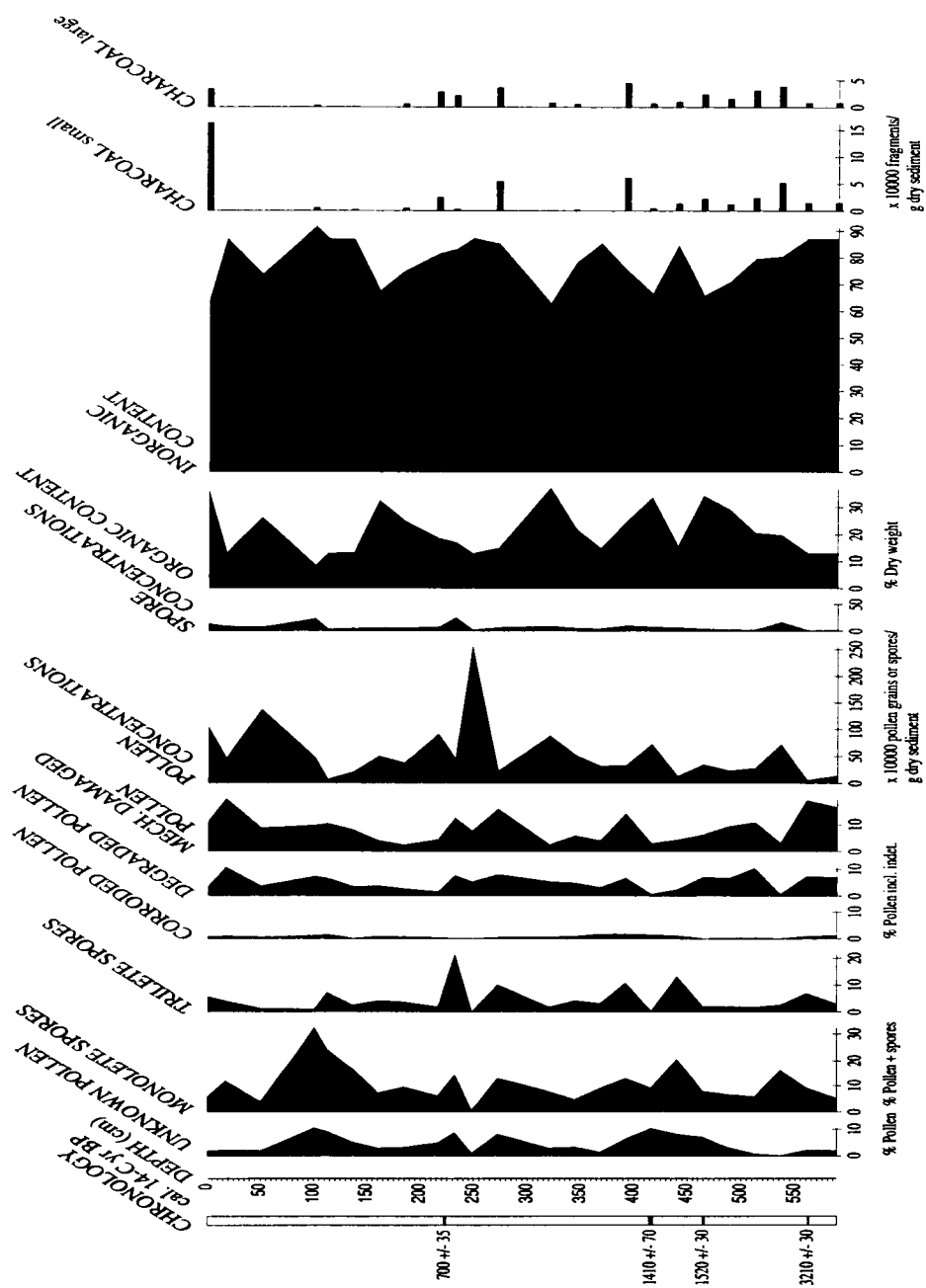


Figure 4.2 Cantarrana Swamp: Unknown Pollen, Spores, Indeterminates, Pollen and Spore Concentrations, Organic Content, and Charcoal

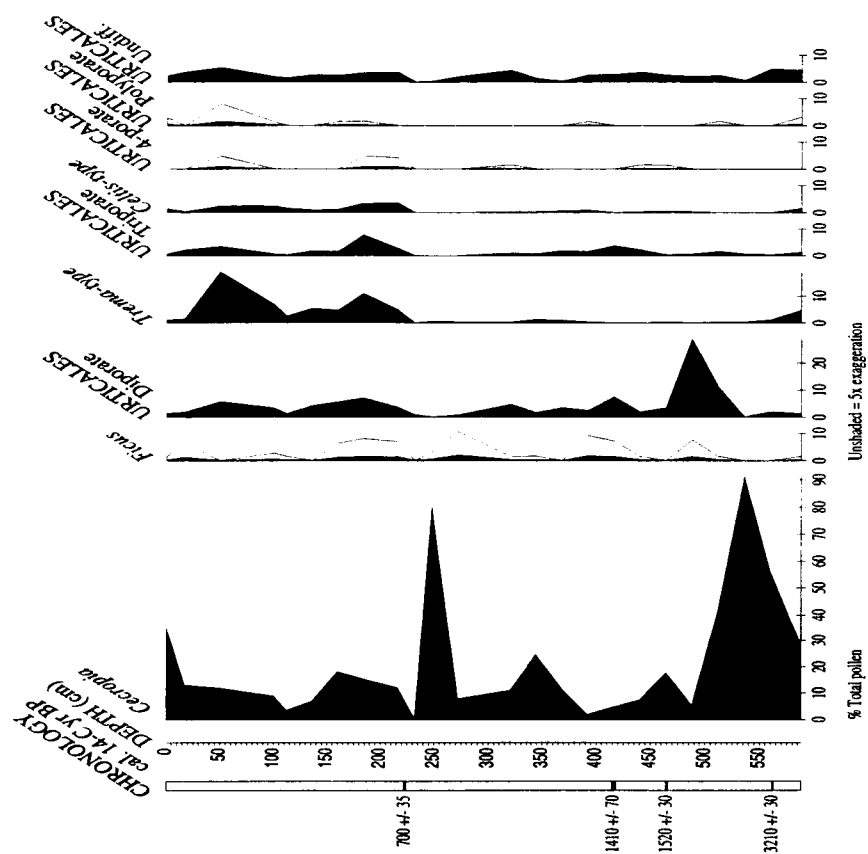


Figure 4.3 Cantarrana Swamp: Urticales Group

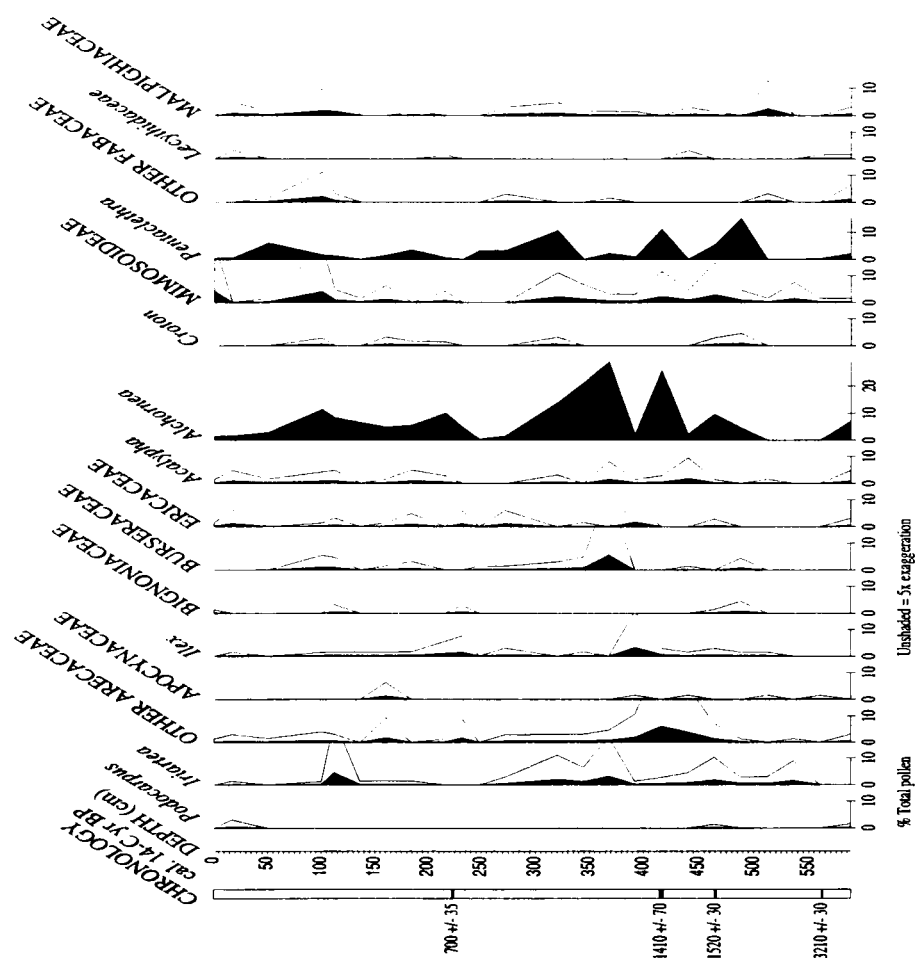


Figure 4.4 Cantarrana Swamp: Selected Lowland Tropical Forest Taxa (I)

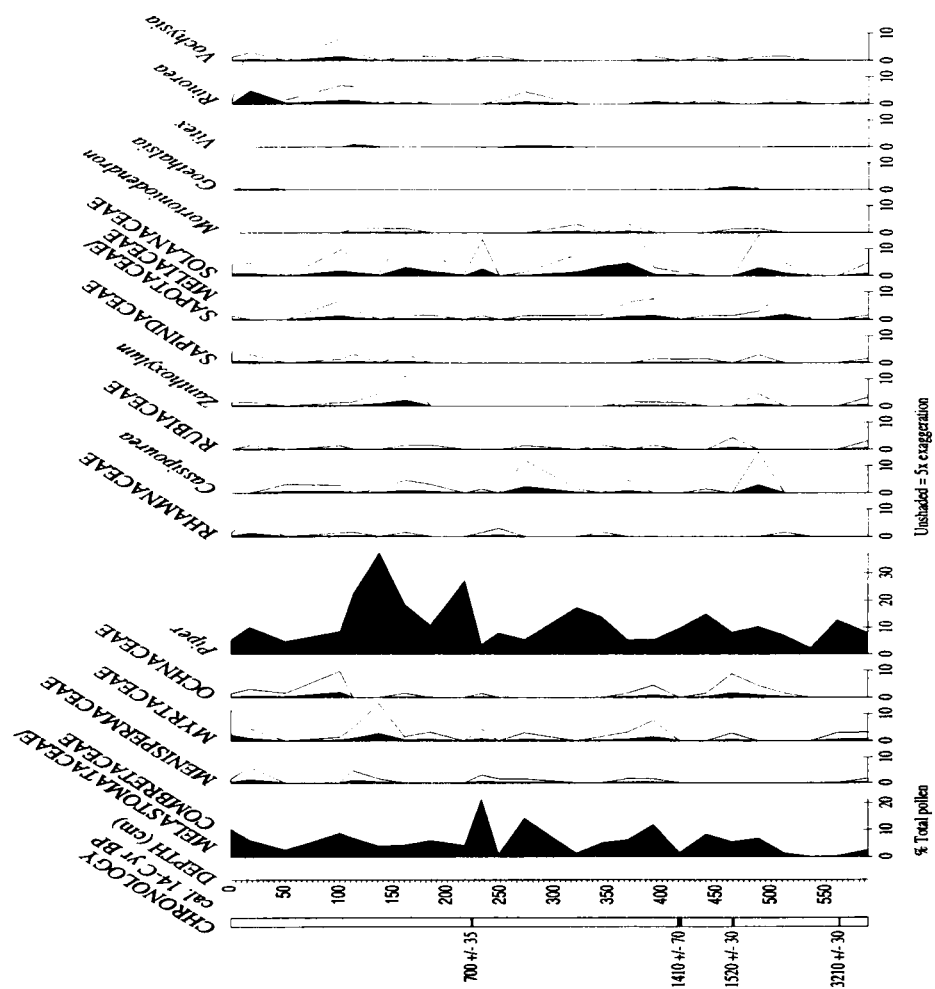


Figure 4.5 Cantarrana Swamp: Selected Lowland Tropical Forest Taxa (II)

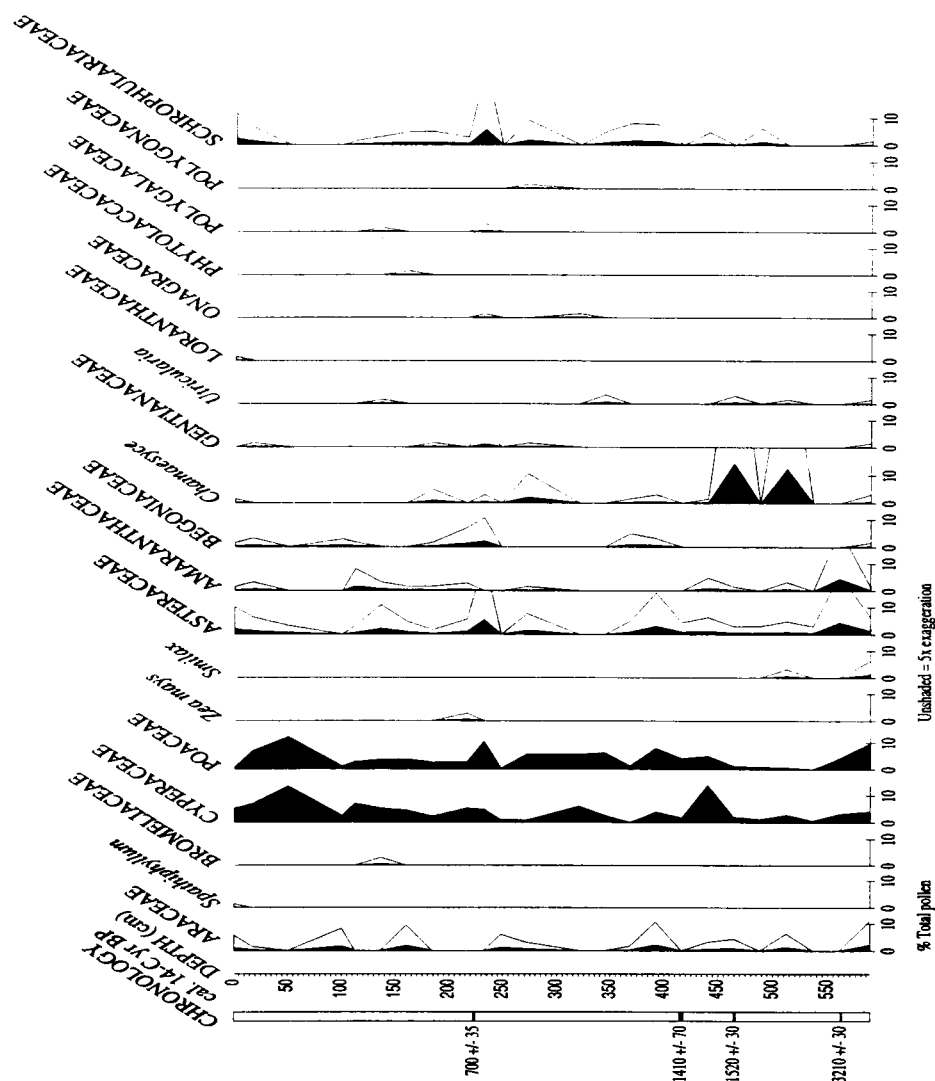


Figure 4.6 Cantarrana Swamp: Selected Non-Arboreal Taxa

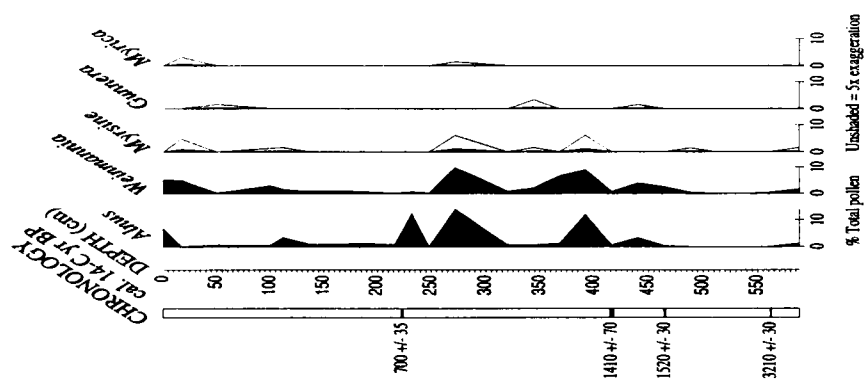


Figure 4.7 Cantarrana Swamp: Premontane and Montane Taxa

together as "damaged" pollen. I excluded those tallied for the "hidden by detritus" class from the pollen diagrams (Figure 4.2). Most indeterminate grains in the Cantarrana sediments were damaged mechanically or by degradation (Table 4.2). Damaged pollen grains from all classes combined ranged from less than 5% to almost 30% of the total pollen (Figure 4.1). Indeterminates were most abundant in levels with low organic content and low pollen concentrations.

Pollen concentrations (Figure 4.2) vary by two orders of magnitude from 4.98×10^4 - 2.54×10^6 grains/g dry sediment (3.70×10^4 - 1.36×10^6 grains/cc wet sediment) (Appendix D). Peaks in pollen concentration are well matched with high levels of organic content, except at 248 cm, where a huge spike in pollen occurs despite relatively low organic content. Overall pollen concentrations in the Cantarrana Swamp are comparable to those reported for other lowland sites in Costa Rica (Northrop and Horn 1996), Guatemala (Leyden *et al.* 1993), Panama (Bush and Colinvaux 1994), and the Ecuadorian Amazon (Liu and Colinvaux 1988, Bush and Colinvaux 1988).

The Cantarrana Pollen Record

The Cantarrana pollen spectra are taxonomically rich. I recognized more than 152 pollen types in 70 families and 120 genera (Appendix C). Many grains were identifiable only to the family level, or to the order in the case of some Urticales pollen. Pollen and spore richness varied between 19 and 80 pollen taxa per sample (Appendix E).

I recorded 107 distinctive types of unknown pollen grains from the Cantarrana sediments. Of the total number of pollen grains tallied (not including indeterminates), about 5.7% were unknowns. Percentages of unknown pollen grains ranged from less than 1% to greater than 11% of the pollen sum for various intervals. The 107 unknown types are separated into classes by morphology and size in Table 4.3. Of the unknown types,

Table 4.2 Percentage of Indeterminate Pollen Grains by Deterioration Class

Deterioration Type ¹	Description ²	% of Total Indeterminate Pollen
Mechanical Damage	Grain broken or crumpled	55%
Degradation	Exine thinned, fusion of sculptural features, or fusion of structural elements forming the wall layers	32%
Corrosion	Exine locally etched, pitted, or perforated	4%
Concealment by Detritus	Grain hidden by mineral or organic debris	9%

^{1,2} Delcourt and Delcourt 1980

Table 4.3 Unknown Pollen Types by Size and Morphology

Morphological Class	Number of Types > 25µm	Number of Types < 25µm	Total	Percent of Total
Tricolporate, Reticulate	17	14	31	29%
Tricolporate, Not Reticulate	7	18	25	23%
Other Than Tricolporate	26	25	51	48%
Total	50	57	107	
Percent of total	47%	53%		100%

29% fell into the tricolporate, reticulate category, a group that is particularly difficult to identify (see Chapter 3).

Most of the pollen grains in the Cantarrana sediments derive from lowland wet forest taxa. Two montane genera, *Alnus* and *Weinmannia*, together comprised nearly 5% of the total pollen grains counted. Some of the most abundant pollen types belong to the Urticales (Figure 4.3); the group as a whole accounts for as much as 90% of the total pollen in some levels in the core. *Cecropia* was the single most abundant pollen type; 21% of all the pollen grains counted in this record were *Cecropia*. Pollen percentages for *Cecropia* fluctuate dramatically between <1% and >90% of the total pollen with prominent peaks at 248 and 536 cm.

The *Trema*-type and other diporate grains were the next most frequently observed among the Urticales pollen types. *Trema*-type is most common in the upper two meters or so of the core. Pollen of diporate Urticales has a relatively stable record (1-7%) through the core with a single prominent peak at 488 cm. *Celtis*-type and other triporate Urticales likewise had higher frequencies in the uppermost two meters. Urticales pollen with more than three pores was rare. *Ficus* pollen was uncommon but consistently present throughout most of the record.

Other pollen types that had values of 10% or higher in at least one level include Poaceae, Cyperaceae, *Chamaesyce* (an herb), Melastomataceae/Combretaceae and *Piper* (mostly large shrubs and small trees in the understory), *Alchornea* (small to medium trees), *Pentaclethra* (large trees), and *Alnus* (tree usually found above 900 m). Most pollen types, however, occurred in low frequencies (less than 2% of the pollen sum at any level) and many appeared in only a few levels of the core (Figures 4.4, 4.5 and 4.6).

Pollen percentages of Melastomataceae/Combretaceae, *Piper*, *Alchornea*, and *Pentaclethra* vary markedly throughout the record. *Pentaclethra* pollen showed three peaks of around 10% of the total pollen in intervals between 300 and 500 cm, roughly the period between 1500 and 700 cal. yr BP. *Alchornea* pollen peaks several times during the same period. The highest peaks in *Piper* (around 30%) are before 700 cal. yr BP. *Piper* is consistently represented throughout the record while the other three taxa show low levels near the bottom of the core that coincide with a spike in *Cecropia*.

Herbaceous taxa are represented by grasses (Poaceae) and sedges (Cyperaceae) and weedy groups such as Asteraceae, Amaranthaceae, *Chamaesyce* and Scrophulariaceae (Figure 4.6). Grass and sedge pollen was present throughout the core with percentages ranging from less than 1% to greater than 10% of the total pollen. These two groups have coincident peaks in the upper meter. *Chamaesyce* (Euphorbiaceae) pollen has a sporadic presence but percentages are higher than 10% in two intervals (464 and 512 cm). No other herbaceous pollen types reach percentages greater than 10%.

Asteraceae pollen is continuously present and reaches 5% in some levels while Amaranthaceae pollen is present in lower percentages in about half of the counted levels. These two families are usually associated with open or successional habitats and often with cultivation. Pollen percentages for both families peak near the bottom (560 cm) of the core. Scrophulariaceae, another family typical of weedy or wet habitats, shows relatively high pollen percentages among the herbs. Araceae (mostly epiphytes of mature forests) is the only other herbaceous pollen type present in more than half of the samples. Interestingly, *Spathiphyllum* (Araceae), the herb that presently dominates much of the swamp, is present only in the surface sample (1 grain). All other herbaceous pollen types are rare.

Five genera (*Alnus*, *Weinmannia*, *Myrsine*, *Gunnera* and *Myrica*) that occur

primarily at higher elevations (outside the La Selva reserve) are grouped together as Premontane/Montane Taxa (Figures 4.1 and 4.7). A few pollen types such as *Ilex*, *Clethra*, Chloranthaceae, and Ericaceae could represent highland or lowland taxa, so were excluded from the Premontane/Montane group. A few grains of pollen from another primarily montane genus, *Podocarpus*, were also present in the Cantarrana sediments. However one species of *Podocarpus* is known from the Caribbean lowlands (Standley 1937-1938) (although not listed in the La Selva flora), so the genus was excluded from the Premontane/Montane group.

Pollen of premontane and montane taxa is consistently present in relatively low percentages (generally less than 10%) in the upper two meters of sediment (about the last 700 years), but has an increasingly spiky record during the period between 1500 and 700 cal. yr BP. In that part of the record, percentages reach as high as 20%. Pollen percentages of the premontane/montane group plummet to 0 near the bottom of the core corresponding to a *Cecropia* spike.

To better understand taphonomic processes in the Cantarrana Swamp, I have explored the relationship between plant reproductive systems and pollen representation in light of a recent conceptual model by Bush (1995). I present this analysis separately from the main text in Appendix F.

Fern Spores

Fern spores made up 17.5% of total pollen and spores recorded in the Cantarrana sediments. Monolete spores were more than twice as abundant as trilete spores (Table 4.4). The two most common sclerine (outer layer of the spore) types of both monolete and trilete spores are psilate (smooth surface) and verrucate ("bubbly" surface). Of the monolete spores, more than half were psilate; trilete spores were more often verrucate.

Peaks in both monolete and trilete spores match peaks in indeterminate pollen grains and dips in pollen concentration.

Maize Pollen

I found two grains of maize (*Zea mays*) pollen in level 216 cm during routine pollen counts. In low magnification scans of one to several slides from 67 levels throughout the core (8 cm intervals), I detected 25 additional maize grains between 92 cm and 312 cm (Table 4.5). Almost all of the maize grains are in levels where microscopic charcoal is also present.

Microscopic and Macroscopic Charcoal

Table 4.5 includes data on the presence/absence of microscopic charcoal in the levels scanned for maize pollen, supplementing the charcoal curves in the diagrams. Results of sieving for macroscopic charcoal in sediments from "counted" levels are presented in Table 4.6.

Table 4.4 Percentages of Fern Spores by Sclerine Type

Sclerine Type	Monolete	Trilete
Psilate	62%	21%
Verrucate	25%	39%
Other	13%	40%
% Total Spores	69.5%	30.5%

Table 4.5 Results of Low Magnification Scanning for Maize Pollen and Microscopic Charcoal

Level (cm)	Slides Examined	Maize Grains	Charcoal Present?	Level (cm)	Slides Examined	Maize Grains	Charcoal Present?
0	3	0	yes	320	3	0	yes
17	3	0	yes	328	3	0	yes
33	3	0	yes	336	3	0	yes
50	3	0	yes	344	3	0	yes
67	3	0	yes	352	3	0	yes
83	3	0	yes	360	3	0	yes
92	3	1	questionable	368	3	0	yes
100	3	1	yes	376	3	0	yes
104	1	3	yes	384	3	0	yes
112	2	1	yes	392	3	0	yes
120	4	1	yes	400	3	0	yes
128	2	1	yes	408	3	0	yes
136	2	2	yes	416	3	0	yes
144	1	1	yes	424	3	0	yes
152	2	1	yes	432	3	0	yes
160	6	0	no	440	3	0	yes
168	3	0	yes	448	3	0	yes
176	1	2	yes	456	3	0	no
184	2	1	yes	464	3	0	yes
191	2	1	yes	472	3	0	yes
200	5	0	yes	480	3	0	yes
208	3	0	yes	488	3	0	yes
216	3	4	yes	506	3	0	yes
224	2	1	yes	512	3	0	yes
232	5	0	yes	520	3	0	yes
240	3	0	yes	528	3	0	yes
248	3	2	yes	536	3	0	yes
256	3	0	yes	544	3	0	yes
264	3	1	yes	552	3	0	yes
272	3	0	yes	560	3	0	yes
279	3	0	yes	568	3	0	yes
304	3	0	yes	576	3	0	yes
312	3	1	yes	584	3	0	yes
total	maize	25		588	3	0	yes

Table 4.6 Macroscopic Charcoal in the Cantarrana Swamp
(+ indicates presence, 0 absence)

Sample Depth (cm)	Charcoal > 250 μm	Charcoal > 500 μm
0-2	0	0
14-19	0	0
48-52	0	0
98-100	+	+
111-113	+	+
135-137	0	0
159-161	0	0
183-185	+	+
215-217	0	0
231-233	0	+
247-249	+	+
271-273	+	+
319-321	0	0
343-345	+	+
367-369	0	0
391-393	+	+
415-416	0	0
439-441	0	0
463-464	+	+
487-489	+	+
511-513	+	+
535-537	+	+
559-561	+	+
587-588	0	0

CHAPTER 5

DISCUSSION

Pollen, charcoal, and other sedimentary evidence from the Cantarrana swamp indicate that La Selva forests have been subjected to episodic disturbances during the late Holocene. Archaeological research suggests that people have occupied the area of the biological station since at least the La Montaña period (3000-2300 yr BP; Quintanilla 1990, Sol 1998)--about the same time period represented by the Cantarrana core. Paleoecological evidence of the long-term disturbance history of the Cantarrana Swamp must therefore be interpreted and discussed within the framework of this human history, which has influenced the landscape and the sediment record.

In this chapter, I begin by discussing the sedimentary evidence of prehistoric agriculture at La Selva. The next section looks at what can (and cannot) be learned about fire history from both microscopic and macroscopic charcoal preserved in the Cantarrana sediments. In the third section, I examine some of the pollen curves as possible signals of past human activity, and natural disturbances such as treefalls and hydrologic change. The fourth section discusses sedimentary evidence of climatic variability.

PREHISTORIC MAIZE CULTIVATION

Prehistoric human activity at La Selva is most evident in the record of maize pollen and charcoal preserved in the Cantarrana swamp sediments (Table 4.5). Linear interpolation between the uppermost radiocarbon dated interval (700 cal. yr BP) and the modern surface would place the most recent occurrence of maize pollen at around 300 years ago. Similar calculations between dated intervals places the lowest occurrence (312 cm) between 1100 and 1000 cal. yr BP (850-950 AD). Given the imprecision of radiocarbon calibrations (see ranges and probabilities in Table 4.1) and the possibility of varying

sedimentation rates between dated intervals, dates assigned to particular levels in the Cantarrana core should be viewed as approximations. These dates for maize cultivation at La Selva are consistent, however with the regional archaeological record.

As mentioned in Chapter 2, most of the archaeological evidence discovered to date at La Selva is from the El Bosque (2300-1500 yr BP) and the La Selva (1500-1000 yr BP) archaeological periods (Quintanilla 1990, Sol 1998). Archaeological sites associated with the more recent La Cabaña period (1000-450 yr BP) occur within 20 km of La Selva (Cubujuquí site; Guttierrez and Mora 1988, Quintanilla 1990), but to date La Selva has yielded only limited archaeological evidence for human activity during this period. The discovery of maize pollen in association with 700 year old charcoal (the radiocarbon dated material) extends the known period of human occupation of La Selva into the La Cabaña period. This period is associated with the highly organized caciques or chieftains who ruled eastern Costa Rica until the arrival of the Spaniards in the 16th century (Snarskis 1981, 1984). The maize pollen also provides the first direct botanical evidence of prehistoric agriculture within the La Selva reserve. However, the scarcity of La Cabaña artifacts at La Selva suggests that populations may have been low during this period.

The sudden decline of maize pollen in the upper meter of the Cantarrana sediments probably signals the approximate time of abandonment of the area by its prehistoric inhabitants. This time frame is consistent with the timing of abandonment of Cubujuquí, a nearby archaeological site which was abandoned around 200 yr BP (Gutierrez and Mora 1988), and of rain forest sites in the Darien, Panama which were abandoned $\approx$ 350 yr BP; (Bush and Colinvaux 1994).

The evidence of maize cultivation at La Selva during the La Cabaña phase is consistent with present understanding of the regional history of maize, which is believed to

have surpassed manioc (*Manihot esculenta*) in dietary importance in the Atlantic lowlands by the beginning of the El Bosque phase more than a millennium earlier (Snarskis 1984). Although the Cantarrana swamp does not have maize pollen from El Bosque age sediments, maize pollen has been discovered in another La Selva swamp core from sediments dated to about 2500 ^{14}C yr BP (Horn and Kennedy, in preparation). The core is from the Machita swamp, located approximately 2 km west of the Cantarrana on the same alluvial terrace (Sollins *et al.* 1994). Lake sediment cores from other paleoecological sites in the Atlantic lowlands also contain maize pollen that dates to the El Bosque phase or slightly earlier (Northrop and Horn 1996, S. Horn and J. Rodgers III, unpublished data). A maize cob was recovered from an El Bosque site near Guácimo some 45 km southeast of La Selva (Snarskis 1981) and macrofossils of maize are also known from Atlantic lowland archaeological sites representing later phases (Snarskis 1984).

I interpret the maize pollen in the Cantarrana sediments as an indication that maize was being grown very near to, or perhaps during drier periods within, the Cantarrana Swamp. *Zea* pollen is transported by wind and gravity, and under calm conditions, most plants are pollinated by their neighbors (Purseglove 1988). Maize pollen generally travels less than 250 m, except in high winds, which may carry it as far as 500 m (Purseglove 1988). Maize pollen dispersal is probably limited to short distances by the grain's large size and lack of elaborate sculpturing, particularly in the wet tropics where winds are rarely strong. The absence of maize pollen from Cantarrana sediments representing earlier archaeological periods does not mean that maize was not being grown elsewhere at La Selva or even near the swamp in earlier times.

I did not tally controls during the scans for maize pollen, so cannot calculate pollen concentrations. Even so, maize pollen concentrations were clearly less than the 1-4% found by Northrop and Horn (1996) in the larger Bonilla and Bonillita lakes. The rarity of

maize pollen in the Cantarrana sediments may be simply a reflection of the swamp's small size, or it may indicate that the pollen source was near some critical distance from the swamp, beyond which it would not have been transported to this site.

Smith (1994-95), has distinguished "first" and "second" categories of evidence of prehistoric cultigens. "First category" status is reserved for seeds, cobs, or other cultivated plant parts that are dated using the Accelerator Mass Spectrometer (AMS) radiocarbon dating method. The maize pollen in the Cantarrana sediments would be considered by Smith (1994-95) to be "second category" evidence and therefore potentially suspect because the grains themselves have not been directly dated. The maize grains in this case are insufficiently concentrated to allow such dating. Maize pollen was the only pollen type found in the Cantarrana sediments that could with certainty be attributed to cultivation.

FIRE HISTORY: EVIDENCE FROM STRATIGRAPHIC CHARCOAL

Charcoal in the Cantarrana sediments may have originated from either (or both) fires started intentionally by people for agricultural or other uses, or wildfires ignited by lightning or accidentally by people. In the first scenario, prehistoric agriculturalists cut down vegetation, let it dry, and then burn it to make areas suitable for cultivation. The second possibility, wildfire, is more difficult to imagine in a wet tropical environment. But wildfires may have been possible in prehistoric forests of La Selva.

Studies of Amazonian forests have shown that wildfires in undisturbed, closed canopy evergreen tropical forests are virtually impossible under average rainfall conditions (Mueller-Dombois 1981, Uhl *et al.* 1988, Uhl and Kauffman 1991). Uhl *et al.* (1988) have suggested that high fuel moisture may be the limiting factor in preventing forest fires in Amazonia. However, soil charcoal in rain forests in Amazonia (Sanford *et al.* 1985, R. Sanford and S. Horn, unpublished data) as well as at La Selva (Horn and Sanford 1992,

and unpublished data) provides evidence that environmental conditions have at times allowed such events to occur. Climatic and human disturbances, which may act alone or in concert, have been found to modify fuel moisture and increase flammability of wet tropical forests. Droughts associated with the 1982-83 El Niño-Southern Oscillation event led to fires in Borneo that burned a parcel of lowland rain forest the size of Taiwan (Malingreau *et al.* 1985, Leighton and Wirawan 1986). In modern Amazonia, human disturbance has transformed practically nonflammable rain forest into much more flammable secondary growth through a cycle of forest clearance, conversion to pastures, and then second growth (Uhl and Kauffmann 1990).

Prehistoric land use at La Selva would not necessarily have paralleled modern human disturbance in Amazonia, but some of the factors thought to make disturbed Amazonian rain forests more likely to burn today may have similarly affected La Selva's forests. Second growth forests in Amazonia are more easily burned (flammable after 8-10 rainless days) than mature forests for several reasons: (1) a more open canopy allows more herbs and grasses to persist in the understory as surface fuels, (2) many pioneer species (e.g., *Cecropia*) drop large numbers of leaves during drought periods, increasing fuel loads, and (3) the modified microclimate (warmer and drier) under a more open canopy results in more rapid loss of fuel moisture (Uhl and Kauffman 1990). Forests selectively logged by modern machinery undergo similar microclimatic changes and may be even more fire prone than secondary growth due to a buildup of fuel at the surface resulting from the timber removal process (Uhl and Kauffman 1990). Uhl and Kauffman (1990) found forests that had undergone mechanized removal of only 1.7% of stems >10 cm dbh (diameter at breast height) became flammable after only five or six rainless days.

Manual forest clearance by prehistoric inhabitants may have affected forests in a similar fashion, making them more susceptible to wildfires ignited by lightning, volcanic

activity, or agricultural or domestic fires that burned out of control. Selective timber removal along with cycles of clearing, cultivation, and abandonment were likely a part of the agricultural system used by early La Selva agriculturalists. These activities would have produced a patchy landscape of cleared and cultivated areas, second growth, selectively harvested forests, and possibly less impacted old growth, that may have been more flammable than the largely intact forests that occupy the reserve today. Such fragmentation would also have increased the ratio of forest edge to interior. The warmer, drier microclimates characteristic of forest edges (Harris 1984) could have further increased the likelihood of fire in such a landscape.

Prehistoric human activities at La Selva probably led to changes in microclimate and fuel buildup that enhanced the probability of wildfires. Such disturbances, when coupled with periodic droughts, could have made La Selva forests more flammable than modern conditions would suggest. Even minor shifts toward warmer, drier conditions are thought to greatly increase the likelihood of fire in undisturbed rain forest (Kauffman 1991). In a more disturbed landscape, drought events such as the one in 1983, when thirty days passed at La Selva without significant rainfall (Sanford *et al.* 1994), might allow forests to burn, especially when ignition sources are abundant.

Interpreting the temporal and spatial patterns of past fires at La Selva from the microscopic charcoal profile is problematic, particularly with a single record from a small swamp. Patterson *et al.* (1987) have suggested that most microscopic charcoal in small ponds (<1 ha) derives from the local area, i.e., within 20 or 30 m of the site. On the other hand, small charcoal particles (< 60 μm) of the size usually found on pollen slides can be transported long distances by wind and thus may have a regional or larger source area (Clark 1988, MacDonald *et al.* 1991, Clark and Royall 1995). Interpreting the source of pollen slide charcoal based on size seems risky given that larger fragments may be reduced

in size through transport and depositional processes as well as by mechanical processes during sample preparation (Clark 1984).

Charcoal production and dispersal are influenced by fire intensity and spatial extent, fuel type, and meteorological conditions such as wind direction and velocity, and rainfall (Chandler *et al.* 1983). These factors vary from place to place, and from fire to fire within a place, making it difficult to interpret the source area of microscopic charcoal. Most recent models of charcoal production and deposition (e.g., Clark 1988 and Clark and Royall 1995) are based on temperate studies. These processes undoubtedly vary in tropical environments under different fire and climate regimes.

Microscopic charcoal is more or less continuously present throughout the Cantarrana record (Table 4.5). This might signal human activity in the general area throughout most of the period represented by the sediment record. However, the low magnification scanning (results in Table 4.5) detected only the presence or absence of charcoal; I did not attempt to measure abundance. The low amounts of microscopic charcoal in some intervals could result from postdepositional mixing and downward movement (Patterson *et al.* 1987) or from a time lag in the transport of charcoal to the site after a fire (Whitlock and Millspaugh 1996). One of these explanations could account for the presence of microscopic charcoal in the uppermost "post-Conquest" levels, when forests of La Selva are presumed to have been abandoned. On the other hand, low concentrations of microscopic charcoal may be "background noise" from distant fires.

The overall abundance of microscopic charcoal in the Cantarrana sediments is lower than that found in another Costa Rican rain forest site with a history of prehistoric human disturbance. The major charcoal peaks in two lakes (< 1 km apart) studied by Northrop and Horn (1996) are about twice as high as peaks in the Cantarrana charcoal profile. This

disparity probably reflects between-site differences in factors influencing charcoal taphonomy, such as source area, accumulation rates, and charcoal production and dispersal. The Cantarrana charcoal is comparable to amounts in swamp cores from the Darien of Panama, which Bush and Colinvaux (1994) studied to provide records of prehistoric human disturbance of lowland tropical rain forest.

Interestingly, microscopic charcoal is most abundant in levels below the zone of maize pollen (92-312 cm), and especially in intervals lower than the one dated at about 700 cal. yr BP (223 cm). One possible explanation is that the general area of La Selva was less populated during the La Cabaña period, when maize was being grown near the swamp, than in earlier times (La Selva and El Bosque phases). If most of the charcoal is associated with prehistoric agriculture, then lower populations would mean less agricultural activity (and fewer human-set fires), hence less charcoal available for transport. Low populations during the La Cabaña period would be consistent with the archaeological evidence currently available. Another possibility is that droughts were more intense, longer or more frequent before about 700 cal. yr BP, producing conditions more conducive both to agriculture (and associated fires) and wildfires. More favorable conditions for agriculture also supports the idea of higher populations during that time versus late La Cabaña.

Similar patterns in the abundance of microscopic charcoal of both size classes ($< 25 \mu\text{m}$ and $\geq 25 \mu\text{m}$) may mean that they are signaling the same fires (Figure 4.2). Four peaks in microscopic charcoal abundance stand out in the record. The most prominent is in the surface sample, which appears to be recording trash burning at the biological station and possibly agricultural and trash burning by station neighbors. The other three are at 272 cm, 392 cm and 560 cm. All four levels also contain macroscopic charcoal $> 500 \mu\text{m}$ in maximum dimension (Table 4.6) documenting local fires. Whether the peaks in microscopic charcoal signal larger-scale fires, more regional burning (contemporaneous

with local fires) or simply fires closer to the basin, is unclear. Both middle peaks (272 cm and 392 cm) precede levels with high mineral content that may be evidence of forest clearance and erosion. Microscopic charcoal not associated with macroscopic charcoal in the Cantarrana sediments may be reflecting both local and wider scale fires (see MacDonald *et al.* 1991).

While the source area of pollen slide charcoal is difficult to interpret, large charcoal (> 60 μm) does not become airborne at normal wind speeds (Clark 1988) and thus is largely reflecting local fires (Clark 1988, MacDonald *et al.* 1991). The presence of macroscopic charcoal in more than half of the samples studied (Table 4.6) indicates that local fires were relatively common throughout the swamp's 3000 year history. The Cantarrana charcoal may result from fires of various origins, but its association with human activities is likely given the archaeological and pollen evidence of contemporaneous occupation. Ongoing study of charcoal in the upland soils (Harrell, Sanford, and Horn, in progress) and in sediments from other swamps in the reserve (Horn, Kennedy, and League, in progress) will help sort out the fire history of the La Selva area and will contribute to understanding of charcoal taphonomy in tropical environments.

DISTURBANCE INDICATORS IN THE POLLEN RECORD

Herbaceous Taxa

Pollen percentages for the weedy families Amaranthaceae and Asteraceae peak in the maize zone and lower in the core where maize pollen is absent (Figure 4.6). These peaks match the charcoal record: highest percentages are in levels with more charcoal. This result supports the idea that increases in charcoal may signify increased cultivation and that nearby areas were being cultivated earlier (before the maize zone) even though I found no maize pollen in deeper sediments of the Cantarrana swamp.

Whether cultivation expanded and contracted periodically on a broad scale or whether these changes were occurring only locally around the Cantarrana swamp is unclear. The source areas for *Amaranthaceae* and *Asteraceae* pollen may be smaller than for those for microscopic charcoal. It is worth mentioning that although their pollen percentages are low, many of these taxa are insect-pollinated and therefore expected to be somewhat underrepresented in the record. In studies of modern pollen rain, *Amaranthaceae* pollen percentages exceeded 2% only in a sample from a modern corn field (Rodgers and Horn 1996, and S. Horn unpublished data). *Asteraceae* pollen grains are found in several Costa Rican vegetation types (Rodgers and Horn 1996), but members of this family are commonly agricultural weeds and inhabitants of disturbed environments. Percentages of *Amaranthaceae* and *Asteraceae* in this record are slightly lower than in pollen records of human disturbance at Laguna Bonillita (Northrop and Horn 1996) and in the Darien, Panama (Bush and Colinvaux 1994).

Pollen percentages of two other weedy, mostly herbaceous taxa, the *Scrophulariaceae* and *Chamaesyce* (*Euphorbiaceae*), also relate fairly well to the abundance of microscopic charcoal. The genus *Chamaesyce* (four species at La Selva, Wilbur *et al.* 1994) is almost exclusively found in sunny, open places and early successional sites (Burger and Huft 1995). At Palo Verde in the seasonally dry lowlands of northwestern Costa Rica, one species of *Chamaesyce* is known to colonize the marsh during the dry season (Hernández and Gómez 1993). Many of the genera and species of *Scrophulariaceae* at La Selva are associated with wet or waste places (Standley 1937-1938). Peaks in these taxa may indicate hydrological changes within the swamp, or agriculture or other disturbances that would open the canopy, or some combination. This evidence may support the link between relatively dry periods and agricultural expansion, including the use of fire, and possibly accidental fires.

Pollen of Poaceae (grasses), another family often associated with human disturbance and agriculture, is consistently present in the record except for a decline in the lowest meter. Some of the peaks also match peaks in the charcoal record. The grass percentages also largely parallel those for Cyperaceae (sedges). The Cyperaceae and Poaceae pollen curves may represent changing water levels in the swamp. A lower water table in the swamp would create emergent areas along the perimeter of the swamp and on microtopographic high points, where local populations of grasses and sedges could flourish. Or standing water might disappear altogether, allowing widespread colonization of the swamp surface. A broad peak in pollen of both families in the upper meter is associated with high organic levels and moderate indeterminate percentages, so it probably does not indicate a drastic decline in water levels during that time period. But even slight or moderate lowering of the water table over a long period time might allow at least seasonal increases in populations around the swamp edges as proposed above, while standing water at the core site would continue to result in organic accumulation and good pollen preservation.

The Urticales Group

Several taxa within the order Urticales are characteristic of disturbed habitats (e.g., *Trema microcantha* (Ulmaceae), *Phenax sonneratii* and (Moraceae), and *Pilea microphylla* (Urticaceae)), but most taxa in the group are found in shaded mature forest sites (Burger 1977a, 1977b). A study of modern pollen rain in Costa Rica shows high percentages of Urticales pollen to be a signature of tropical wet forests (lowland and premontane). Downcore fluctuations in the pollen of Urticales components, other than *Cecropia* (discussed separately below) and "Undifferentiated," follow a highly similar pattern with two marked peaks within the top 200 cm and conspicuously lower percentages below that (Figure 4.3). The one exception is a prominent peak in diporate Urticales at 488 cm. Most

of the pollen peaks for the combined Urticales group (Figure 4.1) lag slightly behind those of *Cecropia* and may be reflecting the recovery of La Selva forests after major disturbances, such as wide scale forest clearance.

Premontane and Montane Taxa

Pollen percentages for premontane and montane taxa (Figure 4.1) may lend support to the interpretation of Urticales peaks as indications of forest recovery after disturbance. Generally, sediments of a small basin, such as the Cantarrana, are not expected to contain high percentages of pollen from distant sources (Jacobsen and Bradshaw 1981). Low percentages of premontane/montane pollen in the top two meters of the core are consistent with that idea. However, if in earlier times forests were cleared (and/or burned) around the swamp or in the larger area, biomass and pollen production of local (lowland) taxa may have been temporarily reduced. And the open area in the canopy above the basin may also have increased in size, increasing the relative importance of pollen influx from distant sources. In this way, pollen percentages of higher elevation taxa may have increased at the expense of local types, with peaks indicating periods of maximum disturbance. Contemporaneous peaks in microscopic charcoal support the interpretation of a relationship between disturbance and increased abundance of premontane/montane pollen.

Pentaclethra macroloba

At present, *Pentaclethra macroloba* trees form the majority of the canopy around the edges of the Cantarrana swamp. As noted in Chapter 2, this versatile species is dominant on all types of terrain at La Selva, including waterlogged swamp soils (Hartshorn and Hammel 1994). *Pentaclethra* is usually thought of as a primary forest species because of its ability to germinate and grow in shade. However, its rapid growth in high light and

abundance in early successional habitats show that the distinction between "shade tolerant" and "gap dependent" species is not necessarily clear (Clark 1994).

Pentaclethra is pollinated by beetles (Kress and Beach 1994) and has relatively large sculptured pollen grains. These characteristics suggest the possibility that *Pentaclethra* pollen, while perhaps abundant, may not be transported very far from its source. If so, then its fluctuating percentages may indicate changing local abundances. The inverse relationship between the *Pentaclethra* and premontane/montane pollen curves may denote a link with disturbance; for example, forest clearance around the swamp basin might have resulted in reduced *Pentaclethra* pollen and increased influx of premontane/montane pollen from distant forests.

The pollen curve for *Pentaclethra* is also noteworthy because of the species' unique importance in La Selva forests (see Chapter 2). Janzen (1970) has speculated that *Pentaclethra*'s dominance in Atlantic lowland forests may be due to its status as a relatively recent newcomer. He suggested that *Pentaclethra* may have left behind its normal complement of seed predators, allowing it unusual population growth in the region. Janzen does not give a time frame for his hypothetical "recent" arrival of *Pentaclethra*. But, we now know from the presence of *Pentaclethra* pollen even in the lowest Cantarrana sediment sample that the species has been present at La Selva for at least 3000 years.

Cecropia and Gap Dynamics

Along with human disturbance, natural disturbances, particularly treefalls, are known to have a significant influence on the structure and dynamics of tropical forests. Gap dynamics have been the focus of many ecological studies at La Selva and other neotropical sites (Denslow 1987, Denslow and Hartshorn 1994, and references therein).

Canopy trees die standing, are uprooted, snap off, and fall or are fallen upon, producing openings in the canopy that allow more light to reach the forest floor and bring about other physical changes in the gap environment. These changes are a source of environmental heterogeneity and may have an important role in the maintenance of species diversity (Denslow and Hartshorn 1994). The small-scale disturbances resulting from treefalls are thought to be even more important at La Selva than at other rain forest sites more prone to hurricanes, landslides and other periodic large-scale disturbances (Denslow and Hartshorn 1994).

High winds, waterlogged soils, and lightning are among the factors contributing to treefalls at La Selva (Denslow and Hartshorn 1994). Hartshorn's (1978) data from the long term research plots at La Selva suggests that gap formation rates may be even higher on alluvial and swamp soils, raising the possibility that forests around the Cantarrana swamp may have higher than average gap formation rates. Floods, bank collapses, and other riverine disturbances along the nearby Río Puerto Viejo and its tributaries, El Surá and El Salto, are also likely to increase the frequency of treefalls around the swamp.

Cecropia (Cecropiaceae) trees are pioneers in treefall gaps and other high-light environments and dominant canopy trees in early successional sites at La Selva (Hartshorn and Hammel 1994) and in tropical lowlands elsewhere (e.g., Gentry 1993). As is typical of pioneer species, they are rapid growers and can reproduce easily within five years. High percentages of *Cecropia* pollen are usually interpreted by paleoecologists as evidence of disturbance. Peaks in *Cecropia* in neotropical pollen records can be associated with gap dynamics and natural regeneration processes, or with forest clearance and later plot abandonment by prehistoric agriculturalists. The dynamic forest history indicated by fluctuations in *Cecropia* pollen percentages likely reflect both natural and human disturbance.

PAST CLIMATIC VARIABILITY

Recent paleoclimatic studies have suggested late Holocene aridity in several areas of tropical America: central Mexico (Metcalf *et al.* 1994 and Metcalf 1995), the Yucatan Peninsula (Hodell *et al.* 1995, Curtis and Hodell 1996), Costa Rica (Horn and Sanford 1992) and the Caribbean (Hodell *et al.* 1991, Curtis and Hodell 1993). One study, based on oxygen isotopes of ostracods and gastropods found in sediments from Punta Laguna, Yucatan (Curtis *et al.* 1996), revealed a detailed record of climate change showing a relatively dry period roughly between 1800 and 1000 ^{14}C yr BP, along with increased intensity and frequency of arid events. The period of maximum aridity suggested by this study and the study of another Yucatecan lake (Chichancanab, Hodell *et al.* 1995) falls between 1225 and 930 ^{14}C yr BP.

In Costa Rica, coeval dates (clustering around 1110-1180 ^{14}C yr BP, and 2430 ^{14}C yr BP) on macroscopic soil charcoal from La Selva and charcoal rich lake sediments from Lago Chirripó in the Cordillera de Talamanca (3819 m), suggested the possibility of widespread fires associated with exceptionally dry periods in Costa Rica (Horn and Sanford 1992). Unequivocal evidence of prehistoric droughts in Costa Rica has yet to be found, although there are hints of droughts in other paleoecological studies (S. Horn and J. Rodgers, III, unpublished data). One of the questions pursued by this study is whether a climate signal could be extracted from the Cantarrana sediment record, in addition to a record of human activities. Oxygen isotope records like those from the Yucatan have the advantage of being relatively immune to influence by human activities, while climate signals in pollen records are often obscured by such disturbance. In the Cantarrana record, increased pollen percentages of weedy taxa and relatively abundant charcoal, during times before about 700 cal. yr BP, may be associated simply with clearing of forests for agriculture. Or, the signal may be complicated by periodic droughts that may have

translated into more favorable conditions for agriculture, more (or more extensive) fires, and increasing forest clearance and post-agricultural succession.

Clues from Indeterminate Pollen Grains

Another possible line of evidence of climatic and hydrologic history are the fluctuations of percentages of indeterminate pollen grains. Pollen assemblages may be altered from their original state by diagenetic processes stemming from deterioration of pollen and spores (Delcourt and Delcourt 1980). Chemical and biochemical oxidation can degrade the exine (outer layer) of pollen grains through thinning and/or fusion or destruction of sculptural elements and corrosion (localized etching, pitting or perforation), (Cushing 1967). Exines weakened by such processes make pollen grains more susceptible to breakage or crumpling (mechanical damage) by sediment compaction (Delcourt and Delcourt 1980). Degradation, corrosion, and mechanical damage often render pollen grains unidentifiable but their presence may still shed light on past environmental conditions.

Delcourt and Delcourt (1980) counted and classified indeterminate pollen grains in sediment cores from four sites in the southeastern U.S. and found that the results provided information on environmental history that clarified and supported other lines of evidence. For two of their sites, high percentages of indeterminates, particularly degraded and mechanically damaged pollen grains, and low organic accumulation coincided with relatively dry periods and lowered water levels indicated by other pollen and sediment analyses. During the drier period, indeterminate pollen grains comprised 10%-25%, percentages two to five times higher than in the rest of the record. In another site, Delcourt and Delcourt (1980) invoked differential preservation in levels with high indeterminate percentages to explain the absence of several major arboreal pollen types from the pollen spectra.

In the Cantarrana swamp core, high percentages of damaged pollen grains (peaks between 20% and 30%, Figure 4.1) in levels with low organic content and low intact pollen concentrations indicate unfavorable conditions for pollen preservation during several intervals of the record. At present, water levels in the Cantarrana swamp remain above the surface most of year, although the water table sometimes sinks below the surface during the short dry season (personal observation, 1994). Both organic content and pollen concentration are relatively high in the surface sample representing modern conditions; lower values may reflect longer or more extreme dry seasons in which the water table was lowered far enough or long enough to permit oxidation of pollen grains. Pollen grains weakened by oxidation may have been crumpled and broken by compaction, and by possible shrinking and expansion of the clay sediments.

Correlations between low pollen and low organic content hint at the possibility of increased erosion rates in the watershed, but chronological control for the core is insufficient to test this idea. Lower pollen production in the source region could also be responsible for lowered pollen concentrations. Both of these scenarios--increased erosion and lower pollen production--might arise from deforestation and fire linked with increased agricultural activity in the area. As previously suggested, increased agricultural activity may have been especially likely during drier periods. Both low pollen and low organics could result simply from drier conditions and poor pollen preservation. Or, the effects of increased human activity in combination with drier conditions may have even further reduced pollen concentrations.

Signals of Environmental Change from Fern Spore Profiles

Downcore changes in fern spore percentages (Figures 4.1 and 4.2) may also reveal shifting environmental conditions in the Cantarrana swamp. Northrop (1994) interpreted

two simultaneous peaks in fern spore, grass pollen, and charcoal in Laguna Bonillita sediments as possible evidence of drier climatic conditions around 1377 and 1151 yr BP. Peak spore percentages (around 30%) in the Cantarrana sediments are slightly lower than for the two major peaks in the Bonillita record ($> 40\%$), but overall fluctuations in the Cantarrana fern spore curves are much more dramatic. There are multiple and perhaps intertwined explanations for these fluctuations.

One explanation might be the differential preservation of fern spores under oxidizing conditions. The outer walls of fern spores are apparently tougher and more resistant to oxidation and breakage than the exines of many pollen grains (Dimbleby 1985). This would cause a higher proportion of spores (compared to pollen) to be preserved under conditions unfavorable to pollen preservation, such as a lowering of the water table in the swamp. Oxidizing conditions such as this might result in high percentages of indeterminate pollen grains. Spore peaks in the upper 4 m of the record are indeed well-matched with indeterminate pollen peaks, supporting this interpretation. But in the lower part of the core the relationship is less strong.

The interpretation of differential preservation is complicated, however, by other effects that drought periods might have on the local environment. For example, if the drier period were long enough, the swamp's surface would be colonized by terrestrial species. Ferns are early colonizers in disturbed environments at La Selva (Grayum and Churchill 1987) and throughout the neotropics (Walker 1994), and may have been among the first plants to move into a temporarily desiccated swamp. Such an increase in local populations of ferns could have given rise to the high spore percentages. However, if nutrient levels are high enough, fast growing grasses, herbs, and trees may prevent fern colonization (Walker 1994).

A broader scale explanation might include increased human activities in the general area of the present-day reserve. Fern spores are dispersed in huge numbers and can travel long distances (Gentry and Dodson 1987). Presumably, a more open (less forested) landscape would aid in long-distance dispersal. Increased cultivation, land abandonment, and fire in the larger area of La Selva would have resulted in a more open landscape with widespread successional patches where ferns may have been common early colonizers. The idea that relatively dry periods would enhance agricultural activities as well as the likelihood of accidental fires would also fit with this explanation. Peaks in both charcoal and the weedy *Amaranthaceae*/*Asteraceae* families further support this "extralocal" interpretation of fern spore fluctuations.

It is entirely possible that all of these related scenarios are together responsible for the fern spore peaks in the Cantarrana record. An additional possibility is that humans directly manipulated the hydrology of the swamp resulting in the fluctuations in both fern spores and indeterminate pollen grains. This possibility highlights the difficulty of separating the evidence of human disturbance from evidence of climate change or other natural disturbances in the pollen record.

Both indeterminate pollen and fern spore percentages may be signaling a record of water table fluctuation in the swamp, but whether the hydrological patterns are related to climatic fluctuations cannot be firmly established by this study. If we do infer episodic droughts in La Selva's climate history, they do not necessarily corroborate the drought periods identified for the Yucatan and other areas of Mesoamerica, i.e., the temporal patterns are not well matched. This may be because the Cantarrana record is reflecting local rather than regional climatic fluctuations, or because there is less stringent chronological control of the sediments (e.g., possible gaps), or because human activity has complicated the sediment record.

CHAPTER 6

CONCLUSION

The most important conclusion of this study is that forests of the La Selva Biological Station are not "virgin", but instead have a long history of human use and modification. Maize pollen grains in a section of the core representing approximately 1100 to 300 cal. yr BP (100-312 cm) provide the first direct botanical evidence of crop cultivation at La Selva. Even the ecological reserve (Reserva Ecológica Rafael Chavarría), where forests are regarded as especially pristine, was cleared and cultivated by prehistoric agriculturalists. The maize evidence is consistent with regional archaeological findings and complements and extends ongoing archaeological research within the La Selva reserve. The maize pollen indicates the presence of at least small human populations at La Selva during the later La Cabaña period, from which no artifacts have yet been found.

That former agricultural lands, such as the ecological reserve at La Selva, could be replaced in the span of only a few centuries by forests that appear undisturbed gives new hope to efforts to reclaim degraded tropical lands. The timing of recovery will of course depend on the nature and magnitude of disturbances, seed sources, and the specific biotic and physical properties of the altered systems. But the story from the Cantarrana Swamp is encouraging.

The Cantarrana pollen, spore, and charcoal profiles, along with characteristics of the sediment, support the current conception of tropical rain forest as a highly dynamic ecosystem influenced by both human and natural disturbances. Dramatic fluctuations in percentages of *Cecropia* and other secondary forest taxa indicate episodic disturbance around the site. Much of the disturbance was probably anthropogenic (e.g., forest clearance, cultivation, and fire). However, the paleoecological record of human

disturbance preserved in the Cantarrana Swamp probably also bears an overprint of natural disturbances. Forest gaps created by treefalls, fluvial processes, hydrological shifts, or lightning fires could provide habitats for some of the same successional species that would be associated with agricultural clearing and burning, or later field abandonment.

Microscopic and macroscopic charcoal in the Cantarrana sediments provide clear evidence of prehistoric fires. Macroscopic charcoal fragments ($> 500 \mu\text{m}$) in half of the samples examined ($n = 25$) indicate fires very near to, or within, the swamp basin. Microscopic charcoal, although present in most of the core, is most abundant in sediments older than 700 cal. yr BP, perhaps because of higher populations or drier conditions (or both) during that period. Most fires at La Selva were probably associated with human activity, but wildfires may have burned intact forest during exceptionally dry periods. Ongoing study of charcoal in other swamp cores (Horn and Kennedy, in progress) and in upland soils (Harrell, Sanford, and Horn, in progress) will help to elucidate the fire history of La Selva.

Other aspects of the Cantarrana sediment record may also record climatic variability. Downcore changes in stratigraphy, and peaks in fern spores and indeterminate pollen grains, suggest hydrologic fluctuations that may signal past drought episodes. Many of these peaks also match charcoal peaks. The discovery of Holocene aridity events in this area would be consistent with evidence emerging from other parts of Costa Rica and the wider Caribbean region (Curtis *et al.* 1996, and references therein). However, more local records need to be studied before we can be certain of the occurrence and nature of Holocene droughts at La Selva.

The fascinating record of maize and other pollen grains, fern spores, and charcoal in the Cantarrana Swamp provides an important point of reference for other tropical paleo-

studies and points to the need for future research in several areas. For this study, as for paleoecological studies elsewhere in the tropics, separating the effects of climatic variability and other natural disturbances from human disturbance proved difficult. Paleoecologists need to develop a better understanding of taphonomic processes (of pollen grains, spores, and charcoal) in tropical settings in order to refine interpretations of tropical sediment records. Further study of modern pollen deposition within a variety of successional sites and along environmental gradients could help to clarify disturbance signals in the Cantarrana and other tropical pollen records. The study of sedimentary microfossils that are less sensitive to human disturbance, such as diatoms (Curtis *et al.* 1996), might also improve the interpretation of such records. Initial work on diatom ecology in Costa Rica has focused on lakes (Haberyan *et al.* 1997), but swamps may also preserve diatom evidence of environmental history. Finally, expanding paleoecological work into other areas of the Caribbean lowlands will strengthen interpretations and enable reconstruction of regional patterns of fire, disturbance and climate.

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APPENDICES

APPENDIX A
PROVISIONAL SPECIES LIST FOR THE CANTARRANA SWAMP

APPENDIX A

PROVISIONAL SPECIES LIST FOR THE CANTARRANA SWAMP

This partial list of the vegetation in and around the Cantarrana Swamp was prepared by Lisa Kennedy based on information provided by station naturalist, Orlando Vargas. Mr. Vargas, an expert on the flora of the La Selva Biological Station, identified plants growing to ≈ 10 m beyond the water's edge, from the boardwalk with binoculars. The list is likely to be more complete for trees than for smaller plants, lianas and epiphytes. Nomenclature follows Wilbur *et al.* (1994) except that alternative family names are used for Gramineae (Poaceae), Palmae (Arecaceae), Compositae (Asteraceae) and Leguminosae (Fabaceae).

TREES ≥ 10 m

ANNONACEAE	<i>Guatteria diospyroides</i> Baillon
ARECACEAE	<i>Prestoea decurrens</i> (H.A. Wendl.) H.E. Moore
ARECACEAE	<i>Socratea durissima</i> (Orsted) H.A. Wendl.
ARECACEAE	<i>Welfia georgii</i> H.A. Wendl. ex Burret
BORAGINACEAE	<i>Cordia lucidula</i> I.M. Johnston
BURSERACEAE	<i>Protium pittieri</i> (Rose) Engler
CAPPARACEAE	<i>Capparis pittieri</i> Standley
CECROPIACEAE	<i>Cecropia obtusifolia</i> Bertol.
CYATHEACEAE	<i>Cyathea</i> sp. (or <i>Dicksonia</i> sp.)?
EUPHORBIACEAE	<i>Alchorneopsis floribunda</i> (Benth) Muell.Arg.
EUPHORBIACEAE	<i>Hyeronima alchorneoides</i> Allemao
FABACEAE	<i>Andira inermis</i> (W. Wright) HBK
FABACEAE	<i>Inga</i> sp. P.Mill
FABACEAE	<i>Pentaclethra maculosa</i> (Willd.) Kuntze
FLACOURTIACEAE	<i>Laetia procera</i> (Poeppig.) Eichl.
FLACOURTIACEAE	<i>Pleuranthodendron lindenii</i> (Tuerch.) Sleumer
LACISTEMACEAE	<i>Lacistema aggregatum</i> (Berg.) Rusby
LAURACEAE	<i>Rhodostemonodaphne kunthiana</i> (Nees) J. Rohwer
MELASTOMATACEAE	<i>Miconia elata</i> (Sw.) DC.
MELASTOMATACEAE	<i>Miconia</i> sp. Ruiz and Pavón
MELIACEAE	<i>Guarea bullata</i> Radlk.
MELIACEAE	<i>Guarea guidonia</i> (L.) Sleumer
MYRISTICACEAE	<i>Virola koschnyi</i> Warb.
MYRISTICACEAE	<i>Virola sebifera</i> Aublet
OLACACEAE	<i>Minquartia guianensis</i> Aublet
PIPERACEAE	<i>Piper colonense</i> C.DC.
PIPERACEAE	<i>Piper</i> sp.L
RHAMNACEAE	<i>Colubrina spinosa</i> J.D. Sm.
RUBIACEAE	<i>Coussarea hondensis</i> (Standley) C.M.Taylor & W.Burger
RUBIACEAE	<i>Coussarea impatiolalis</i> J.D. Sm.
RUBIACEAE	<i>Psychotria panamensis</i> var. <i>compressicaulis</i> (K.Krause) C. Hamilton
RUBIACEAE	<i>Simira maxonii</i> (Standley) Steyererm.
RUBIACEAE	<i>Warszewiczia coccinea</i> (Vahl) Klotzsch
SAPINDACEAE	<i>Cupania livida</i> (Radlk.) Croat
TILIACEAE	<i>Apeiba membranacea</i> Spruce ex Benth.
TILIACEAE	<i>Goethalsia meiantha</i> (J.D. Sm.) Burret

TREES ≥ 10 m (cont.)

TIACEAE	<i>Leuhea semannii</i> Triana & Planchon
ULMACEAE	<i>Ampelocera macrocarpa</i> A. Gentry & Forero
VERBENACEAE	<i>Vitex cooperi</i> Standley

SMALL TREES AND SHRUBS < 10 m

ANNONACEAE	<i>Xylopia bocatorena</i> Schery
ARECACEAE	<i>Asterogyne martiana</i> H.A. Wendl. ex Burret
ARECACEAE	<i>Bactris longiseta</i> H.A. Wendl. ex Hemsley
ARECACEAE	<i>Calyptranthes ghiesbreghtiana</i> (Linden & H.A. Wendl.) H.A. Wendl.
ARECACEAE	<i>Geonoma congesta</i> H.A. Wendl. ex Spruce
FABACEAE	<i>Swartzia simplex</i> (Sw.) Sprengel
GESNERIACEAE	<i>Besleria columneoides</i> Hanst.
HELICONIACEAE	<i>Heliconia irrasa</i> Lane ex R.R. Sm.
LAURACEAE	<i>Ocotea atirrensensis</i> Mez & J. D. Sm. ex Mez
MELASTOMATACEAE	<i>Miconia</i> sp. Ruiz and Pavón
MONIMIACEAE	<i>Siparuna pauciflora</i> (Burl.) A. DC.
MORACEAE	<i>Ficus maxima</i> P.Mill.
MYRSINACEAE	<i>Ardisia nigropunctata</i> Oersted
NYCTAGINACEAE	<i>Neea psychotrioides</i> J. D. Sm.
PIPERACEAE	<i>Piper biseriatum</i> C. D.C.
RUBIACEAE	<i>Hamelia patens</i> Jacq.
RUBIACEAE	<i>Pentagonia donnell-smithii</i> (Standley) Standley
RUBIACEAE	<i>Psychotria graciliflora</i> Benth.
RUBIACEAE	<i>Psychotria</i> sp. L.
SOLANACEAE	<i>Cyphomandra hartwegii</i> (Miers) Dunal
VIOLACEAE	<i>Rinorea deflexiflora</i> Bartlett
ZINGIBERACEAE	<i>Renealmia cernua</i> (Sw.) Macbr.

HERBS AND VERY LOW SHRUBS

ARACEAE	<i>Philodendron</i> Schott spp.
ARACEAE	<i>Spathiphyllum friedrichsthali</i> Schott
ARACEAE	<i>Syngonium</i> sp. Schott sp.
CONVOLVULACEAE	<i>Ipomea</i> sp. L.
COSTACEAE	<i>Costus</i> sp. L.
CYPERACEAE	<i>Scleria</i> sp.?
MELASTOMATACEAE	?
PIPERACEAE	<i>Piper visarantum</i> ?
POACEAE	<i>Paspalum</i> sp. L.
POLYGONACEAE	<i>Polygonum punctatum</i> Elliott
RUBIACEAE	<i>Sabicea villosa</i> Roemer & Schultes
SOLANACEAE	<i>Solanum lancaefolium</i> Jacq.

LIANAS

ARECACEAE	<i>Desmoncus costaricensis</i> (Kuntze) Burret
BIGNONIACEAE	?
FABACEAE	<i>Bauhinia guianensis</i> Aublet
SAPINDACEAE	<i>Paullinea</i> L. spp.

EPIPHYTES

ARACEAE

Anthurium spp. Schott

ARACEAE

Philodendron spp. Schott

ARACEAE

Syngonium spp. Schott

BROMELIACEAE

?

CACTACEAE

Rhipsalis baccifera (J. S. Mill) Stearn

CYCLANTHACEAE

Asplundia sp. Harling

ERICACEAE

Satyria elongata A. C. Sm.

ORCHIDACEAE

?

APPENDIX B
CANTARRANA SWAMP SEDIMENT PROCESSING SCHEDULE

APPENDIX B

CANTARRANA SWAMP SEDIMENT PROCESSING SCHEDULE

I used this schedule (PROC-JR2) to extract pollen from the Cantarrana Swamp sediment core. The process takes about six hours to complete on a batch of six samples. Dr. Sally Horn and John Rodgers III developed the process based on standard techniques (Berglund 1986).

PROC-JR2

NOTES:

This process should be performed in a laboratory fume hood. We used an IEC tabletop centrifuge, model MB, at ~ 2500 rpm. The Alconox solution in step 10 is made by dissolving 1/2 tsp. Alconox powder in 1000 ml distilled water.

1. Place 0.25 cc wet sediment in preweighed, 15 ml polypropylene centrifuge tubes and reweigh.
2. Add 1 *Lycopodium* tablet to each tube.
3. Add a few ml 10% HCl, and let reaction proceed; slowly fill tubes until there is about 10 ml in each tube. Stir well, and place in hot water bath for 3 minutes. Remove from bath, centrifuge for 2 minutes, and decant.
4. Add 10 ml hot distilled water to each tube, stir, centrifuge for 2 minutes and decant. Repeat for a total of two washes.
5. Add about 10 ml 5% KOH, stir, remove stick, and place in boiling bath for 10 minutes, stirring after 5 minutes. Remove from bath and stir again. Centrifuge 2 minutes and decant.
6. Wash 4 times with hot distilled water. Centrifuge for 2 minutes each time.

7. Fill tubes about 1/2 way with distilled water, stir, and pour through 125 μm mesh screen, collecting liquid in a labeled beaker underneath. Wash out material remaining in test tube with more distilled water. Wash screen with a powerful jet of distilled water.
8. Centrifuge down material in beaker by repeatedly pouring beaker contents into correct tube, centrifuging for 2 minutes, and decanting.
9. Add 8 ml of 52% HF and stir. Place tubes in boiling bath for 20 minutes, stirring after 10 minutes. Centrifuge 2 minutes and decant into waste receptacle.
NOTE: HF is dangerous! Wear protective gloves and clothing, and an HF respirator.
10. Add 10 ml hot Alconox solution to each tube. Stir well and let sit for 5 minutes. Then centrifuge and decant.
11. Add about 12 ml hot distilled water to each tube, so top of water comes close to top of tube. Stir, centrifuge for 2 minutes, and decant. Check top of tubes for an oily residue after decanting the hot water. If present, remove carefully with a bit of clean paper towel. Also at this time, examine the tubes to see if they still contain silica. If silica is still present, repeat steps 9-11. Assuming that no samples need retreatment with HF, continue washing with hot distilled water as above for a total of 3 water washes.
12. Add 10 ml of glacial acetic acid, stir, centrifuge for 2 minutes, and decant into waste receptacle.
13. Make acetolysis mixture by mixing together 9 parts acetic anhydride and 1 part concentrated sulfuric acid. Add about 8 ml to each tube and stir. Remove sticks and place in boiling bath for 5 minutes. Stir after 2.5 minutes. Centrifuge for 2 minutes and decant.
14. Add 10 ml glacial acetic acid, stir, centrifuge for 2 minutes and decant.

15. Wash with hot distilled water, centrifuge and decant.
16. Add 10 ml 5% KOH, stir, remove sticks, and heat in vigorously boiling bath for 5 minutes, stirring after 2.5 minutes. Centrifuge for 2 minutes and decant.
17. Add 10 ml hot distilled water, centrifuge for 2 minutes, and decant for a total of 3 washes.
18. After decanting last water wash, use a vortex mixer for 20 seconds to mix sediment in tube.
19. Add one drop 1% safranin stain to each tube. Use vortex mixer for 10 seconds. Add distilled water to make 10 ml. Stir, centrifuge for 2 minutes, and decant.
20. Add a few ml TBA, vortex for 20 seconds. Fill to 10 ml with TBA, stir, centrifuge for 2 minutes, and decant.
21. Add 10 ml TBA, stir, centrifuge 2 minutes and decant.
22. Agitate samples using the vortex mixer to mix the microfossils with the TBA left in the tubes. Carefully transfer the liquid to clean, labeled glass vials. Centrifuge down vials and decant.
23. Add several drops of silicone oil (2000 cs viscosity) to each vial (add more oil if there is a lot of sample). Stir with a clean toothpick.
24. Place uncorked samples in a dust-free cabinet to let the residual TBA evaporate.
25. Stir again after one hour, adding more silicone oil if necessary.
26. Check the samples after 24 hours; if there is no alcohol smell, cap the samples.

APPENDIX C
POLLEN AND SPORE TAXONOMY FOR THE CANTARRANA SWAMP

APPENDIX C

POLLEN AND SPORE TAXONOMY FOR THE CANTARRANA SWAMP

This table includes all of the pollen types that I recognized in the sediments of the Cantarrana Swamp. I combined many taxa from this list for illustration in the pollen diagrams (Figures 4.1-4.7). Pollen taxa that are designated "types" matched reference specimens or descriptions and photographs from published keys, but could not with certainty be separated from other taxa in the same group. The table also includes information on sexual systems, pollinator types, growth form, habitat and taxonomic richness for each taxon where known. Taxonomy follows Wilbur *et al.* (1994) except for species not covered in that work, in which case it follows Burger (1977-1995), or Standley (1937-1938).

FAMILY	GENUS / SPECIES / AUTHORITY	NOTES ON GROWTH FORM, HABITAT, TAXONOMIC RICHNESS	SEXUAL SYSTEM	POLLINATOR TYPE ²
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PTERIDOPHYTES

CYATHEACEAE	<i>Cyathea</i> -type J.E. Sm.	5 spp. at L.S., ³ some spp. are represented in upland primary forest, riparian habitats and swamp forest. ⁴		
HYMENOPHYLLACEAE	<i>Danaea</i> -type J.E. Sm.	5 spp. at L.S., ³ terrestrial genus of ferns, one sp. a primary forest type (<i>D. wendlandii</i>). ⁴		
POLYPODIACEAE	<i>Pteris</i> L.	5 spp. at L.S., ³ they have a range of habitats including primary forest, swamp forest, alluvial forest and weedy areas. ⁴		
SELAGINELLACEAE	<i>Selaginella</i> -type Beauv.	9 spp. at L.S., ³ a terrestrial genus, several spp. are associated with alluvial forest, riparian habitats, secondary growth and rocky streams. ⁴		
OTHER PTERIDOPHYTES	[classified by spore morphology]	the richest group of plants at L.S., about 173 spp. in 45 genera. ⁴		

GYMNOSPERMS

PODOCARPACEAE	<i>Podocarpus</i>	<i>P. guatemalensis</i> is not listed for L.S. but is a lowland forest sp., ⁵ while other spp. in CR are found in higher elevations. ⁶	M ⁷	wind ⁷
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MONOCOTS

ARACEAE	<i>Anthurium</i> -type Schott	largest genus in the family, most spp. are epiphytic, some are terrestrial, ⁶ 25 spp. at L.S. ³	H ⁸ M ⁶	med. bee ⁸
ARACEAE	<i>Dieffenbachia</i> -type Schott	terrestrial genus, about 1 m high, ⁶ 7 spp. at L.S. ³	M ⁸	beetle ⁸
ARACEAE	<i>Montrichardia</i> -type Crueger	only 1 sp. in CR, common on Atlantic coast growing in shallow water, quiet streams or open swamps, up to 3 m high, only 1 sp. in CR, ⁶ not listed in L.S. checklist. ³		

ARACEAE	<i>Philadendron grandipes</i> type Schott	no info on this species, other species of <i>Philadendron</i> epiphytic or terrestrial, 31 spp. at L.S. ³	M ⁸	beetle ⁸
ARACEAE	<i>Spathiphyllum</i> Schott	large terrestrial herbs, ⁶ 5 spp. at L.S., ³ <i>S. friedrichsthalii</i> is abundant in open swamps at L.S. ⁵	H ⁸ (SC)	med. bee ⁸
ARECACEAE	<i>Bactris</i> Jacq ex Scop.	low palms, abundant in the wet lowlands where they form dense thickets, especially plentiful in swampy places, ⁶ 4 spp. at L.S. ³	M ⁸	beetle ⁸
ARECACEAE	<i>Iriarteia deltoidea</i> Ruiz and Pavón	the only sp. in CR, ⁶ a tall palm, important in both primary forest on rolling terrain and in swamps at L.S. ⁵	M ⁸	med. bee ⁸
ARECACEAE	<i>Socratea durissima</i> -type H. A. Wendl.	the only sp. in CR, ⁶ important in primary forest both on rolling terrain and on terraces in L.S. ⁵	M ⁸	beetle/bee ⁸
ARECACEAE	undifferentiated	18 genera of palms at L.S., ³ subcanopy palms are an especially abundant and distinctive part of primary forests on rolling terrain ⁷	M/D ⁷	s.g.i. ⁷
BROMELIACEAE	<i>Guzmania</i> -type Ruiz and Pavón	4 spp. at L.S., ³ all are epiphytic. ⁶	H ⁸	hummer ⁸
COMMELINACEAE-TYPE		7 genera at L.S., ³ small to large herbs in various habitats, mostly in lowlands of CR. ⁶		
CYPERACEAE	<i>Fimbristylus</i> -type Vahl.	2 spp. at L.S. ³	M ⁷	wind ⁷
CYPERACEAE	undifferentiated	10 genera with more than 30 spp., the sedges make up 5% of the herb species at L.S. ⁵	M ⁷	wind ⁷
POACEAE	<i>Zea mays</i> L.	cultivated maize (corn)		wind ⁹
POACEAE	undifferentiated	42 genera with more than 60 spp., grasses make up 11% of the herb species at L.S. ⁵	M ⁷	wind ⁷
SMILACACEAE	<i>Smilax</i> L.	the only genus in the family contains 3 spp. at L.S., ³ all are vines. ⁶		

DICOTS

AMARANTHACEAE	<i>Alternanthera</i> -type Forssk.	3 spp. at L.S., ³ herbs or subshrubs, <i>A. laguroides</i> , of moist evergreen formations, 0-1500 m; <i>A. sessilis</i> , pioneer weeds in open sites and wet depressions, 0-1200 m; <i>A. tenella</i> , open sunny early secondary growth, 0-500 m. ¹⁰	H ⁷	bee ⁷
AMARANTHACEAE	<i>Amaranthus</i> -type L.	1 sp. at L.S., ³ <i>A. spinosus</i> , open sites and secondary growth, 0-1600 m. ¹⁰	H ⁷	bee ⁷
AMARANTHACEAE	<i>Chamissoa</i> -type HBK/ <i>Iresine</i> -type Humb. & Bonpl. ex Willd.	1 sp. of each genus at L.S., ³ <i>C. altissima</i> , shrub to 2 m or liana to 10 m, in evergreen wet and seasonally dry formations, 0-1500 m; <i>I. diffusa</i> , herbs, subshrubs or shrubs to 3 (5) m, secondary growth in open, sunny or partially shaded sites in both very wet and seasonally dry formations, 0-2600 m. ¹⁰	H/M ¹⁰	

AMARANTHACEAE	<i>Cyathula</i> -type Lour.	2 spp. at L.S., ³ herbs or subshrubs both weedy, found in open or partially shaded disturbed sites, stream beds and early successional vegetation, 1-1000 m. ¹⁰	H ¹⁰	?
AMARANTHACEAE	<i>Gomphrena</i> L // <i>Jamesbondia</i> -type Mears ined.	1 sp. of <i>Gomphrena</i> at L.S., ³ <i>G. serrata</i> , sm. herbs, common weeds in open sites, 0-1200 m, ¹⁰ no info. on <i>Jamesbondia</i> .	H ⁷	bee ⁷
ANACARDIACEAE	<i>Spondias</i> -type L.	3 spp. at L.S., ³ shrubs to medium trees, widely distributed, some with edible fruits, used as living fence posts. ⁶	D ⁷	s.d.i. ⁷
ANACARDIACEAE	<i>Tapirira guainensis</i> -type Aublet	widespread and prevalent in lowland forests ¹¹	D ⁷	s.g.i. ⁷
ANNONACEAE	<i>Annona</i> L.	3 spp. at L.S., ³ small to medium trees or shrubs, some with edible or otherwise useful fruits ⁶	H ⁸	beetle ⁸
APOCYNACEAE	<i>Forsteronia</i> -type G.W.F. Meyer (similar to <i>Prestonia</i>)	1 sp. at L.S., <i>A. viridescens</i> , ³ the genus contains lianas, ⁶ anthers usually exserted ¹¹	H ¹¹	
APOCYNACEAE	<i>Stemmadenia</i> -type Benth.	<i>S. donnell-smithii</i> is a widespread tree of disturbed habitats such as riparian forest, secondary forest, edges and pastures on Pacific slope, ¹² no info. on the ecology of the species at L.S.	H ⁸	Euglossine. bee ⁸
APOCYNACEAE	<i>Tabernaemontana</i> - type L.	2 sp. at L.S., ³ shrubs or small trees. ⁶	H ⁸	moth ⁸
AQUIFOLIACEAE	<i>Ilex</i> L.	<i>I. skutchii</i> is lowland sp., ⁵ others in CR are premontane and montane ^{6,5}	D ⁸	s.d.i. ⁸
ASTERACEAE	classified by pollen morphology as "high-spine" or "low-spine"	34 genera, more than 40 spp. (all Composites combined) at L.S., ³ more than half are exotics; at least 1 sp., <i>Erechtites heiracifolia</i> , is a classic pioneer at L.S. ⁵	M/H ⁶	s.g.i., and butterfly (Tubuliflorae) ⁷
ASTERACEAE	<i>Pseudoelephantopus</i> - type Rohr (fenestrate)	2 spp. at L.S., ³ one of them, <i>P. spicatus</i> , is described as a common weed in waste places, cultivated ground and pastures ⁶		
BEGONIACEAE	<i>Begonia</i> L.	herbs or shrubs sometimes annuals, often succulent, ⁶ this is the only genus at L.S. with 5 spp. and some undetermined types ³	M ⁸	sm. bee ⁸
BETULACEAE	<i>Alnus acuminata</i> HBK	trees 5-20m, 1500-3100m, esp. on landslides and in other disturbed areas, ¹⁰ one herbarium specimen from the Museo Nacional, CR was collected at 900 m elevation (personal observation)	M ¹⁰	wind ¹⁰
BIGNONIACEAE	<i>Arrabidaea</i> -type DC.	3 spp. at L.S., ³ probably all lianas ⁶	H ⁷	bee ⁷
BIGNONIACEAE	<i>Tabebuia chrysantha</i> -type (Jacq.) G. Nicholson	3 spp. of <i>Tabebuia</i> at L.S. ³	H ⁸	med.-lg. bee ⁸
BORAGINACEAE	<i>Tournefortia</i> L.	2 spp. at L.S., ³ shrubs (often scandent and forming thickets), large vines, or possibly small trees? ⁶	H ⁷	butterfly ⁷

BORAGINACEAE	<i>Cordia</i> L.	11 spp. at L.S., ³ shrubs to large trees, ⁶ some of L.S. forests were converted to plantations of one timber sp., <i>C. alliodora</i> ⁵ (C. <i>porcata</i> is SI)	H, S ⁸	moth / butter. ⁸
BURSERACEAE	<i>Protium</i> Burm. f.	3 spp. at L.S., ³ all are abundant subcanopy spp. in primary forest ⁷	D ⁸	s.d.i. ⁸
CECROPIACEAE	<i>Cecropia</i> Loebl.	2 spp. at L.S. <i>C. insignis</i> and <i>C. obtusifolia</i> , ³ along with other spp. dominate the secondary forest canopy at L.S., ⁵ 2 other spp. in CR: <i>C. peltata</i> , rare on Caribbean side, secondary growth, and <i>C. polyphlebia</i> , 1400-2400 m ⁴	D ⁷	wind and possibly bat ⁷
CHRYSOBALANACEAE	<i>Hirtella</i> -type L.	<i>H. lemsii</i> , a subcanopy tree and the only sp. at L.S., is known only from the northern Caribbean lowlands and the Osa peninsula in CR, no records from the southern Caribbean lowlands ⁷	H ⁸	bee ⁸
CLETHRACEAE	<i>Clethra</i> L.	shrubs or trees to 12 m, usually found between 1200 and 1900 m elevation, ⁶ <i>C. lanata</i> only species at L.S., ³ the family is more sp. rich at higher elevations (500-2500 m) ⁵	H ⁶	?
CLUSIACEAE	<i>Clusia</i> L.	10 spp. at L.S., ³ the genus contains shrubs or small to med. trees (apparently some subcanopy trees at L.S.) often beginning as epiphytes ⁶	D ⁸	lg. bee / beetle ⁸
CLUSIACEAE	<i>Garcinia</i> -type L.	= <i>Rheedea</i> , trees ¹¹	D ¹¹	
CUNONIACEAE	<i>Weinmannia</i> L.	shrubs or small trees common on the slopes of the central volcanoes at elevations above 1200 m, ⁶ small white flowers		probably wind
ELAEOCARPACEAE	<i>Muntingia</i> -type L.	A weedy, second-growth tree, ¹¹ according to Stanley (1937-38) there is only 1 sp. in Central America on the Pacific coast, this "type" may be one of the <i>Sloanea</i> sp. for which we do not have a ref. sample	H ⁷	s.g.i./bee ⁷
ELAEOCARPACEAE	<i>Sloanea</i> -type L.	6 spp. at L.S., ³ large canopy trees in lowland and mid-elev. forests, ¹¹ at least one, <i>S. latifolia</i> , is an emergent tree ⁷	H ⁷	s.g.i./bee ⁷
ERICACEAE		there are 2 genera (2 sp.) at L.S., <i>Satyria elongata</i> and <i>Sphyrropermum buxifolium</i> , ³ both are shrubs, the family is more typical of higher elevations, ⁵ Standley (1937-38) reports <i>S. elongata</i> from above 500 m and <i>S. buxifolium</i> from over 1000 m ⁶	H ⁷	wind ⁷
EUPHORBIACEAE	<i>Acalypha diversifolia</i> -type Jacq., Hort. Schoenbr.	common shrubs or small trees of evergreen formations 20-1100 m, monoecious, rarely bisexual ¹⁰	M ⁸	s.g.i. ⁷
EUPHORBIACEAE	<i>Acalypha</i> L.	possibly 7 spp. at L.S., ³ herbs, shrubs or small trees, usually unisexual, many are weedy plants of open sites ¹⁰	M/D ⁷	s.g.i. ⁷

EUPHORBIACEAE	<i>Alchornea costaricensis</i> Pax & K. Hoffm.	usually small trees, 0-800m ¹⁰	D ⁷	wind ⁷
EUPHORBIACEAE	<i>Alchornea latifolia</i> Sw.	trees 6-25 m tall, lower montane (40) 300-1600 (2300) m ¹⁰	D ⁷	wind ⁷
EUPHORBIACEAE	<i>Chamaesyce</i> S.F.Gray	4 spp. at L.S., ³ this genus formerly <i>Euphorbia</i> ; herbs or subshrubs, found in open, sunny or early successional sites, often assoc. with disturbance or sandy/gravelly soils, latex possibly caustic, not eaten by livestock or insects, ¹⁰ at Palo Verde, it occupies the swamp when the surface dries out ¹⁴	M ⁷	s.g.i. ⁷
EUPHORBIACEAE	<i>Croton</i> L.	trees, shrubs or herbs, bisexual or unisexual, many species are components in open weedy or early secondary vegetation ¹⁰	M ⁷ D ¹⁰	s.g.i. ⁷
EUPHORBIACEAE	<i>Hyeronima</i> Allemao	2 spp. at L.S., ³ <i>H. alchorneoides</i> , tree to 40 m, lowland evergreen forest, 5-700 (900) m, ¹⁰ grows on alluvial soils at L.S., ⁵ <i>H. oblonga</i> , a tree 4-25 m evergreen forest (100)500-2400 m, ¹⁰ occurs only along streams and on ridges in southern portion of L.S. ⁵	D ⁷	s.g.i. ⁷
EUPHORBIACEAE	<i>Sapium</i> P.Br.	2 spp. at L.S., ³ <i>S. aucuparium</i> , trees 5-20 m, monoecious, in evergreen and deciduous forests, collected most often bet. 900-2000 m; <i>S. oligoneurum</i> ¹⁰	M ⁷	s.g.i. ⁷
FABACEAE - Caesalpinioideae	<i>Bauhinia-type</i> L.	a common liana ("monkey's ladder") in primary forests of L.S. with dehiscent pods that explode at the end of the dry season, regenerates especially well in gaps and along trails ⁵	H ⁷	bee ⁷
FABACEAE - Caesalpinioideae	undifferentiated	4 other genera (8 spp.) at L.S. ³		
FABACEAE - Mimosoideae	<i>Acacia</i> P. Mill.	3 spp. at L.S., ³ trees or shrubs usually armed with spines or prickles ⁶	H ⁷	bee ⁷
FABACEAE - Mimosoideae	<i>Mimosa pigra</i> L.	Standley (1937-38) reports this shrub (1-2 m) only in the Meseta Central to the Pacific coast (although expected on the Atlantic side) as abundant in wet swampy places, sometimes growing in shallow water, also stream and lake margins; Janzen (1983) says only on roadsides and in pastures in the Atlantic lowland foothills	H ⁷	bee ⁷
FABACEAE - Mimosoideae	<i>Mimosa pudica-type</i> L.	a low herb, abundant and weedy in every inhabited part of Central America, growing around dwellings, cultivated or waste places and abandoned fields, ⁶ also called "sensitive" plant for its leaves that fold together when touched ⁶	H ⁷	bee ⁷
FABACEAE - Mimosoideae	undifferentiated	herbs, shrubs and trees, ⁶ 7 genera (39 spp.) altogether in the Mimosoideae at L.S. ³	H ⁷	bee ⁷

FABACEAE - Mimosoideae	<i>Pentaclethra macroloba</i> (Willd.) Kuntze	a canopy tree, this is the only species in the genus ⁶ , most abundant in Caribbean lowlands of Central America, dominant at L.S. ⁵	H ⁸ (SI)	sm. beetle ⁸
FABACEAE - Papilionoideae	<i>Andira inermis</i> - type (W.Wright) HBK	the only species in CR, an unarmed tree 9- 15 m common in lowland forests, possesses poisonous properties ⁶ , has unusual supra-annual flowering pattern at L.S. with some trees flowering only once in 12 years, possibly flowering more frequently on forest margins ⁹ .	H ⁸	med. bee ⁸
FABACEAE - Papilionoideae	<i>Machaerium</i> -type Pittier	2 spp. + undetermined sp. at L.S., ³ <i>M.</i> <i>floribundum</i> , a shrub or small tree, and <i>M.</i> <i>seemanii</i> an unarmed liana ⁶	H ⁷	bee ⁷
FABACEAE - Papilionoideae	<i>Swartzia</i> Schreber (probably <i>S. simplex</i>)	2 spp. at L.S., <i>S. simplex</i> is a small tree or shrub (2-3 m) common in La Selva but appearing to be restricted to the Caribbean lowlands; a larger <i>Swartzia</i> (to 10 m) is relatively rare at L.S., but widely distributed in Central America; identified by some specialists as the same species, but L.S. researchers have considered them the same ⁵	H ⁸ (SI)	lg. bee ⁸
FABACEAE - Papilionoideae	undifferentiated	altogether 25 genera (about 50 spp., some that cannot be determined to species) at L.S. ³	H ⁷	bee ⁷
FLACOURTIACEAE	<i>Laetia</i> -type Loefl.ex L.	<i>L. procera</i> , the only sp. of <i>Laetia</i> at L.S., ³ is a canopy tree that dominates in secondary forest at L.S. ⁵	H ⁸	med. bee ⁸
FLACOURTIACEAE	<i>Casearea</i> -type	5 spp. at L.S., ³ subcanopy trees ⁸ , <i>C. corymbosa</i> a tree of alluvial soils, ¹² <i>C. arborea</i> a rapid grower ¹⁰	H ⁸	s.d.i. ⁸
GENTIANACEAE	<i>Chelonanthus</i> -type	annual or perennial herbs ⁶ ; genus not listed at L.S., one other sp. of Gentian, <i>Lisianthus skinneri</i> , is listed for L.S., ³ may be <i>Lisianthus</i> , we have no reference material or descriptions of the pollen of that genus	H ⁶	
GENTIANACEAE	<i>Voyria</i> Aublet	1 sp., <i>V. tenella</i> (?) at L.S.	H ⁶	
GESNERIACEAE		9 genera (31 spp.) at L.S., ³ mostly herbs, shrubs or subwoody epiphytic climbers of wet or cloud forest habitat ¹¹	H ⁸ (at least 1 sp. is SC) ⁸	hummer /bee ⁸
GUNNERACEAE	<i>Gunnera</i>	massive perennial herbs generally at high elevations ⁶		
LECYTHIDACEAE	<i>Eschweilera</i> -type Martius ex. DC.	subcanopy trees ⁸ , 2 spp. at L.S. ³	H ⁸	lg. bee ⁸
LENTIBULARIACEAE	<i>Utricularia</i> L.	not listed at L.S. ³ ; herbs growing in water or on wet soil, only genus in CR ⁶ .		
LORANTHACEAE (often treated as one family with Viscaceae) ⁵	<i>Struthanthus</i> -type Martius	4 spp. at L.S. ³ ; parasitic epiphytes ⁷ .	H ⁶	

MALPIGHIACEAE	<i>Byrsonima</i> L. C. Rich. ex HBK	2 spp. at L.S., <i>B. crassipes</i> is cultivated at L.S., <i>B. crispa</i> (canopy tree ⁸) has bimodal distribution--Caribbean lowlands and Osa Peninsula ⁵	H ⁸	med.-lg. bee ⁸
MALPIGHIACEAE	<i>Heteropteris</i> HBK.	2 spp. at L.S., ³ lianas ⁶	H ⁷	bee ⁷
MALPIGHIACEAE	<i>Hiraea</i> -type Jacq.	2 spp. at L.S., ³ shrubs, or small trees ⁶	H ⁷	bee ⁷
MALPIGHIACEAE	<i>Spachea</i> -type Adr. Juss.	large canopy tree restricted to the Caribbean lowlands and Osa Peninsula in CR ⁷	H ⁷	bee ⁷
MALPIGHIACEAE	undifferentiated	10 genera (15 spp.) altogether at L.S., ³ lianas, shrubs or small trees ⁶	H ⁷	bee ⁷
MALVACEAE	<i>Hampea appendiculata</i> (J.D. Smed.) Standley	subcanopy tree, ⁸ early successional at L.S. ¹¹⁰	D ⁸	sm.-med. bee ⁸
MELASTOMACEAE/ COMBRETACEAE	undifferentiated	Melastomataceae is the 5th largest family at L.S. with about 90 spp., ⁵ herbs, shrubs and small trees in the understory to subcanopy, as canopy sp. only in the case of <i>Terminalia</i> (COMB), ⁸ only 2 genera (4 spp.) in Combretaceae at L.S., ³ mostly buzz-pollinated, anthers opening by terminal pores ¹¹	H ⁷	bee ⁷
MELIACEAE	<i>Trichilia</i> -type P.Br.	2 spp. at L.S., ³ small trees or shrubs ⁶	D ⁸	s.d.i. ⁸
MELIACEAE (see Sapotaceae / Meliaceae)	undifferentiated	3 spp. (not incl. <i>Trichilia</i>), ³ canopy and subcanopy trees, ⁸ one emergent, <i>Carapa guianensis</i> , is a dominant in forested swamps at L.S. ⁵	M, D ⁸	moth ⁸
MENISPERMACEAE	<i>Abuta</i> -type Aublet	1 sp., <i>A. panamensis</i> (= <i>Hyperbaena panamensis</i>), ³ liana in forests of Atlantic lowlands ⁶	D ¹¹	
MENISPERMACEAE	<i>Cissampelos</i> -type L.	3 spp. at L.S., ³ scandent herbs or shrubs and large vines/lianas ⁶	D ¹¹	
MONIMIACEAE	<i>Siparuna</i> Aublet	4 spp. at L.S., ³ shrubs or small trees ⁵	D ⁷	s.g.i. ⁷
MORACEAE	<i>Ficus</i> L.	16 spp. at L.S., ³ small to large trees or shrubs, rarely climbers (<i>Ficus shippii</i>) ¹⁰	M ⁸	wasp ⁸
MORACEAE (see also URTICALES)	<i>Maquira costaricana</i> -type (Standley) C.C. Berg (stephanoporate)	shrubs or small trees (2-10 m, rarely 20 m), in wet evergreen formations on both Pacific and Caribbean sides of CR, unisexual ¹⁰ .	D ⁸	wind ⁸
MYRICACEAE	<i>Myrica</i> L.	shrubs to small trees, growing from 800-2800 m, unisexual ¹⁰	D rarely M ¹⁰	?
MYRSINACEAE	<i>Myrsine</i>	= <i>Rapanea</i> , shrubs or small trees mostly from mid elevations, 1000-1800 m, ⁶ no <i>Myrsine</i> spp. at L.S.	H ⁷	bee ⁷
MYRSINACEAE	<i>Parathesis</i> -type (A.DC.) Hook. f.	3 spp. at L.S., ³ small trees and shrubs that are similar to <i>Ardisia</i> ¹¹		
MYRTACEAE	<i>Eugenia</i> L.	about 7 spp. (5 indeterminate and 1 cultivated) at L.S. ³	H ⁷	bee ⁷

MYRTACEAE	<i>Psidium</i> -type L.	only 1 sp., <i>P. guajava</i> , is known at L.S., ³ this small tree is planted and wild all over CR up to 1400 m ⁶	H ⁷	bee ⁷
MYRTACEAE	undifferentiated	Besides the 2 genera above there are 3 others at L.S., ³ the family is mostly shrubs and small trees and many spp. occur at higher elevations (1000-2800 m) ⁶		
OCHNACEAE	<i>Cespedezia macrophylla</i> Seemann	canopy tree, ⁸ only sp. in CR (and N.Am.) ⁶	H ⁸	med.-lg. bee ⁸
OCHNACEAE	<i>Ouratea</i> Aublet	3 spp. at L.S., probably shrubs or small trees (?) ^{6,8}	H ⁸	bee ⁸
OLACACEAE	<i>Heisteria</i> -type Jacq.	lianas, shrubs or small trees, the 3 spp. from L.S. ⁵ are usually found in moist and wet evergreen forests from 0-800 m ¹⁰	H ¹⁰	?
ONAGRACEAE	<i>Ludwigia</i> L.	= <i>Jussiaea</i> , 6 spp. at L.S., widely distributed (in the tropics) herbs, mostly in wet, swampy or muddy areas ⁶	H ⁷	bee ⁷
PHYTOLACCACEAE	<i>Phytolacca</i> -type L.	<i>P. rivinoides</i> the only sp. at L.S., ³ herbs or subshrubs of open disturbed or early successional sites, 0-1300 (1800) m, ¹⁰ known as a pioneer sp. at L.S.; barely persisting into the 2nd year, ⁵ 4 other genera present at L.S., ³ some of them weedy ¹⁰	H ¹⁰	?
PIPERACEAE	<i>Peperomia</i> Ruiz and Pavón	herbaceous plants with thick fleshy leaves, mostly epiphytic but a few are terrestrial, ¹⁰ 16 spp. at L.S. ³		
PIPERACEAE	<i>Piper</i> L.	the richest genus at L.S., ³ there are 45-48 spp. at L.S., mostly small to medium sized shrubs 1-3 m, a few are large shrubs or treelets (to 5 m) and vines, some are shade-tolerant understory sp., some are light-demanding pioneers and successional spp. ¹⁶	H ⁷	bee ⁷
POLYGALACEAE	<i>Polygala</i> -type L.	<i>P. paniculata</i> , the only sp. at L.S., ³ a herb common in pastures, other grassy areas and sometimes in cultivated ground from the Meseta Central to the coast in CR.	H ⁷	bee ⁷
POLYGONACEAE	<i>Polygonum</i> L.	2 spp. at L.S., ³ <i>P. hydropiperoides</i> , herbs, 0-200 m on Caribbean side, plants of river edges, wet depressions or sandy/gravelly soils near water; <i>P. punctatum</i> , herbs of wet depressions, stream sides and forest edges, 0-2000 m, most commonly encountered <i>Polygonum</i> sp. in Central America ¹⁰	H ⁷	bee ⁷
RHAMNACEAE	<i>Colubrina spinosa</i> J.D. Sm.	subcanopy tree, 9th most important tree in primary forest of swamp at L.S. ⁵	H ⁸	s.d.i. ⁸
RHAMNACEAE	<i>Gouania lupuloides</i> (L.) Urban	the only sp. at L.S., ³ a scandent shrub, common in thickets and open woods of the lowlands ⁶	H ⁷	bee ⁷

RHIZOPHORACEAE	<i>Cassipourea guianensis</i> Aublet	= <i>C. elliptica</i> , the only sp. at L.S., ³ typical in the understory of primary forest on rolling terrain ⁵	H ⁸	sm. bee ⁸
RUBIACEAE	<i>Hamelia</i> -type Jacq	2 spp. at L.S., ³ <i>H. patens</i> a shrub or small tree common in early secondary growth, ¹⁰ <i>H. xerocarpa</i> , shrubs or small trees in evergreen lowland forests ¹⁰	H ⁸	hummer ⁸
RUBIACEAE	<i>Psychotria</i> -type L. (inaperturate, rugulate)	shrubs, small to med. trees, rarely lianas, ¹⁰ 2nd most speciose genus at L.S. (almost 40 spp.) and one of the largest genera of Angiosperms, ^{10,5} especially common in the understory of evergreen forests and forest edges ¹⁰	S/H ⁸	various ⁸
RUBIACEAE	<i>Sabicea villosa</i> -type Willd. ex Roem. & Schult.	liana/climbing shrub in thickets of the Atlantic lowlands, ⁶ 0-600 m ¹⁰	H ¹⁰	?
RUBIACEAE	<i>Uncaria tomentosa</i> -type Schreber.	large liana in thickets and swamps of the Atlantic lowlands, often growing into the canopy (30 m), a troublesome weed; 10-300 m ¹⁰	H ¹⁰	?
RUBIACEAE	<i>Warszewiczia coccinea</i> (Vahl) Klotzsch	subcanopy tree, locally abundant in primary forest on old terrace at La Selva, ⁵ according to <u>Flora Costaricensis</u> , grows from 10-300 m in light gaps, edges and secondary growth ¹⁰	H ⁸	butter / hummer ⁸
RUTACEAE	<i>Zanthoxylum</i> L.	2 spp. at L.S., ³ both canopy trees ⁵	D ⁸	s.d.i. ⁸
SAPINDACEAE	<i>Paullinia</i> -type L.	10 spp. at L.S., ³ lianas	H ¹¹	
SAPINDACEAE	<i>Serjania</i> -type P. Mill	4 spp. at L.S., ³ lianas	H/D ⁷	bee ⁷
SAPOTACEAE	<i>Pouteria</i> -type Aublet	7 spp. at L.S., ³ lowland forest trees ¹¹	H/D ⁷	bee/s.g.i. ⁷
SAPOTACEAE (classified as Sapotaceae/Meliaceae)	undifferentiated	the only other genus in Sapotaceae at L.S. is <i>Chrysophyllum</i> (4 spp.) ³ , med. to large trees, ⁶ there is some overlap in the morphologies of pollen grains of Sapotaceae and Meliaceae so these families were grouped unless a specific type was recognized	H ¹¹	
SAXIFRAGACEAE-TYPE	possibly <i>Hydrangea</i>	hemiepiphytic liana, usually mid elevation, ¹¹ not listed at L.S.	H ¹¹	
SCROPHULARIACEAE	<i>Mecardonia</i> -type Ruiz. and Pavón	= <i>Bacopa procumbens</i> , ³ small herbs common in moist places, often sandy stream beds, widely distributed ⁶	H ¹¹	
SCROPHULARIACEAE	undifferentiated	7 genera at L.S., ³ herbs, rarely shrubs, many spp. are characteristic of wet areas or waste places, ¹⁰ tubular flowers ¹¹	H ¹¹	
SOLANACEAE	<i>Solanum</i> -type L.	large genus, highly variable in habit (herbs, shrubs, trees and lianas), ¹¹ esp. common in disturbed habitats.	H ⁷	bee ⁷
SOLANACEAE	undifferentiated	10 genera at L.S., ³ mostly small trees and shrubs in the understory and some lianas ^{8,5}	H ⁷	bee ⁷
STERCULIACEAE	<i>Byttneria</i> -type Loefl.	lianas ¹¹ , 1 sp., <i>B. aculeata</i> , at L.S., ³ 4 other genera of Sterculiaceae, (6 spp.) at L.S., ³ herbs, shrubs or trees, ⁶	H ¹¹	

TILIACEAE	<i>Goethalsia</i> -type Pittier	1 sp., <i>meiantha</i> , at L.S., ³ common in canopy of secondary forest at L.S. and in primary forest ⁵	H ⁸ (SI)	s.d.i. ⁸
TILIACEAE	<i>Mortoniendron</i> Standley & Steierm.	2 spp. at L.S., ³ common in tropical wet forest but also occurs in tropical moist forest ¹¹	H ⁷	bee ⁷
ULMACEAE	<i>Celtis</i> -type L.	only 2 spp. at L.S., ³ <i>C. iguanaea</i> has variety of growth forms, vines, lianas, shrubs or small trees, bisexual, <i>C. schippii</i> tree 10-30 m, bisexual ¹⁰	M/D ⁷	s.g.i. ⁷
ULMACEAE	<i>Trema</i> Lour.	trees 4-12 m, 0-2100 m but rare at lower elevations on Caribbean side, on open or partly shaded sites and in secondary growth ¹⁰	M ⁸	s.d.i. ⁸
URTICALES - Moraceae ¹⁵	genera other than <i>Ficus</i> and <i>Maquira</i> (described above)	10 genera (15 spp.) other than <i>Ficus</i> and <i>Maquira</i> at L.S., ³ trees or shrubs, rarely herbs or climbers, common in lowland evergreen tropical forests ¹⁰	M/D ⁷	wind ⁷
URTICALES - Urticaceae ¹⁵		6 genera (17 spp.) at L.S., ³ herbs, shrubs and small trees, especially along streams and in wet sites, some spp. of these genera are common in successional habitats	M/D ⁷	wind ⁷
URTICALES	<i>diporate</i>	some possible genera represented: <i>Boehmeria</i> , <i>Laportia</i> , <i>Phenax</i> , <i>Pilea</i> , <i>Urera</i> (all Urticaceae); <i>Artocarpus</i> , <i>Brosimum</i> , <i>Trophis</i> , <i>Perebea</i> (all Moraceae); <i>Coussapoa</i> , <i>Pourouma</i> (Cecropiaceae; some spp. of <i>Pourouma</i> are common in successional habitats) ¹¹	M/D ⁷	wind ⁷
URTICALES	<i>triporate</i>	some possible genera represented: <i>Boehmeria</i> , <i>Myriocarpa</i> , <i>Urera</i> , <i>Urtica</i> (Urticaceae), <i>Castilla</i> (Moraceae)	M/D ⁷	wind ⁷
URTICALES	<i>4-porate</i>	some 4-porate and polyporate Urticales pollen may be from the genus <i>Maquira</i> (Moraceae) described above	M/D ⁷	wind ⁷
URTICALES	<i>polyporate</i>	taxa uncertain	M/D ⁷	wind ⁷
VERBENACEAE	<i>Vitex cooperi</i> Standley	a canopy tree, the only sp. at L.S. ⁸	H ⁸ (SI)	med. bee ⁸
VIOLACEAE	<i>Rinorea deflexiflora</i> Bartlett	the only sp. at L.S., common understory tree in primary forest on rolling terrain ⁵	H ⁸	sm. bee ⁸
VITACEAE	<i>Vitis</i> L.	a large vine common in forests and thickets to 1500 m, <i>V. tilifolia</i> is the only native sp. in CR. ⁶ 1 other genus at L.S. contains 3 spp. ³	H ¹¹	
VOCHYSIACEAE	<i>Qualea</i> -type Aublet	at L.S. <i>Qualea</i> is known only from a few individuals on a ridge in the Sarapiquí annex, also occurs on hills north of Puerto Viejo and Chilamate ⁵	H ¹¹	
VOCHYSIACEAE	<i>Vochysia</i> Aublet	2 spp. at L.S., <i>V. ferruginea</i> (an abundant tree) ¹⁰ and <i>V. hondurensis</i> , ³ both canopy trees ⁸	H ⁸ <i>V. ferruginea</i> is (SC)	butter/bee ⁸

C.R. = Costa Rica, L.S. = La Selva

¹ Sexual Systems: H = hermaphroditic, M = monoecious, D = dioecious. (SI) = self incompatible, (SC) = self compatible

² Pollinator Types: sm. = small, med. = medium, lg. = large; butter = butterfly, hummer = hummingbird, s.g.i. = small generalist insects (after Bush 1995), s.d.i. = small diverse insects (after Kress and Beach 1994) [s.g.i. and s.d.i. are basically the same, see Appendix F].

³ Wilbur *et al.* 1994

⁴ Grayum and Churchill 1987

⁵ Hartshorn and Hammel 1994

⁶ Standley 1937-1938

⁷ Bush 1995

⁸ Kress and Beach 1994

⁹ Purseglove 1988

¹⁰ Burger, W. 1971-1995

¹¹ Gentry 1993

¹² Foster and McDiarmid 1983

¹³ Hernández and Gómez 1993

¹⁴ Fetcher *et al.* 1994

¹⁵ I did not classify any grains specifically to this family but likely some grains classified as Urticales are in this family.

¹⁶ Grieg 1993

APPENDIX D
POLLEN AND SPORE CONCENTRATIONS: CANTARRANA SWAMP

APPENDIX D

POLLEN AND SPORE CONCENTRATIONS: CANTARRANA SWAMP

Sample Depth (cm)	Pollen Grains/ g Dry Sediment	Pollen Grains/ cc Wet Sediment	Spores/ g Dry Sediment	Spores/ cc Wet Sediment
0	1.04×10^6	3.21×10^5	1.36×10^5	4.19×10^4
17*	4.59×10^5	2.47×10^5	8.56×10^4	4.62×10^4
50*	1.37×10^6	3.65×10^5	7.51×10^4	2.00×10^4
100*	4.71×10^5	3.36×10^5	2.34×10^5	1.67×10^5
112	6.44×10^4	4.40×10^4	2.99×10^4	2.04×10^4
136	2.09×10^5	1.23×10^5	4.95×10^4	2.91×10^4
160	4.99×10^5	1.43×10^5	6.50×10^4	1.86×10^4
184	3.70×10^5	1.15×10^5	5.64×10^4	1.75×10^4
216	9.08×10^5	4.30×10^5	7.86×10^4	3.72×10^4
232	4.55×10^5	2.04×10^5	2.51×10^5	1.12×10^5
248	2.54×10^6	1.36×10^6	1.56×10^4	8.31×10^7
272	2.22×10^5	1.26×10^5	6.60×10^4	3.73×10^4
320	8.76×10^5	2.01×10^5	9.15×10^4	2.10×10^4
344	5.19×10^5	2.01×10^5	5.16×10^4	2.00×10^4
368	3.16×10^5	1.29×10^5	4.37×10^4	1.79×10^4
392	3.33×10^5	1.04×10^5	1.03×10^5	3.21×10^4
416	7.19×10^5	1.59×10^5	7.46×10^4	1.65×10^4
440	1.27×10^5	7.24×10^4	6.45×10^4	3.68×10^4
464	3.45×10^5	9.90×10^4	3.85×10^4	1.10×10^4
488	2.30×10^5	9.11×10^4	2.16×10^4	8.58×10^7
512	2.79×10^5	1.36×10^5	2.32×10^4	1.13×10^4
536	7.16×10^5	4.75×10^5	1.65×10^5	1.09×10^5
560	4.98×10^4	3.70×10^4	9.59×10^7	7.11×10^7
588	1.40×10^5	9.92×10^4	1.25×10^4	8.84×10^7

* Adjusted depths (see Chapter 3)

APPENDIX E
TAXONOMIC RICHNESS OF POLLEN AND SPORES:
CANTARRANA SWAMP

APPENDIX E

TAXONOMIC RICHNESS OF POLLEN AND SPORES:
CANTARRANA SWAMP

Level (cm)	Pollen Taxa (including unknowns)	Total Pollen Counted	Unknown Pollen Taxa	Spore Taxa	Total Spores Counted	Pollen and Spore Taxa
0	51	345	7	11	45	62
17	55	316	9	7	59	62
50	31	311	6	4	17	35
100	54	361	12	7	179	61
112	65	313	16	15	145	80
136	51	325	15	9	77	60
160	53	315	6	7	41	60
184	45	306	8	9	47	54
216	38	358	9	9	31	47
232	56	332	19	13	183	69
248	21	327	2	1	2	22
272	62	330	19	11	98	73
320	40	316	10	9	33	49
344	41	302	8	10	30	51
368	41	311	6	10	43	51
392	48	327	14	11	101	59
416	30	347	9	5	36	35
440	57	319	18	14	162	71
464	53	341	15	15	38	68
488	46	329	11	13	31	59
512	37	313	2	9	26	46
536	11	334	0	8	77	19
560	25	338	6	8	156	33
588	50	314	9	12	28	62

APPENDIX F

**RELATIONSHIPS BETWEEN REPRODUCTIVE SYSTEMS OF LA SELVA
PLANTS AND THEIR REPRESENTATION IN THE POLLEN RECORD:
COMPARISON WITH A RECENT CONCEPTUAL MODEL**

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**RELATIONSHIPS BETWEEN REPRODUCTIVE SYSTEMS OF LA SELVA
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COMPARISON WITH A RECENT CONCEPTUAL MODEL**

Understanding the taphonomic processes that underlie fossil pollen spectra is important for predicting which taxa are likely to be under- or overrepresented in pollen records, and thus for interpreting patterns in such data. Pollen grains from the Cantarrana Swamp at the La Selva Biological Station, Costa Rica, are notably more diverse than are pollen spectra from other humid lowland sites in Costa Rica (Northrop and Horn 1996, Gray 1995, Horn and Rodgers, in progress). This contrast gives rise to questions of how taphonomic processes (e.g., pollen production, transport, and preservation) might vary from site to site.

Taphonomic processes in temperate ecosystems are relatively well studied (e.g., Tauber 1967, Davis and Brubaker 1973, Janssen 1973, Currier and Kapp 1974, Delcourt and Delcourt 1980, Jacobson and Bradshaw 1981, Davis *et al.* 1984), while in tropical areas, taphonomy has yet to receive much research attention. Mark Bush (1995) has been one of the first to consider the ways in which tropical taphonomic processes may differ from those in temperate areas. His 1995 paper introduces the first conceptual model (Figure A1) to explain and predict the abundance of individual pollen taxa in neotropical sediment records. Bush (1995) analyzed pollen records from Central and South America to study the potential for using a knowledge of a plant's reproductive system to predict its representation in the pollen record. The Cantarrana Swamp record provides an excellent opportunity to replicate this type of analysis in an area where the ecology of the modern

Pollination System:
wind > small insects > bat > bee > moth > hummingbird > cleistogamy (self-pollination)

Sexual System:
dioecy > monoecy > hermaphroditism (protogyny > protandry > distyly > monostyly)

Self-Compatibility:
allogamy > autogamy

Likelihood of Direct Contribution:
aquatic and riparian taxa > terra firma taxa

Figure A1 Bush's (1995) Model of Tropical Pollen Representation in Sediment Records: A Ranking of Pollinators, Sexual Systems and Compatibility in Terms of Outcrossing Potential (subheadings added by author)

vegetation is well documented (McDade *et al.* 1995). In this appendix, I report the results of a similar analysis of the Cantarrana pollen data. I first briefly summarize the Bush (1995) study and model. Then I describe relationships between plant reproductive systems in the La Selva flora and their representation in the Cantarrana pollen record. Lastly, I compare patterns in the Cantarrana pollen record to the model and results of Bush (1995).

BACKGROUND AND MODEL OF BUSH (1995)

The predominance of entomophily (insect pollination) in the lowland tropics was once thought to be a major stumbling block to meaningful pollen analysis in the tropics (Faegri 1966). Faegri (1966) thought that pollen of the rare, and generally weedy, anemophilous (wind-pollinated) trees would dominate tropical pollen records, and reduce their usefulness. In temperate regions, pollen records do represent primarily anemophilous taxa, while entomophilous species are largely underrepresented. Bush (1995) contends that such a "temperate" view of tropical ecosystems is invalid. Instead of viewing entomophily versus anemophily as the best predictor of taxonomic representation in the

pollen record, he suggests that palynologists consider outcrossing potential as a predictive character.

Bush's model suggests that a plant's pollination system, sexual system, and potential for self-pollination--all of which affect its potential for outcrossing--are the major factors influencing its representation in the pollen record. Anemophily, for example, is a common outcrossing mechanism in temperate areas, where anemophilous taxa are the major component of the pollen rain (Faegri and Iversen 1989). However, anemophily is not so effective in the lowland, wet tropics where most species are rare, trees are always in leaf, and winds are relatively weak especially beneath the canopy. Bush (1995) suggests that the role of small generalist insects in tropical pollination is similar to that of wind in temperate areas.

According to Bush (1995), sexual systems and self-compatibility are also important when measuring outcrossing potential. Dioecy guarantees outcrossing and is generally associated with massive pollen production (Bawa and Opler 1975). Bush's (1995) model suggests that wind pollinated, self-incompatible, dioecious taxa represent the highest potential for outcrossing, and therefore have the greatest likelihood of incorporation into the pollen record. Self-compatible hermaphroditic taxa (e.g., *Heliconia*, *Ludwigia*, *Vochysia ferruginea*) would represent the other extreme, and are least likely to appear. Finally, plant location is also important given that plants with any type of reproductive system may be represented in the record if their flowers are contributed directly to the water body, such as is the case with aquatic and riparian taxa (Bush 1995).

DATABASE FOR THE BUSH (1995) ANALYSIS

To develop his model, Bush reviewed 16 neotropical lowland pollen records from lakes and swamps in Brazil, Ecuador, and Panama. He ranked 162 reported pollen taxa based on both frequency of occurrence per record and abundance in the total pollen rain. His classes 1-3 (Table A1) represent taxa that were abundant in pollen records at several sites, while classes 4-6 comprise taxa that occur regularly but as a minor component, and at fewer sites. Comparison of these data with information on reproductive systems of the taxa showed that abundant pollen types are primarily from monoecious or dioecious plants that are pollinated by wind or small insects. Plants with long corolla tubes and specialized pollinators such as hummingbirds, moths, and butterflies are generally underrepresented in the pollen record.

THE CANTARRANA SWAMP ANALYSIS

To better understand taphonomic processes at the Cantarrana Swamp and the extent to which the pollen spectra follow Bush's model, I compared the reproductive systems of fossil pollen taxa to their representation and abundance in the pollen record. My main questions were 1) how well do the pollen spectra of the Cantarrana Swamp adhere to Bush's model?, and 2) how well do the reproductive systems of the fossil pollen spectra appear to represent those of the present La Selva forests? For this analysis, I looked only at the lowland taxa represented in the record and did not include any taxa that I classified as premontane or montane.

METHODS

I determined likely pollinators and sexual systems for each taxon based on the literature (results included in Appendix C). I excluded taxa (only a few) for which I could not find information on reproductive systems. To clarify terminology that is sometimes

Table A1 Most Abundant Pollen Taxa (Groups 1-3) in 16 Neotropical Records: Rank, Sexual Structure, and Pollinator Type (Bush 1995: Appendix, Table A1)

Pollen Type	Rank ¹	Structure ²	Pollinator ³
<i>Alchornea</i>	1	D	anem.
<i>Cecropia</i>	1	D	anem./bat
Combretaceae/ Melastomataceae	1	H	bee
Cyperaceae	1	M	anem.
Gramineae (Poaceae)	1	M	anem.
<i>Mauritia</i>	1	D	s.g.i.
Myrtaceae	1	H	bee
Urticaceae/ Moraceae	1	M/D	anem.
Euphorbiaceae	2	M/D	s.g.i./bee
<i>Iriarte</i>	2	M	bee
<i>Symmeria</i>	2	D	s.g.i.
Tubuliflorae (subfamily of Asteraceae)	2	H	s.g.i./butter.
<i>Acalypha</i>	3	M/D	s.g.i.
<i>Anacardium</i>	3	D	s.g.i.
Arecaceae	3	M/D	s.g.i.
<i>Celtis</i>	3	M/D	s.g.i.
<i>Chenopodium/ Amaranthus</i>	3	H	bee
<i>Didymopanax</i>	3	H	bee
<i>Ilex</i>	3	D/H	s.g.i.
<i>Mabea</i>	3	M	bee
<i>Pilea</i> (Urticaceae)	3	M/D	anem.
<i>Piper</i>	3	H	bee
<i>Trema</i>	3	M	s.g.i.
<i>Typha</i>	3	D	anem.

¹ Rank 1 = presence in > 10% of tot. pollen rain in 8 or more records, Rank 2 = presence in > 10 % of the tot. pollen rain in 4 - 7 records, and Rank 3 = presence in > 5% of the tot. pollen rain in 4- 7 records.

² M = monoecious, D = dioecious, H = hermaphroditic.

³ Anem. = (anemophilous, or wind-pollinated), s.g.i. = small generalist insect, butter. = butterfly.

variously used, I defined hermaphroditic as individual plants with bisexual (or perfect) flowers, monoecy as having separate male and female flowers on the same plant, and dioecy as a system in which individual plants are unisexual.

Sexual Systems

To compare how well different sexual systems were represented by the pollen taxa, I scored one point in each category (monoecious, dioecious, or hermaphroditic) for every pollen taxon (Appendix C) employing that type of system. For any taxon that employed more than one system, I counted one half point for each. For example, *Acalypha* (Euphorbiaceae) scored one-half point each for both "monoecious" and "dioecious". For the problematic Urticales (other than *Cecropia*, *Ficus*, *Celtis*-type and *Trema*-type), I assigned only one point for each of the following taxonomic and morphological groups: Urticaceae, Moraceae, diporate, triporate, 4-porate and polyporate, knowing that each of these groups may (or may not) represent several genera and species.

I compared the abundance of pollen grains representing each type of sexual system by assigning the total pollen count for each taxonomic group to the corresponding sexual system. I used the same groupings as for pollen diagrams rather than every individual taxon listed in Appendix C. For example, although I recognized several different types of Malpighiaceae grains, I grouped these all together for this analysis (as for the pollen diagrams). For the Malpighiaceae group, I assigned 38 (the total number of grains in all levels combined) to "hermaphroditic". If more than one sexual system was employed by any group, I arbitrarily assigned half the pollen count to each. These cases were rare and the pollen counts were small with one exception: for the "other Urticales" group, 692 pollen grains were divided between the monoecious and dioecious categories. The worst case error (i.e., if all the pollen represented only one of these systems) for this method

would make total pollen representation for each of these two sexual systems off by about 5%.

Pollination Systems

I analyzed the fossil pollen representation of different pollination systems by first assigning each pollen taxon to one or more of five pollinator classes: 1) *wind*; 2) *small generalist insects* (s.g.i. and s.d.i. in Appendix C), which includes a variety of relatively small insects such as small bees, beetles, flies, thrips, small wasps and butterflies (Kress and Beach 1994, Bawa *et al.* 1985a); 3) *bees*; 4) *fig wasps*; 6) *other*, which includes moths, hummingbirds and bats. I have used the term "small generalist insects" (after Bush 1995) in this paper to include the category "small diverse insects" used by Kress and Beach (1994) and Bawa *et al.* (1985). The published studies indicate that these authors are using slightly different names for more or less the same group of small insect pollinators.

Researchers have sometimes placed taxa in this category when no single most important pollinator could be detected (Kress and Beach 1994, Bawa *et al.* 1985a). A caveat to this categorization is that a significant proportion of the taxa that are assigned to the "small diverse insect"-pollinated group at La Selva may upon further study prove to be primarily bee-pollinated, according to Kress and Beach (1994). Although beetle pollination has been assigned to many of the taxa in Appendix C (usually by Kress and Beach 1994), for clearer comparison with Bush (1995), I have attempted to follow what I interpret to have been his approach, which was to group beetle-pollinated taxa with small generalist insect-pollinated taxa. But I also show beetle pollination data separately.

I tallied pollination system data in two ways. First, to look at taxonomic representation of each pollination system, I scored the taxa in the same way as for the sexual system analysis, adding one or one-half point to each pollinator category for every

pollen taxon representing it. For example, one point was scored in the "wind" category for Poaceae, and 0.5 in both "small generalist insects" and in "butterflies" for Asteraceae. The number of taxa used in the comparison of sexual systems is higher than for pollinator comparison because information on sexual systems was more widely available than for pollination systems.

Second, to look at what proportion of the pollen record was represented by each pollination system, I attributed the total pollen count for each taxon to the corresponding pollinator class. In a few cases, small generalist insects were listed for a taxon along with a specific pollinator such as beetle or bee. For these taxa, I attributed the full pollen count to the s.g.i. category, with the idea that that taxon may also be pollinated by small insects other than bees or beetles. I counted *Cecropia* pollen as wind-pollinated although bat pollination may be possible (Bush 1995). I counted Solanaceae as bee-pollinated although a couple of genera may be moth-pollinated. I counted pollen of the order Urticales (excluding the distinctive genera outlined above) as wind-pollinated (which most appear to be) although other forms of pollination may be possible for some species.

In assigning the total pollen counts to pollinator types, I used the same groupings of taxa as for the pollen analysis and diagrams (as described above). In a few cases, for example with the Rubiaceae, the grouping made assigning a single pollination syndrome impossible, so those families or genera were excluded.

I compared the results of these analyses with data on the reproductive systems of La Selva plant taxa (Kress and Beach 1994), and with the similar data on fossil pollen spectra compiled from 16 neotropical lowland records by Bush (1995).

RESULTS

Although a diversity of pollen taxa (> 100) appear in the Cantarrana pollen record, almost 3/4 of the total pollen was made up of only 13 lowland pollen taxa (Table A2). More than half of the taxa represented are pollinated by bees, but in terms of abundance of pollen grains, wind pollination is best represented (53.5% of total pollen grains, Table A3). Wind-pollinated taxa are more frequent in the Cantarrana sediments than they are in Bush's (1995) 16 sites combined, (Table A3). Anemophilous taxa are dramatically overrepresented (4x), while bee and small generalist insect-pollinated taxa are only slightly overrepresented when compared with expected values (Table A4). Proportions of bee and small generalist insect-pollinated taxa in the Cantarrana sediments are very similar to Bush's (1995) data. Taxa pollinated by moths, hummingbirds, and bats are the only group ("Other" in Table A4) that is largely underrepresented in the Cantarrana pollen record compared to its representation in the modern landscape (Kress and Beach 1994). Taxa with pollination system in the "Other" category are about 3.5x less frequent than expected at La Selva (Kress and Beach 1994), based on the modern flora, and half as frequent as in the combined neotropical records reviewed by Bush (1995). In terms of abundance, they represent less than 0.1% of the total number of pollen grains in the record.

Taxonomically, monoecious taxa appear to be somewhat overrepresented in the Cantarrana record while hermaphroditic taxa appear slightly underrepresented, when compared to the modern vegetation data (Table A4). But values for all sexual systems are close to the expected frequencies (Kress and Beach 1994), and remarkably similar to Bush's (1995) data (Table A4). Pollen grains of dioecious taxa are the most abundant type in the pollen record.

**Table A2 Lowland Pollen Taxa >1% Total Pollen: Cantarrana Swamp
(Purely High Elevation Taxa Not Included)**

Taxon	Total Pollen Grains	% of Total Pollen	Pollination System ¹	Sexual System ¹
1) <i>Cecropia</i> (Cecropiaceae)	1648	20.9%	wind	D
2) <i>Piper</i> (Piperaceae)	908	11.5%	bee	H
3) Other Urticales	692	8.8%	wind	M/D
4) <i>Alchornea</i> (Euphorbiaceae)	569	7.2%	wind	D
5) Melastomataceae/Combretaceae	466	5.9%	bee	H
6) Cyperaceae	328	4.2%	wind	M
7) Poaceae	323	4.1%	wind	M
8) <i>Pentaclethra</i> (Fabaceae)	233	3.0%	sm. beetle ^{2,3}	H ²
9) <i>Trema</i> -type (Ulmaceae)	220	2.8%	s.g.i.	M
10) Arecaceae (including <i>Iriarteia</i>)	144	1.8%	s.g.i./bee/beetle	M, D
11) <i>Chamaesyce</i>	107	1.4%	s.g.i.	M
12) Asteraceae (all types combined)	101	1.3%	s.g.i./butterflies	M
13) Mimosoideae	89	1.1%	sm. beetle ³	H
Totals	5828	74.0 %		

¹ Except where otherwise noted data are from Bush (1995).

² Kress and Beach (1994).

³ Grouped with s.g.i. for analysis.

Table A3 Representation of Pollination Systems in the Cantarrana Pollen Record: Comparison With Representation in the Present Vegetation and in Pollen Records from Other Neotropical Sites

Pollinator Type	Number of Taxa Cant. Swamp	Pollen Representation: Cantarrana Swamp (% Total Pollen)	Taxonomic Representation: Cantarrana Swamp (% Total Taxa)	Expected Value for La Selva ¹ (% Total Taxa)	Tax. Represent. Other Neotropical Sites (Bush 1995)
Wind	11	53.5%	11.5%	2.5%	6.5%
Bees	51	30.0%	53.1%	38.4%	50.5%
S. G.	25.5	15.6%	26.6%	23.9% ²	27.8%
Insects ³ (Beetles) ⁴	(6)	(3.6%)	(6.3%)	(12.7%)	
Fig Wasps	1	0.8%	1.0%	No Data	No Data
Other ⁵	7.5	<0.1%	7.8%	26.5%	14.8%
Totals	96	100%	100%	91.3%⁶	99.6%⁶

¹ Based on 276 La Selva plant species studied by Kress and Beach (1994).

² Small bees, beetles, flies, thrips, some wasps and butterflies (Bush 1995, Kress and Beach 1994, and Bawa *et al.* 1985a).

³ Combined small diverse insects and beetle categories from Kress and Beach (1994) to make comparable with Bush (1995).

⁴ Beetles are included in small generalist insect totals, but also shown here separately.

⁵ Includes moths, hummingbirds and bats.

⁶ Total is not 100% because these authors had other categories not comparable to my data.

Table A4 Sexual System Representation in the Cantarrana Pollen Record: Comparison With Representation in Present Vegetation and With Pollen Records from Other Neotropical Sites.

Sexual System	Number of Taxa Cant. Swamp	Pollen Representation Cantarrana Swamp (% Total Pollen)	Taxonomic Representation Cantarrana Swamp (% Total Taxa)	Expected Value for La Selva ¹ (% Total Taxa)	Tax. Represent. Other Neotropical Sites (Bush 1995)
Dioecy	22.5	41.7%	19.1%	17.4%	19.1%
Monoecy	21	21.9%	17.8%	12.4%	16.4%
Hermaphroditism	74.5	36.4%	63.1%	70.2%	64.5%
Totals	118	100 %	100 %	100 %	100 %

¹ Based on 507 La Selva plant species studied by Kress and Beach (1994).

DISCUSSION

Comparison with Modern Vegetation

Pollination and Sexual Systems

Of 276 flowering plant species with known pollination systems at La Selva, 2.5% are wind-pollinated (Kress and Beach 1994, Bawa *et al.* 1985a). In the pollen record, the abundance of pollen grains from wind-pollinated taxa (56% of the total counted) is striking and supports Faegri's (1966) assumption that anemophilous taxa are overrepresented in tropical lowland pollen records (as they are in temperate records). Also as Faegri (1966) predicted, many of the wind-pollinated taxa in this record (*Cecropia*, *Alchornea*, Cyperaceae, Poaceae, and at least some of the Urticales) probably represent weedy/successional vegetation reflecting local disturbance. But contra Faegri's (1966) predictions about the uninformative nature of tropical pollen records, these tropical wind-pollinated taxa tell a story. Significant downcore fluctuations in their pollen percentages

clearly indicate the dynamic disturbance history of forests around the Cantarrana Swamp (see Chapters 4, 5, and 6).

According to Kress and Beach (1994), no canopy trees at La Selva are known to be wind-pollinated; however, they note that the syndrome is easily overlooked and is more prevalent in lower strata. The Kress and Beach (1994) study did not include *Cecropia*, a wind (and possibly bat)-pollinated tree that dominates the canopy of secondary forest and many treefall gaps at La Selva. *Cecropia* is the most abundant taxon (20.9% of total pollen) in the Cantarrana pollen record.

Hermaphroditic taxa are well represented in the pollen record, but within that group it is important to note that only the types that are pollinated by bees, beetles and small generalist insects are likely to be common in the pollen record. Hermaphroditism is associated with several pollination systems at La Selva. However, all hummingbird and butterfly-pollinated taxa and 80% of bat-pollinated taxa are hermaphroditic (Kress and Beach 1995). These are the hermaphroditic taxa that are clearly underrepresented in the pollen record at La Selva (Table A3), or are absent altogether.

Breeding Systems (Compatibility)

Most tropical rain forest trees are now known to possess strong barriers to self-fertilization (Bawa *et al.* 1985b, Kress and Beach 1994). At La Selva, 88% of the studied canopy and subcanopy trees are self-incompatible (Kress and Beach 1994). The prevalence of dioecism or self-compatibility barriers guarantees outcrossing in most trees in the upper strata (Kress and Beach 1994). The vast majority of known self-compatible species at La Selva are understory components, particularly herbs (Kress and Beach 1994).

According to Bush (1995), self-compatibility in a taxon may reduce the chance of

its pollen being incorporated into sedimentary deposits and thus potentially into a pollen record. It is true that few taxa with known self-compatible members (e.g., *Spathiphyllum*, *Canna*, *Costus*, *Heliconia*, Marantaceae, Zingiberaceae, and Annonaceae) are represented in pollen records. This is the case even in the Cantarrana Swamp, a small basin where local and rare taxa are more frequently represented than in sediments of larger water bodies. However, self-compatibility alone provides no clear mechanism on which to base this assumption, unless self-compatibility is combined with low pollen production or low pollen release into the atmosphere. Flower morphologies such as long tubular or closed petals may inhibit pollen release such that most pollen remains with the flower as it drops and decays. Time spent in the detrital environment maximizes the likelihood that pollen will decay, and minimizes the chance that it will be transported to accumulate as sediment in a swamp or pond.

Low pollen production and enclosed flower morphologies do seem to appear in many self-compatible taxa. For example, self-pollinated flowers have fewer pollen tubes (Kress 1983), and selfers set fewer flowers and fruit (Kress and Beach 1994, Bawa *et al* 1985b, and references therein), characteristics which hint at the possibility of relatively low pollen production. And, although self-compatibility has not been proven to be associated with any particular pollination systems, 85% of the known hummingbird-pollinated species at La Selva (N = 20) are self-compatible (Kress and Beach 1994). If selfers do often have the long tubular flowers that are commonly associated with hummingbird pollination, that might help to explain their rarity or absence in the pollen record.

A case in point is the *Heliconia* (Heliconiaceae), an almost entirely self-compatible genus with deep-throated hermaphroditic flowers pollinated exclusively by hummingbirds (Kress and Beach 1994). *Heliconia* species are common elements in the understory of both closed forests, and forest edges and open habitats (Kress and Beach 1994), and yet the

genus has no representation at all in the Cantarrana pollen record. Kress and Beach (1994) suggest that an association between self-compatibility and hummingbird pollination may emerge as more species are studied. It may be that the low daily flower production combined with the long, curved floral tubes of most *Heliconias* (Kress and Beach 1994) has a negative effect on its chance of becoming part of a sediment record. In contrast, *Heliconias* adapted to more open sites produce many flowers daily and have short, straight perianth tubes (Kress and Beach 1994), but these are not represented in the Cantarrana pollen record either. So, it appears that none of the components of the reproductive system necessarily adequately explain the absence of *Heliconia* pollen from the sediment record.

The absence of *Heliconia* and of *Spathiphyllum friedrichsthali* from the Cantarrana pollen record may be indicative of another very important influence on taxonomic representation in sediments, that of pollen preservation. *Spathiphyllum* is a self-compatible aroid that presently dominates sections of the Cantarrana Swamp. Considering its current importance in the swamp, it is noteworthy that I found only one grain (in the surface sample) in the entire pollen record.

Pollen preservation depends on several factors, but most importantly, the composition of the exine of particular pollen types (Jarzen and Nichols 1996). Pollen grains have variable susceptibility to oxidation (such as occurs when the water table drops below the surface of a swamp) and other types of damage from physical, chemical and biological processes that occur during transport of sediments and in situ. The same pollen grains (with weaker exines) that are susceptible to oxidation are also likely to be susceptible to destruction by acetolysis used in processing sediments for pollen analysis (Moore *et al.* 1991, p.57; Roubik and Moreno 1991). Pollen of *Spathiphyllum*, *Heliconia*, Bromeliaceae, Marantaceae, and Zingiberaceae are among those known to be vulnerable to damage by acetolysis (Roubik and Moreno 1991), and may also be more sensitive to

damage from processes of transport, deposition or diagenesis. For some of these plant taxa, differential preservation may be more important than reproductive factors, or combine with them, in influencing their representation in the pollen record.

Self-incompatibility is relevant as an outcrossing mechanism only for hermaphroditic taxa at La Selva, because many monoecious taxa have self-pollination barriers (Kress and Beach 1994). It is also mostly important for understory herbs given that obligate outcrossing has already been confirmed for most tree species (Kress and Beach 1994). Hermaphrodites comprise about 75% of the understory species (N = 507) studied at La Selva. Interestingly, although self-compatibility is common in the understory (except in the Rubiaceae) at La Selva, systems that enhance outcrossing predominate (Kress and Beach 1994). Self-compatibility therefore may reduce, but does not preclude, outcrossing in plants. Kress and Beach (1994) consider the prevalence of two types of reproductive systems to be responsible for common cross-fertilization in the understory: 1) low daily flower production coupled with reliable long-distance pollinators such as euglossine bees and hummingbirds, and 2) monoecy, protogyny, and beetle pollination.

Comparison to Data From Other Neotropical Sites and to the Bush (1995) Model

One of the few discrepancies between the Cantarrana Swamp pollen record and the compilation of records from other neotropical sites is in taxonomic representation of anemophilous taxa (Table A3). The proportion of anemophiles in the Cantarrana pollen taxa (11.5%) is almost twice as high as in Bush's compilation of sites (6.5%). This inconsistency may be a result of differences between our studies in taxonomic assignment of the Urticales. As previously mentioned, pollen of the Urticales is sometimes difficult to identify to genus or family. Differences in classification are common between sites and between researchers.

Of greater interest are the striking similarities between our data. All of the top ten most abundant taxa in the Cantarrana pollen record are also included in Bush's pollen classes 1-3 (Table A1) except *Pentaclethra*. *Pentaclethra*'s abundance is unique to Caribbean lowlands of Central America and the genus is not listed in Bush's compilation. The similarity in our abundant taxa is consistent with Bush's prediction that taxa in his classes 1-3 are the most likely to be abundant in lowland tropical pollen records. The representation of pollination systems (Table A3) is similar to other neotropical sites (Bush 1995), especially for bees and small generalist insects. Data on sexual systems represented in the Cantarrana pollen record (Table A4) are remarkably similar to the data compiled by Bush (1995).

Clearly, the Cantarrana pollen record supports the two extreme relationships between fossil pollen representation and reproductive systems modeled by Bush (1995): 1) wind-pollinated, dioecious taxa (obligate outcrossers) are most likely to be abundant in the pollen record, and 2) autogamous taxa (self-pollinators) are least likely to be part of the pollen rain. However, in between the two extreme cases, there are some discrepancies between the model's predictions and the Cantarrana Swamp data. One example is that the two hermaphrodites most abundantly represented in the Cantarrana record (combined they make up 17.4% of total pollen), *Piper* and Melastomataceae / Combretaceae, are reportedly pollinated by bees (Bush 1995), rather than small generalist insects as might be predicted by the Bush (1995) model. Semple (1974), however, has reported small flies and small beetles, along with bees, pollinating *Piper*.

The Cantarrana data, however, do agree with the Bush *data* (if not with the model), i.e., pollen of *Piper* (Rank 3) and Melastomataceae / Combretaceae (Rank 1) are also abundant in his sites, along with several other bee-pollinated taxa (Table A1). Bees are such important pollinators at La Selva, transporting pollen for almost 40% of the studied

taxa (not including any bees that are part of the small generalist insect category), that the sheer abundance of bee-pollinated taxa may insure good taxonomic representation in the Cantarrana Swamp. But why are bee-pollinated taxa among the most abundant types in the pollen spectra at La Selva? The abundance of pollen from bee-pollinated taxa in the Cantarrana record, and in Bush's (1995) sites, hints at possible incongruities in the ranking of pollinators in the Bush model.

While monoecy and dioecy do generate frequent and even obligatory outcrossing, and prevent selfing, they apparently do not guarantee abundant fossil pollen representation except for plants that are pollinated by wind or small insects. Many monoecious and dioecious taxa are present, but not abundant, in the Cantarrana record and in other neotropical lowland sites (Bush 1995). Their relative rarity in the pollen record may be because they represent relatively rare taxa, or because other taphonomic processes are more important than outcrossing potential, or because outcrossing potential is not truly greater for plants with unisexual flowers (monoecious and dioecious) versus plants with perfect flowers (hermaphroditic).

Outcrossing is widespread among tropical plants, even in self-compatible species (Kress and Beach 1994). I would argue that outcrossing potential is difficult to measure, even in a relative sense, and that its usefulness in predicting fossil pollen representation is limited. For example, anemophily, ranked as having the highest potential among modes of outcrossing in Bush's model, is an efficient means of dispersing huge quantities of pollen (hence its abundant representation in tropical pollen records), but its randomness may render it relatively inefficient as an outcrossing mechanism in the lowland tropics where species are rare and winds unreliable.

Reliable long-distance pollinators like euglossine bees and hermit hummingbirds

provide an interesting contrast. These highly-specialized pollinators carry their cargo to widely dispersed understory species (e.g., *Heliconias*, gingers, gesneriads) that are self-compatible and have low daily flower production, but still accomplish cross-fertilization. That reproductive strategy seems to yield high potential for outcrossing, and yet plants using that strategy are not well represented in the pollen record. And bats, also specialized pollinators, which are ranked above bees in Bush's model, would seem to increase outcrossing potential, yet bat-pollinated plants are not well represented in pollen spectra from the Cantarrana swamp (nor in Bush's records from other tropical sites). While several components of the Bush model seem to be valid, the "potential for outcrossing" as a framing concept appears to break down between the extremes.

The data from Bush (1995) and this study do indicate a clear relationship between reproductive systems and fossil pollen representation. I interpret the Cantarrana and the Bush (1995) data as supporting the following: wind-pollinated and self-pollinated taxa are the extreme examples of the relationship between reproductive systems and pollen representation in tropical records. Other than those groups, self-incompatible taxa (outcrossers) of any sexual system that are pollinated by bees or other small insect pollinators are more abundant in the pollen record than those taxa of any sexual system that are pollinated by large and sometimes more specialized pollinators.

The major mechanisms that affect fossil pollen representation are pollen production, flower morphology and dispersal mode(s), the likelihood of direct deposition (determined for the most part by aquatic vs. terrestrial habitat, as in Bush (1995)), and pollen preservability. Superimposed on all of those are the possible effects of pollen reworking in a site, i.e., sorting by grain size, shape, or density, and sedimentary resuspension and redeposition, that influences the observed pollen assemblage (Delcourt and Delcourt 1980). As pointed out by Bush (1995), these mechanisms are not well-understood in the tropics,

and temperate region "rules" cannot be applied to tropical areas. Therefore, searching for more accessible "surrogate" predictors, such as Bush's model of outcrossing potential, is a worthwhile exercise.

We know almost nothing about the pollen production of most tropical plants, but perhaps it is suggested to some degree by pollinator types and flower morphology. Flower morphology is clearly a part of the pollination system, and is associated with particular pollinator types. Small pollinators may be good indicators of fossil pollen representation because they are associated with smaller, more abundant flowers that may result in higher pollen production. Taxa pollinated by large pollinators may be assumed to have larger and perhaps fewer flowers and possibly lower pollen production. Bush (1995) points out that flower morphology determines accidental release of pollen, which is most likely on open structured flowers versus tubular flowers that are usually pollinated by the larger long-tongued pollinators such as bats, hummingbirds and some moths. Open flowered species with protruding stamens, such as the Mimosoid legumes, would be more likely to spill pollen or lose it to the wind or rain than flowers with stamens inserted in tubular corollas. Bush (1995) notes that this may account to some degree for the abundant pollen representation of "buzz-pollinated" taxa such as *Melastoma*.

These are some of the known relationships between plant reproductive systems and pollen representation, most of which are well-reviewed by Bush (1995). By learning more about these relationships, and perhaps discovering new ones, we will be better able to understand taphonomic processes in the tropics. For example, documentation of relationships between pollen production and any other aspect of the reproductive system might allow us to extrapolate (carefully) to as yet unstudied taxa. Another interesting possibility is that a relationship exists between some aspect of the reproductive system and pollen preservability. For example, why are pollen grains of so many self-compatible taxa

susceptible to damage by acetolysis? This kind of information, if uncovered, could help tropical paleoecologists make better predictions of which taxa might be underrepresented or not represented at all in a pollen record, and in this way contribute to our ability to reconstruct past environments from fossil pollen.

CONCLUSION

This analysis shows that Bush's model of potential for outcrossing can help elucidate and predict taxonomic representation in the fossil pollen record, especially with regard to extremes of pollen representation. However, outcrossing potential as modeled by Bush (1995) does not adequately explain why some hermaphroditic taxa are so abundant and some obligate outcrossers are so rare in the Cantarrana sediments and in sediments from other neotropical sites. For these taxa, other factors, such as pollen production, flower morphology, and/or pollen preservability--none of which are fully incorporated into Bush's (1995) model--probably outweigh any effects of outcrossing potential.

VITA

Lisa Marie Kennedy was born in Indianapolis, Indiana on May 2, 1957. She graduated from Cascade High School (Hendricks County) in 1975 and continued to live and work in rural central Indiana for several years. She worked first as an orchardist, and then in the family greenhouse and produce business while earning a Bachelor of Arts (With Highest Distinction) in geography from Indiana University - Purdue University in Indianapolis. Her Bachelor's degree emphasis was in physical geography and she participated in field courses in the Rocky Mountains (biogeography and microclimatology) and in Costa Rica (tropical biology) that fueled her interests in vegetation dynamics and tropical landscapes. She entered the geography graduate program at the University of Tennessee in 1993 to focus on tropical vegetation change and environmental history, especially prehistoric human influence on vegetation.

Lisa has participated in research in Costa Rica and the Dominican Republic funded by the National Geographic Society, the National Science Foundation, and The A.W. Mellon Foundation. She spent the summer of 1994 in a plant systematics course offered by the Organization for Tropical Studies in Costa Rica. In 1996 she presented research at the International Conference on Quaternary Glaciation and Paleoclimate held in Venezuela, and participated in a post-conference field trip in the Andes.

Lisa was as a Hilton A. Smith Fellow for two years and also worked as a Teaching Assistant for introductory physical geography. Recently she has been a Research Assistant on a project funded by a grant to her advisor, Sally P. Horn, from The A.W. Mellon Foundation. She received her Master of Science degree in May, 1998 and will continue work on a Ph.D. in the Department of Geography at the University of Tennessee. She plans to continue to study vegetation dynamics and environmental history in the tropics.