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MODERN POLLEN RAIN IN COSTA RICA

A Thesis

Presented for the

Master of Science

Degree

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John C. Rodgers III

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ABSTRACT

The modern pollen rain of 29 sites in Costa Rica was characterized by analyzing pollen spectra in surface lake and pond sediments and soils. The sites were located within nine principal vegetation types: mangrove, tropical dry forest, derived savanna, tropical moist forest, tropical wet forest, premontane rain forest, montane rain forest, montane bog, and páramo. Pollen data were analyzed using cluster analysis and detrended correspondence analysis (DCA). Sites with similar vegetation showed similar pollen percentages and were clustered together in the cluster analysis and DCA. Results demonstrate that different vegetation types in Costa Rica can be distinguished by their modern pollen rain.

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CHAPTER 1

INTRODUCTION

The tremendous biological diversity of tropical rain forest environments has long attracted attention. Originally, it was believed that environmental stability over long periods of time in tropical regions was the cause for the high species diversity (Slobodkin and Sanders, 1969). Stable environments with unchanging climates would have allowed organisms unlimited time to evolve and seek out new environmental roles. More recently, scientists have argued that it is instability, rather than stability, that has produced highly diverse tropical ecosystems. There are two major theories that ascribe importance to unstable environments. The first is the "Pleistocene refuge theory," which attributes tropical diversity in South America to long-term oscillations in climate (Colinvaux, 1987). The theory postulates the existence of dry periods in the low latitudes during Pleistocene glacial episodes. During these drier periods, the Amazon rain forest is thought to have been fragmented, with rain forest species restricted to areas of persistent moisture or "refuges." Wetter conditions are thought to have returned during interglacial intervals, allowing rain forest species to migrate out of their refuges and intermix with species from other refuges. This migration of species into and out of refuges, driven by long-term climatic instability, is believed by some to be the major cause of high species diversity in the Amazon and adjacent areas of the neotropics [though the idea is not without its detractors, see for example Colinvaux (1987)].

The second theory that relates instability to diversity focuses on short-term environmental instability. This "intermediate disturbance theory" holds that repeated small-scale forest disturbances (from tree falls, storms, landslides, fires, and/or aboriginal humans) are

responsible for high tropical diversity. These disturbances are believed to continually create new opportunities and shift competitive balances of tropical species, thereby preventing the forest from ever reaching the "climax" successional stage (Connell, 1979). By reducing selective pressures on less competitive species, the intermediate disturbances are thought to lower extinction rates and lead to a higher accumulation rate of species over time.

Understanding causes for high species diversity in the tropics will be important in predicting how present rain forests habitats will respond to the increased environmental pressures that plague tropical regions. Paleoecological research can shed light on past human and natural disturbances and climate change in tropical environments, and on vegetation responses to them. Pollen grains, spores, charcoal fragments, diatoms, and other plant fossils in ancient sediments can reveal how tropical vegetation has changed over time periods of hundreds or thousands of years. The pollen records that result from these analyses can then be used to test ideas about the role of climatic change and disturbance in shaping biotic communities in particular areas of the tropics.

Interpreting past vegetation from fossil pollen requires a clear understanding of how different vegetation is represented in the pollen record. The usual approach is to determine how pollen from the modern vegetation is represented in sediment and how these modern pollen assemblages in the sediment vary across different habitats. Such studies are referred to as modern "pollen rain" studies because their aim is to characterize the "rain" of pollen that occurs at different sites. Modern pollen rain is defined as pollen from the modern vegetation that accumulates in adjacent sediments (Moore, *et al.*, 1991).

Some modern pollen rain studies make use of devices to trap pollen present in the air or washed out by rain (Tauber, 1974; Bush, 1992), but more often researchers utilize "natural" traps provided by lakes and

ponds, whose surface sediments contain pollen derived from present day vegetation. Moss polsters also trap pollen and can provide samples for modern pollen rain studies (Delcourt and Pittillo, 1986). Finally, surface soils can trap pollen and can be used in modern pollen studies, although preservation is sometimes poor.

The objective of this thesis is to characterize the "pollen signatures" (*i.e.*, the pollen percentages, indicator pollen types, and levels of pollen diversity) for different vegetation types in Costa Rica. I use cluster analysis and detrended correspondence analysis to test the hypothesis that the vegetation types of Costa Rica can be distinguished by their modern pollen rain. My thesis research investigates the pollen content of 27 surface lake sediment and soil samples collected by Sally Horn and collaborators, and two surface soil samples collected by myself. This thesis will provide the basis for interpreting fossil pollen spectra in sediment cores from Costa Rica and other neotropical areas.

This research is part of a wider study of Costa Rican lakes and their sediments that is being carried out by Sally Horn and Kurt Haberyan and collaborators (Horn and Haberyan, 1993). Their study is supported by grants from the National Geographic Society, the National Science Foundation, the Association of American Geographers, the University of Tennessee, and Troy State University. Companion studies have examined diatom assemblages in the sediment samples (Haberyan and Horn, 1993), and modern plankton communities in the lakes (Haberyan et al., 1993). Many of the lake sites included in this analysis of modern pollen assemblages have been cored for paleoecological studies.

CHAPTER 2

LITERATURE REVIEW: MODERN POLLEN RAIN IN TROPICAL ENVIRONMENTS

Many modern pollen rain studies have been carried out in the temperate regions (*e.g.*, Janssen, 1966 and 1967; Wright, 1967; Whitehead and Tan, 1968; Davis and Webb, 1974; Webb, 1974; Delcourt and Pittillo, 1986; and Jackson, 1990). The literature on tropical pollen rain is more limited, but has begun to develop. This chapter reviews previous pollen rain studies in tropical areas, with an emphasis on research in the New World tropics.

Flenley (1973) was one of the first to systematically investigate modern pollen rain in tropical environments. His work was motivated in part by a desire to test the feasibility of tropical pollen work. As described by Flenley, pollen analysis was once thought to be impossible in tropical regions. Major perceived limitations to tropical pollen work were (1) that the high plant diversity in tropical environments would hinder identification of pollen types, (2) that most tropical vegetation would produce low amounts of pollen because they are predominately animal pollinated rather than wind pollinated, and (3) that the scarcity of winds in tropical forest would limit dispersal of pollen grains (Flenley, 1973). Through modern pollen rain studies conducted by himself and others, Flenley demonstrated that these perceived difficulties did not in fact limit tropical pollen work. He found that diversity, though high, was manageable (especially through knowledge gained by studying pollen spectra deposited in areas of known vegetation). Flenley found that even though many tropical pollen taxa were never or only rarely encountered in samples, enough pollen grains were present that he could successfully relate modern pollen spectra to vegetation.

In his 1973 paper, Flenley reviewed modern pollen studies in East Africa, Southeast Asia, and tropical South America conducted through the 1970s. Among more recent studies in the Old World tropics is that of Burney (1988), who analyzed the pollen rain of different vegetation types in Madagascar. Burney found that dry mesic forest, xerophilous bush and thickets, rain forest, secondary forest, montane forest, sclerophyllous forest, and savanna and steppe vegetation types were distinguishable by their modern pollen rain (Burney, 1988). In the American tropics, Fine (1978) distinguished differences in the modern pollen spectra among the pine, subdeciduous tropical, and mangrove forests of Sinaloa and Nayarit Provinces, Mexico. Other neotropical pollen rain studies include Grabandt and Nieuwland (1985), who described relationships between modern pollen rain and montane vegetation in the Colombian Cordillera Oriental, and Bartlett and Barghoorn (1973), who related modern pollen rain to forest vegetation of Barro Colorado Island, Panama, as an adjunct to core studies from Gatun Lake.

Bush (1991) recently summarized data on pollen spectra in surficial sediments from 21 lakes in Central and South America. He found that many tropical lowland vegetation types were distinct in their modern pollen rain. Bush has established a network of pollen traps in different areas of Costa Rica, Panama, and other neotropical areas to determine differences in the air-borne pollen rain of different vegetation types (Bush, 1993; S. Horn, pers. communication, 1994). As part of this work, he has devoted attention to understanding the pollination modes of plants represented in pollen records. He has found that outcrossing taxa, the few that are wind-pollinated, and also those pollinated by small generalist insects, are commonly represented in pollen records (Bush, 1993).

In Costa Rica, Horn (1985a, 1993) previously investigated pollen in surface soils from mangrove and savanna sites in Santa Rosa National Park, and in surface lake sediments and moss polsters from páramo and

montane forest sites in Chirripó National Park. But prior to the present thesis, no attempt had been made to understand pollen deposition in the country of Costa Rica as a whole.

Until recently, fossil pollen work in Costa Rica also was limited. Paul Martin (1964) was the first to conduct paleoecological studies in this region. In a sediment core from a montane mire, he found evidence of shifts in montane forest vegetation as a result of climate cooling during the Late Pleistocene. Twenty years later, Kesel (1983) collected surface exposures of sediment from a former lake on the lower slope of the Cordillera de Talamanca that suggested that savanna vegetation had been present in the area since the Late Pleistocene (Kesel, 1983). Clary (1990), working in connection with the Tilarán Archaeological Project, made inferences about human habitation and human subsistence in the Cordillera de Tilarán during the Tronadora phase (2000 B.C. - 500 B. C.) based on the pollen content of soil samples from archaeological sites. More recently, Hooghiemstra *et al.* (1992) have examined pollen records from the La Chonta bog and nearby sites in the Cordillera de Talamanca that reveal altitudinal shifts in forest vegetation during the Pleistocene.

Aside from the work of Hooghiemstra and colleagues, all recent paleoecological research in Costa Rica has been conducted by Sally Horn and her students and collaborators. Horn's paleoecological research in Costa Rica began with investigations of marine sediments. Short cores from Golfo Dulce provided preliminary evidence of late Holocene vegetation history in southwestern Costa Rica (Horn, 1985b), while longer cores from Deep Sea Drilling Project Site 565 offshore of the Nicoya Peninsula yielded evidence of major shifts in montane forest communities likely associated with Pleistocene glacial cooling (Horn, 1985a). Pollen analysis and radiocarbon dating of sediment cores from glacial lakes in the Chirripó highlands of the Cordillera de Talamanca showed that the region has supported treeless páramo vegetation since

deglaciation some 10,000 years ago (Horn, 1990, 1993). Charcoal fragments in cores reveal that fires due to natural or human causes have repeatedly burned the páramo (Horn, 1989a, 1993). Fragments of charcoal in soil cores collected under forest at the La Selva Biological Station in the Atlantic lowlands reveal that this area also burned during the Holocene (Horn and Sanford, 1992). Whether fires burned only on plots cleared for agriculture or also spread into intact forest remains to be resolved, as does the possible significance of the intriguing match of radiocarbon dates on charcoal fragments and charcoal-rich sediment from La Selva and Chirripó.

Sally Horn and her students are presently examining microfossils in lake and swamp sediment cores from a number of sites in Costa Rica, including several of the sites whose modern sediments were examined in this study (Northrop and Horn, 1993; Killefer and Horn, 1993; Gray and Horn, 1994). The purpose of their research is to document long-term vegetation history in Costa Rica, especially as related to prehistoric human use of forests and natural climatic variability and change. These studies will require knowledge of the relationships between modern vegetation and pollen rain. My master's thesis research was designed to provide this information.

CHAPTER 3

DESCRIPTION OF SAMPLING SITES

The twenty-nine pollen sampling sites included in this thesis range in elevation from sea-level to 3820 meters on Costa Rica's highest peak. Mean annual temperatures at the sites range from over 28° C to below 5° C, and annual precipitation ranges from about 1500 mm at sampling sites in the seasonally dry northwestern Pacific lowlands to 4000 mm or more on the rainy Atlantic slope (Coen, 1983). Seven principal Holdridge bioclimatic life zones (Holdridge et al., 1971; Tosi, 1969) are included. Holdridge life zones are defined on the basis of temperature and moisture availability, but are given names that correspond to the expected mature or primary (non-disturbed) vegetation of the bioclimatic zone (Hartshorn, 1983). Although the Holdridge life zone system is a *climatic*, rather than *vegetation* classification, it is often used to describe vegetation types in Costa Rica (e.g., Burger, 1977; Hartshorn, 1983). That is, mature forest vegetation in areas with climatic conditions that fall within the premontane rain forest life zone is referred to as premontane rain forest. In this thesis, I have followed the convention of using Holdridge life zone names to describe vegetation types, except in cases where common usage or special edaphic or anthropogenic factors dictate otherwise. In naming vegetation in these special situations, I have used classifications offered by Hartshorn (1983) and Gómez (1986). The principal vegetation types sampled for this thesis were: mangrove forest, tropical dry forest, derived savanna, tropical moist forest, tropical wet forest, lowland tropical swamp, premontane rain forest, montane rain forest, montane bog, and páramo.

Twenty-seven of the samples I analyzed in this study were collected by Sally Horn and collaborators, mainly in July/August 1991. I collected two of the samples in August 1992. Figure 1 shows the location of the 29 sampling sites in Costa Rica. Table 1 lists the elevation, life zone, vegetation type, sample type, sample collector, and sampling date for each site. The life zone designation provides information on the climatic characteristics of the sites, which can be determined by examining the "Holdridge triangle" in Appendix I. Life zones were determined from the ecological (life zone) map prepared by Tosi (1969). I did not distinguish between major and transitional life zones in making life zone determinations and naming forest vegetation. Five sites that were mapped within the "tropical wet forest, transition to premontane" life zone (sites 11, 12, 13, 14, and 15) were included in the tropical wet life zone. Following Hartshorn (1983, 1988) and Holdridge *et al.* (1971), seasonally dry sites in lowland Guanacaste province that were mapped by Tosi (1969) as transitional between the tropical dry forest and premontane moist forest (sites 1, 2, 3, 4, and 5) were considered to be in the tropical dry forest life zone.

The following pages briefly describe the vegetation types sampled and the location and vegetation of the sampling sites. I begin with lowland mangrove forest, and from there move inland and upslope.

MANGROVE FOREST

Mangrove forests occur in protected sites along both coasts of Costa Rica. Five genera are present (though not all at every site): the red mangrove (*Rhizophora* spp.), the black mangrove (*Avicennia* spp.), the tea mangrove (*Pelliciera rhizophorae*), the white mangrove (*Laguncularia racemosa*), and the buttonwood mangrove (*Conocarpus erecta*) (Simberloff, 1983).

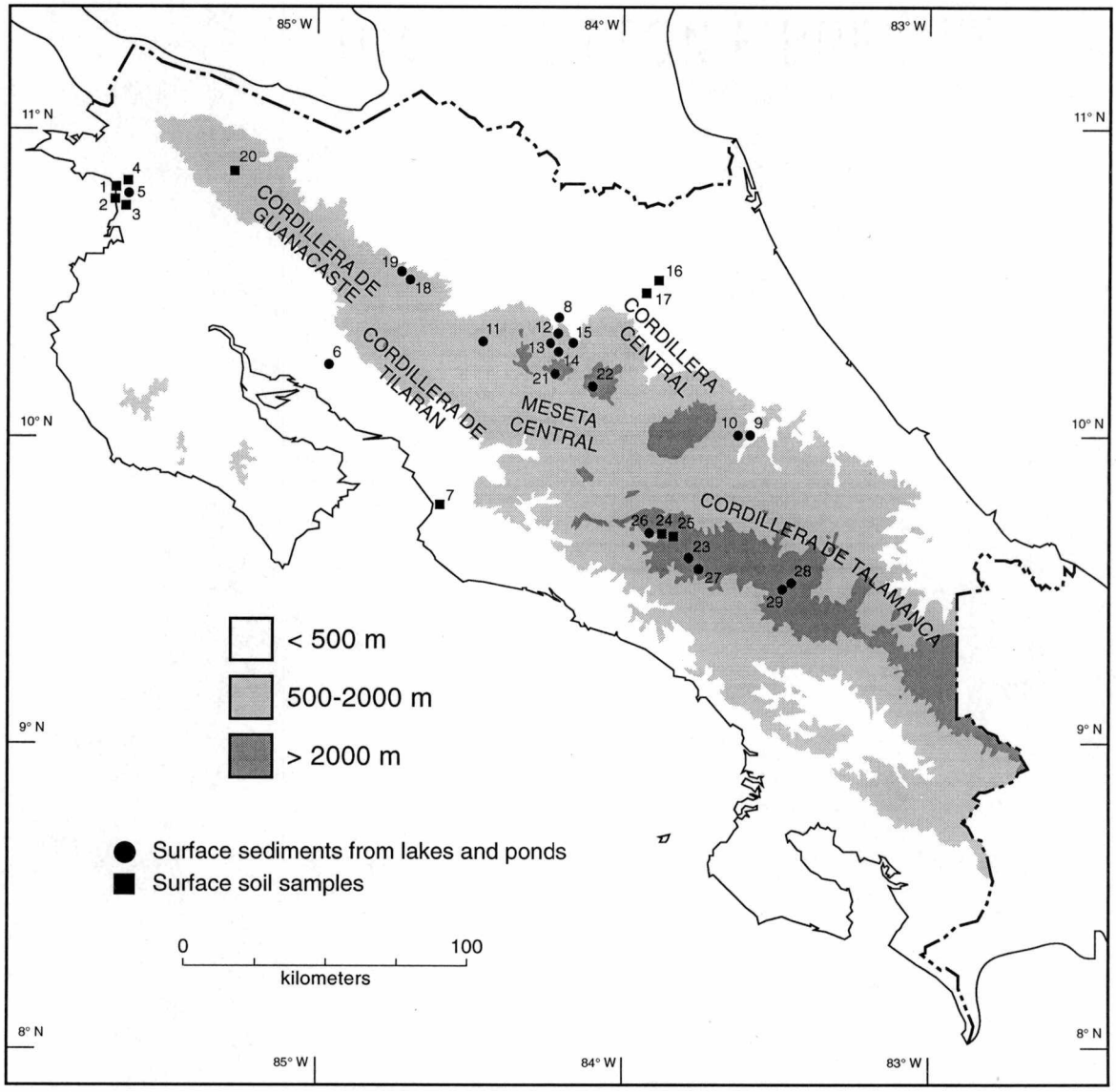

Figure 1: Modern pollen rain sampling sites, Costa Rica.

Table 1: Modern Pollen Samples

Site	Elevation	Life Zone	Vegetation Type	Sample type	Collector & Date
SRNP Mangrove (1)	0 m	tropical dry forest	mangrove forest	surface soil	Horn; March, 1991
SRNP Mangrove (2)	ca. 1 m	tropical dry forest	mangrove forest	surface soil	Horn; March, 1991
SRNP Tropical Dry Forest (3)	280 m	tropical dry forest	tropical dry forest	surface soil	Horn; March, 1991
SRNP Savanna (4)	280 m	tropical dry forest	derived savanna	surface soil	Horn; March, 1991
Escondido (5)	280 m	tropical dry forest	derived savanna	pond sediment	Horn; March, 1991
Palmita (6)	60 m	tropical dry forest	derived savanna	lake sediment	Horn & others; July/August, 1991
Carara (7)	35 m	tropical moist forest	tropical moist forest	surface soil	Rodgers, August, 1992
Río Cuarto (8)	380 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August 1991
Bonilla (9)	380 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
Bonillita (10)	450 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
González (11)	710 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
Congo (12)	740 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
Bosque Alegre (13)	740 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
Hule (14)	740 m	tropical wet forest,	tropical wet forest	lake sediment	Horn & others; July/August, 1991
María Aguilar (15)	770 m	tropical wet forest	tropical wet forest	lake sediment	Horn & others; July/August, 1991
La Selva Cantarrana (16)	36 m	tropical wet forest	lowland tropical swamp	surface soil	Horn & other; June/July, 1992
La Selva Suampo (17)	40 m	tropical wet forest	lowland tropical swamp	surface soil	Horn & others; June/July, 1992
La Palma (18)	610 m	premontane rain forest	premontane rain forest	lake sediment	Horn & others; June/July, 1992

Table 1: (continued)

Site	Elevation	Life Zone	Vegetation Type	Sample Type	Collector & Date
Cedeño (19)	610 m	premontane rain forest	premontane rain forest	lake sediment	Horn & others; July/August, 1991
Volcán Cacao (20)	1000 m	premontane rain forest	premontane rain forest	surface soil	Rodgers; August, 1992
Botos (21)	2600 m	montane rain forest	montane rain forest	lake sediment	Horn & others; July/August, 1991
Barva (22)	2840 m	montane rain forest	montane rain forest	lake sediment	Horn & others; July/August, 1991
Quebrador (23)	3040 m	montane rain forest	montane rain forest	lake sediment	Horn & others; July/August, 1991
Bog 68 (24)	2670 m	montane rain forest	montane bog	surface soil	Horn; March, 1985
Bog 70 (25)	2670 m	montane rain forest	montane bog	surface soil	Horn; March 1985
Tres de Junio (26)	2670 m	montane rain forest	montane bog	lake sediment	Horn & others; July/August, 1991
Asunción (27)	3340 m	montane rain forest	páramo	lake sediment	Horn & others; July/August, 1991
Morrenas (28)	3480 m	subalpine páramo	páramo	lake sediment	Horn & others; January, 1989
Chirripó (29)	3520 m	subalpine páramo	páramo	lake sediment	Horn; February, 1985

SRNP Mangrove (site 1 and site 2):

Two surface samples were collected from the mangrove forest behind Playa Naranjo, along the northwestern Pacific coast in Santa Rosa National Park (SRNP). The topography of this park in the Guanacaste province consists of an upper plateau that descends by a series of terraces to the Pacific ocean. A small area of mangrove forest occurs inland of Playa Naranjo (Hartshorn, 1983). Bonoff and Janzen (1980) described the vegetation as a nearly pure stand of *Avicennia germinans*, with scattered individuals of *Conocarpus erecta* and *Rhizophora mangle* found closer to the estuary. The white mangrove (*Laguncularia racemosa*) and the pantropical coastal tree *Hibiscus tiliaceous* are also present (Crease *et al.*, 1982; Hartshorn, 1983). The first SRNP mangrove sample (site 1) was collected adjacent to the estuary behind the northern end of Playa Naranjo. In a project for an Organization for Tropical Studies field course, Crease *et al.* (1982) studied the distribution of mangrove species along a transect that began near the sampling site and extended inland 150 meters at right angle to the coast. They found that *Rhizophora mangle* had the highest relative frequency but *Laguncularia racemosa* had the highest relative density. The relative frequencies (rf) and relative densities (rd) for the mangrove species were: *Avicennia germinans* rf = 10 and rd = 10; *Laguncularia racemosa* rf = 29 and rd = 41; *Rhizophora mangle* rf = 41 and rd = 29; *Hibiscus tiliaceous* rf = 20 and rd = 20. Crease *et al.* (1982) also found that *R. mangle* was most abundant near the coast (where the sample was collected) with *L. racemosa* and *H. tiliaceous* increasing in dominance away from the coast.

The second SRNP mangrove site (site 2) was located about 0.5 km inland from the coast, about 3 km southeast of the first site, at the site of an old salt extraction enterprise. The vegetation consists of a nearly pure stand of the black mangrove *Avicennia germinans*. Tropical dry forests surround the site on three sides. Bonoff and Janzen (1980)

listed the following taxa as present in these forests: *Caesalpinia coriaria, Prosopis luliflora, Manilkara zapote, Thouinidium decandrum, Licania arborea, Enterolobium cyclocarpum, Andira inermis, Bursera simaruba, Bombacopsis quinata, Cocoloba sp., Guaiacum sanctum, Tabebuia spp., Cedrela odorata, Swietenia macrophylla, Aphelandra deppeana, Casearia corymbosa, Allophylus occidenalis, Psychotria spp., Randia spp., Piper spp., Acacia spp., Stemmadenia obovata, Acalypha garnieri, Hamelia patens, Pithecolobium saman, Brosimum alicastrum, Hura crepitans, Terminalia chiriquensis, Pisonia,* EUPHORBIACEAE, APOCYNACEAE, and SAPINDACEAE (Bonoff and Janzen, 1980).

TROPICAL DRY FOREST

The **tropical dry forest** is a semideciduous forest consisting of only two layers. The canopy trees range from 20-30m tall with mimosoid and caesalpinoid leguminous trees dominating. The understory is 10-20m tall and is dominated by plants in the RUBIACEAE (Hartshorn, 1983). Most of the tropical dry forest that originally occurred in Costa Rica has been cleared for agriculture and cattle grazing (Janzen, 1986).

SRNP Tropical Dry Forest (site 3):

The tropical dry forest sample was collected within the forest along the nature trail near the casona (old estate house) on the upper plateau of Santa Rosa National Park. This forest is a secondary forest about 100 years old that has regenerated after selective logging and clearing for pastures. Taxa include *Hymenaea courbaril, Andira inermis, Trichilia spp., Exostemma mexicana, Bursera simaruba, B. tomentosa, Luehea sp., Guazuma ulmifolia, Ateleia herbert-smithii, Calycophyllum candidissimum, Plumeria ruba, Hemiangium excelsum, Manilkara zapota, Chlorophora tinctoria, Bombacopsis quinata, Acacia tenuifolia,*

A. collinsii, Machaerium biovulatum, Panicum maximum, Casearia corymbosa, C. sylvestris, Jatropha curcas, Aphelandra deppeana, Piper amalgo, Sapranthus palanga, Tetracera volubilis, Psychotria spp., Randia echinocarpa, R. karstenii, Rourea glabra, Selaginella sp., Banisteriopsis muricata, Forsteronia spicata, Serjania schiedeana, and *Byttneria catalpifolia* (Bonoff and Janzen, 1980).

DERIVED SAVANNA

Seasonally-parched **derived savannas** occur where tropical dry forests have been cleared and burned for pasture establishment. Scattered, fire-resistant trees are often present (Hartshorn, 1983, 1988).

SRNP Savanna (site 4):

The SRNP savanna site is located on the upper plateau of Santa Rosa National Park. According to Hartshorn (1983), here derived savanna vegetation is the result of the clearing and burning of an original forest dominated by the evergreen oak *Quercus oleoides*. The vegetation is dominated by introduced African grasses (especially *Hyparrhenia rufa*) with scattered trees. *Crecentia alata* (BIGNONIACEAE) is especially common in microdepressions, whereas the fire-resistant trees *Brysonima crassifolia* (MALPIGHIACEAE) and *Curatella americana* (DILLENIACEAE) are more common on drier ridges (Hartshorn, 1983; Vargas, 1987). Increasingly strict control of fire in Santa Rosa National Park has allowed a diversity of non-fire resistant woody species to invade the savannas, including *Tabebuia ochraceae, Cochlospermun vitifolium, Luehea candida, Dalbergia retusa, Spondias mombin, Bursera simaruba, Psidium guineense, Guazuma ulmifolia, Genipa americana, Eugenia salamanensis,*

Gliricidia sepium, Alibertia edulis, Cassia biflora, Cordia guanacastensis, Chomelia spinosa, and *Xylosma seemannii* (Vargas, 1987).

Escondido (site 5):

Laguna Escondido is a pond on the upper plateau of Santa Rosa National Park. The pond is an old cattle watering area that was constructed in the early part of this century (S. Horn, per. communication, 1994). As at site 4, the vegetation surrounding Escondido is largely derived savanna with scattered islands of trees. No site specific vegetation data are available, but many of the taxa listed under sites 3 and 4 may be represented.

Palmita (site 6):

Palmita is a man-made lake in the lowland Guanacaste Province (outside of Santa Rosa National Park) (Horn and Haberyan, 1993). The surrounding vegetation is mostly derived savanna used for pasture, probably consisting largely of African grasses as in Santa Rosa National Park. Scattered trees occur adjacent to the lake and in surrounding pastures. Taxa likely include some of the tropical dry forest species listed above for sites 3 and 4.

TROPICAL MOIST FOREST

Tropical moist forest was once the most extensive vegetation type in Costa Rica, but today only small pockets remain. It is a multi-layered, semideciduous or evergreen forest that includes many palm species and abundant herbaceous vines and woody lianas. In general terms, tropical moist forests can be thought of as intermediate in

characteristics between tropical dry and tropical wet forest (Goodland, 1969).

Carara Biological Reserve (site 7):

The Carara Biological reserve is located in the central Pacific lowlands, along the lower course of the Rio Grande de Tárcoles (Vargas, 1992). The reserve falls within the tropical moist forest life zone as mapped by Tosi (1969). According to Vargas (1992), 75% of the reserve consists of mature forest. The Carara sample was collected in an area of late successional forest that includes many species of the mature forest. The sample was collected from the nature trail off the Costanera Highway, about 0.5 km south of the reserve administration area. The specific sampling site was approximately 50 meters east of the trialhead, where a stream runs across the path. Vargas (1992) noted that three species are of particular importance in the late successional forests in this part of the reserve: *Schizolobium parahybum* (a tree fern), *Guazuma ulmifolia*, and *Cordia alliodora*. These species seem to comprise an intermediate stratum within the forest. Canopy trees include *Brosimum utile, B. costaricanum, Terminalia lucida, Spondias mombin, Tabebuia rosea*, and *Apeiba tibourbou*. The understory is open and dominated by palms such as *Scheelea rostrata* (Vargas, 1992). Strangler figs (*Ficus sp.*) also occur in the forest (S. Horn, pers. communication, 1994).

TROPICAL WET FOREST

The tropical wet forest is a tall, multilayered evergreen forest found in the wettest lowlands of Costa Rica. It is the most species-rich vegetation type in Costa Rica. Canopy trees range from 45-55 m tall, subcanopy trees from 30-40 m tall, and understory trees from

10-25 m tall. Palms and broad-leaved herbs are common in the understory but the ground layer is not thickly grown (Hartshorn, 1983).

Río Cuarto (site 8):

Río Cuarto occupies an explosion crater on the lower northern slope of Volcán Poás in the Cordillera Central. Remnant tropical wet forests grow along the crater walls, but the surrounding volcanic plain has been cleared for cattle pasture (Horn and Haberyan, 1993).

Laguna Bonilla (site 9) and Laguna Bonillita (site 10):

Lagunas Bonilla and Bonillita are located on the lower eastern slope of Volcán Turrialba, the southernmost volcano in the Cordillera Central. Both lakes are on terraces of the Río Reventazón; Bonillita is one third the size of Bonilla and is located higher than Bonilla on an older river terrace. The lakes are less than one kilometer from each other and are surrounded by pastures and small patches of remnant tropical wet forest. A preliminary study of arboreal vegetation near the lakes found the dominant plant families to be MORACEAE (51.57%), LEGUMINOSAE (27.7%), LAURACEAE (12.12%), and MYRTACEAE (9.09%) (Acuna *et al.*, 1983).

Laguna González (site 11):

González is a small, landslide-dammed lake near Ciudad Quesada on the northern end of the Cordillera Central. Most of the area surrounding the lake is in pasture, but tropical wet forest grows on the steep slope that slid in the landslide. A radiocarbon date on basal sediments of a 2.2 m sediment core from Laguna González indicates that

the lake, and hence the forest on the landslide scar, is about 350 years old (Horn and Haberyan, 1993).

Laguna Congo (site 12), Laguna Bosque Alegre (site 13), and Laguna Hule (site 14):

Congo, Bosque Alegre, and Hule are lakes occupying a single volcanic explosion crater on the north slope of Volcán Poás in the Cordillera Central. Tropical wet forest grows on the interior crater walls and the central subsidiary cone, but there is extensive clearing on the surrounding rim and on parts of the crater floor (Horn and Haberyan, 1993).

Laguna María Aguilar (site 15):

Laguna María Aguilar is located 2 km east of the Hule crater; it is a natural lake dammed by a volcanic flow. The lake is surrounded by cattle pastures but there is a small area of tropical wet forest on its western edge (Horn and Haberyan, 1993).

LOWLAND TROPICAL SWAMP

Lowland tropical swamp vegetation occurs within tropical wet forests, in low-lying areas subjected to flooding or persistent inundation.

La Selva Cantarrana (site 16) and La Selva Suampo (site 17):

The Cantarrana and Suampo sites are both located at the La Selva Biological Station in the Atlantic Lowlands of Costa Rica. Cantarrana is an open swamp dominated by the terrestrial aroid *Spathiphyllum sp.*

and other herbs. The tropical wet forest surrounding Cantarrana and throughout La Selva is dominated by *Pentaclethra macroloba*. Other taxa present near the swamp include *Luehea seemannii, Virola sebifera, Terminalia oblonga, Dipteryx panamensis* and a diversity of palms. Areas of old cacao (*Theobroma cacao*) plantation and recent tree falls near the swamp provide habitats for a number of successional species including *Cecropia sp.* (Farnsworth and González, 1989; Hartshorn, 1983; S. Horn, pers. communication, 1994).

The Suampo site is a large, forested swamp along the Sendero Suampo. The sample was collected near the northern corner of the area known as Plot II (Hartshorn, 1983). The vegetation is dominated by *Pentaclethra macroloba* and *Carapa guianensis*. Also abundant are *Apeiba membranacea, Adelia triloba, Astrocaryum alatum, Bactris longiseta, Colubrina spinosa, Dialyanthera otoba, Iriartea gigantea, Piper cenocladum, Pterocarpus officinalis, P. hayesii,* and *Welfia georgii* (Hartshorn, 1983).

PREMONTANE RAIN FOREST

The **premontane rain forest** is an evergreen forest with two to three layers. The sub-canopy and understory trees are very dense, with tree ferns and palms common. The ground layer consists of a dense covering of ferns, *Selaginella*, and broad-leaved herbs. Epiphytes, woody vines, and herbaceous climbers are very abundant.

Laguna La Palma (site 18) and Laguna Cedeño (site 19):

Lagunas La Palma and Cedeño are located on the north slope of Volcán Arenal, on the southern end of the Cordillera de Guanacaste. The vegetation near the lakes consists of a mosaic of premontane rain forest and pasture (Horn and Haberyan, 1993). Forests adjacent to and upslope

from the lakes are developed on prehistoric to recent lava flows and lahars, and are in various stages of succession (Vargas, 1985). Forest vegetation adjacent to Laguna La Palma is denser and in some areas, older (see aerial photograph in Horn and Haberyan, 1993). No site specific vegetation data are available, but the forests probably include some of the taxa recorded by Vargas (1985) in late successional forest elsewhere on the slopes of Arenal. Taxa listed for this forest type include *Trema micrantha, Lonchocarpus monofoliaris, Heliocarpus popayensis, Schizolobium parahybum, Cassia reticulata, C. fruticosa, Cecropia sp., Cedrela odorata, Alfaroa costaricensis, Peltogyne purpurea, Cordia alliodora, Guarea sp. Dendropanax arboreum, Iriartea gigantea, Socratea durissima, Asterogyne martiana, Chamaedorea sp., Piper spp., Guettarda crispiflora, Bauhinia cook, Clethra mexicana, Malvaviscus arboreus*, and *Cleome spinosa* (Vargas, 1985).

Volcán Cacao (site 20):

Volcán Cacao is located about 30 km south of the Costa Rican/ Nicaraguan border in the Cordillera de Guanacaste. The sample was collected along the trail to the Volcán Cacao field station (1000 m elevation). According to Janzen (1986), areas above 1000 meters on Volcán Cacao and adjacent Volcán Orosí are bathed in clouds at least eleven months of the year. The forest is dwarfed and trees are heavily covered with epiphytes. I noticed *Ficus, Piper, Urera,* and shrubby MELASTOMATACEAE to be present at the sampling site, but no other vegetation data are available.

MONTANE RAIN FOREST

Montane rain forest covers extensive areas in the Cordillera de Talamanca of Costa Rica, with small outliers surrounding volcanic peaks

of the Cordillera Central (Hartshorn, 1983). It is an evergreen forest that is thickly covered with mosses, small herbaceous epiphytes, orchids, and ferns. Tree ferns are common in the understory and the shrub layer is dense and may include dwarf bamboos (Hartshorn, 1983).

Laguna Botos (site 21):

Laguna Botos is a crater lake on Volcán Poás in the Cordillera Central (Horn and Haberyan, 1993). The vegetation of the crater has been described by Macey (1975). Montane rain forest dominated by *Clusia odorata, Weinmannia triana,* and *Didymopanax pittieri* grows on the steep crater walls that encompass the lake. A secondary layer of small trees includes taxa such as *Ardisia pleurobotrya, Miconia biperulifera, Cavendishia costaricensis, Myrrhidendron, Chusquea,* ERICACEAE and BROMELIACEAE. Lower montane wet forest grows directly downslope from the cloud forest, on the exterior slopes of the crater. This forest is dominated by *Miconia biperulifera.* Other important taxa include *Quercus spp., Ardisia, Didymopanax pittieri, Podocarpus, Chusquea, Bomarea acutifolia, Escallonia poasana, Hesperomeles obovata* and *H. heterophylla.*

Laguna Barva (site 22):

Laguna Barva is a crater lake on Volcán Barva in the Cordillera Central (Horn and Haberyan, 1993). The steep crater walls are covered with montane rain forest. The forest above 2600 meters elevation includes taxa such as *Ardisia sp., Brunellia costaricensis, Dendropanax sp., Ilex vulcanicola,* and *Viburnum mexicana* (Heaney and Proctor, 1990). The forest below the crater at about 2000 meters elevation includes taxa such as *Ardisia palmana, Brunellia costaricensis, Cinclima sp., Didymopanax pittieri, Hieronyma poasana, Miconia sp., Turpinia*

occidentalis, Tetrorchidium sp., Viburnum mexicanum, CYATHACEAE, HAMAMELIDACEAE, and MELASTOMATACEAE (Heaney and Proctor, 1990).

Quebrador (site 23):

Quebrador is a pond that lies in a steep-sided quarry along the Inter-American highway in the Cordillera de Talamanca (Horn and Haberyan, 1993). This area was once covered in dense montane rain forest dominated by *Quercus costaricensis* and *Q. copeyensis*, but following the construction of the highway in the 1940s, the most accessible areas were cleared for charcoal and timber production and converted to cattle pasture (Schubel, 1980). Oaks remain plentiful in pastures and in remnant areas of forest near the highway, and dominate extensive areas outside of the relatively narrow cleared zone along the road. Other arboreal species include *Weinmannia spp., Escallonia poasana, Schefflera pittieri, Drimys granadensis, Cleyera theaeoides, Garrya laurifolia, Ilex pallida, Miconia spp.*, and *Podocarpus spp.*; palms and *Chusquea spp.* are well represented in the forest understory (Weber, 1959; Gómez, 1986; Kappelle, 1991; Kappelle *et al.*, 1991). The rocky slopes immediately adjacent to Quebrador pond are covered with grasses and other herbaceous plants and low shrubs characteristic of disturbed sites (S. Horn, pers. communication, 1994).

MONTANE BOG

Montane bogs occur in poorly drained areas within montane rain forests in the Cordillera de Talamanca. Three sites were sampled in the "Madre Selva" region along the Inter-American highway. General descriptions of the vegetation of this area are included in Weber (1959), Gómez (1986), and Horn (1988).

Bog 68 (site 24):

Bog 68 (site 24) occupies a small depression near kilometer mark 68 along the Inter-American highway (east side of road). The surface of the bog is dominated by the terrestrial bromeliad *Puya dasilyroides*. Other nonwoody taxa present at the sampling site include *Sphagnum* and other mosses, grasses, sedges, pteridophytes, and *Xyris* (S. Horn, pers. communication, 1994). Woody plants include the arborescent fern *Blechnum buchtienii*, bamboo in the genus *Chusquea*, *Vaccinium consanguineum* and other ericaceous shrubs, *Ageratina sp.*, *Weinmannia spp.*, and *Rubus sp.* Montane rain forest dominated by oaks surrounds the bog. When sampled in March, 1985, there were a number of burned and downed *Blechnum* trunks at the site, indicating a past fire. Judging from the vegetation cover, this fire seems to have predated the 1984 fire at the nearby km 68.5 bog, studied by Horn (1988) (S. Horn, pers. communication, 1994).

Bog 70 (site 25):

Bog 70 (site 25) is located about 2 km from Bog 68, near km mark 70 on the west side of the highway. The vegetation of this site is more strongly reminiscent of the páramos found several hundred meters higher in elevation. *Puya dasilyroides* is less common here than at Bog 68; the dominant large plants are bamboo in the genus *Chusquea*. As at Bog 68, *Sphagnum* and other mosses are well-represented, along with grasses and sedges, and species of *Lycopodium* and *Jamesonia*. The small shrub *Hypericum strictum* is common within the bog. Woody plants occurring along the bog margin include *Blechnum buchtienii, Escallonia poasana, Vaccinium consanguineum, Diplostephium costaricensis, Senecio multivenius, Ageratina kupperi, Hesperomeles heterophylla,*

Myrica pubescens, *Oreopanax sp.*, and *Quercus sp.* (S. Horn, pers. communication, 1994).

Tres de Junio (site 26):

Tres de Junio (site 26) is a shallow bog pond very near to the Bog 68 sampling site (Horn and Haberyan, 1993). The surrounding vegetation is as described for Bog 68.

PARAMO

The highest peaks of the Cordillera de Talamanca extend above the upper elevational limit of montane rain forest, and are covered in treeless **páramo** vegetation of Andean affinity. This vegetation type is dominated by bamboo and other grasses and evergreen shrubs (Weber, 1959; Gómez, 1986; Horn, 1989b).

Asunción (site 27):

The Asunción site is a small pond near the summit of Cerro Asunción in the Buenavista páramo of the Cordillera de Talamanca. The páramo vegetation surrounding the pond is dominated by the bamboo *Chusquea subtessellata* and by evergreen shrubs in the ERICACEAE, HYPERICACEAE, and COMPOSITAE families. General descriptions of the vegetation of the páramo are included in Weber (1959) and Horn (1989b and 1989c). Janzen (1973a) examined vegetation recovery after a fire at the site in 1969.

Although the Asunción site supports páramo vegetation that shows close similarity with that of the more extensive Chirripó páramo, the area is mapped by Tosi (1969) as falling within the montane rain forest

life zone. Janzen (1973b, 1983a) has stated that this area along the Inter-American highway supported low montane rain forest, rather than páramo, prior to extensive clearing; however, its present treeless condition predates the construction of the highway (Horn, 1989b).

Morrenas (site 28):

Lago Morrenas is located at the base of Cerro Chirripó, the highest peak in the Cordillera de Talamanca and in all of Costa Rica (Horn and Haberyan, 1993). The páramo vegetation surrounding the lake is dominated by the bamboo *Chusquea subtessellata*, which reaches a relative cover of over 90% in some areas (Horn, 1989c). Intermixed evergreen shrubs include *Hypericum strictum, H. irazuense, Vaccinium consanguineum, Escallonia myrtilliodes, Diplostephium costaricense, Clethra gelida, Gaiadendron punctatum, Myrsine pittieri, Rhamnus oreodendron,* and *Ugni myricoides* (Kappelle, 1991). Tussock grass, sedges, dicotyledonous herbs, prostrate shrubs, pteridophytes, and mosses grow beneath the shrub canopy and in more open areas (Weber, 1959; Horn, 1989c, 1993). Moving downslope from the páramo, *Chusquea subtessellata* leads into *C. talamancensis* and arboreal taxa become dominant (Kappelle, 1991). The uppermost forests include *Vaccinium consanguineum, Weinmannia trianae, Diplostephium costaricense, Miconia spp., Myrsine pittieri, Schefflera pittieri, Gaiadendron punctatum, Ugni myricoides, Rhamnus oreodendron, Drimys granadensis, Oreopanax capitatum,* and *Quercus costaricensis* (Kappelle, 1991). Further downslope, the forest are dominated by *Quercus costaricensis* mixed in with *Chusquea talamancensis, C. subtessellata, Schefflera pittieri, Drimys granadensis, Weinmannia trianae, Myrsine pittieri, Q. copeyensis, Cleyera theaeoides, Ilex pallida, Podocarpus oleifolius, Saurauia veraguasensis, Persea sp., Ardisia sp.,* and *Styrax argenteus* (Kappelle, 1991).

Lago Chirripó (site 29):

Lago Chirripó occupies a second glaciated valley at the base of Cerro Chirripó. It is the highest and largest lake in a chain of three lakes dammed by rock thresholds and moraines (Horn, 1989a, 1993). Vegetation is as described for the Morrenas site.

CHAPTER 4

METHODS

EXPERIMENTAL DESIGN

The hypothesis being tested in this thesis is that the different vegetation types of Costa Rica can be distinguished by their modern pollen spectra. The experimental design consisted of collecting samples from different vegetation types, processing these samples to expose the pollen grains, identifying and counting pollen grains from each sample, and then determining how the pollen percentages for the individual samples and vegetation types compared. To test whether the pollen rain of different vegetation types is distinct, pollen percentage data for pollen types found in each sample were analyzed by both cluster analysis, which is a clustering technique that statistically groups similar sites, and detrended correspondence analysis, which is an ordination technique that plots similar sites close to each other. This chapter outlines in detail the steps used in this experimental design to test the hypothesis.

SAMPLE COLLECTION

The majority of samples consisted of lake or pond sediment collected from the mud/water interface with a dredge or other sediment sampling device. Surface soil samples were used in areas where no lakes exist. Most of the lake and pond samples were collected with a modified Peterson dredge (Haberyan and Horn, 1993); the Lago Morrenas sample was dredged with a weighted bucket. The dredge and weighted bucket collected the top 5-10 cm of surface lake sediment. Most of the samples were taken near the centers of the lakes or ponds. After collection,

samples were stored in polyethylene or glass bottles and refrigerated at 6° C.

The Lago Chirripó sample was taken from the top centimeter of Horn's Chirripó 1 sediment core (Horn, 1989a). This sediment core was raised in January, 1985 using a PVC pipe fitted with a rubber piston (Horn, 1989a). Further information on this and a second core from Lago Chirripó can be found in Horn (1989a) and Horn (1993).

The surface soil samples were collected by taking ten random pinches (Adam and Mehringer, 1975) of the top one to two centimeters of soil in an area of ca. 50 to 100 m^2.

Because all samples were collected on or just below the soil or sediment surface, the pollen within the samples was from the modern vegetation. The soil samples probably preserve the pollen rain of the past one to five years, whereas the sediment samples may integrate the pollen rain of the past 5-50 years. Thus, even in watersheds that have been recently deforested, the surface lake sediments may contain some pollen from the earlier forest communities.

SEDIMENT PROCESSING

The surface lake sediment and soil samples were processed using standard palynological techniques (Faegeri and Iversen, 1975). I used a basic processing schedule developed by Dr. Horn and students, with some modification for sediments that clumped strongly when processed using the original procedure. Both processing schedules are described in Appendix II. *Lycopodium* control spores were added to most of the samples (Stockmarr, 1971). *Lycopodium* control spores make it possible to calculate pollen concentrations and serve as a check on the pollen processing method. The control spores were not added to samples from sites 3, 5, 9, 11, 24, 25, 28, and 29. At the time those samples were

processed, the *Lycopodium* tablets were suspected of causing samples to clump, an interpretation that turned out to be incorrect.

Initial sample preparation differed for the surface lake sediments, core top sample, and surface soils. The surface lake and pond sediments were first stirred manually in their storage bottles for two minutes to produce a homogeneous mixture. A sample of 0.6 ml of sediment was then taken from the bottles and placed in a pre-weighed, 15 ml polypropylene test tube. The sample was reweighed to determine the wet weight of the sediment sample, then processed for pollen analysis. A duplicate 0.6 ml of sediment was taken immediately after the first and place in a pre-weighed crucible. The crucible plus wet sediment was weighed and then dried at 100°C for 24 hours. After drying, the sample was reweighed to determine the amount of water in the sediment. The crucible and sediment were then ignited at 550°C for one hour and reweighed to determine the amount of organic material in the sample. (Dean, 1974).

Preparation of the Chirripó sample involved taking 0.25 cc of sediment from the top centimeter of the core. The 0.25 cc sample was placed into a pre-weighed, 15 ml polypropylene test tube. The wet weight was determined, as described above, and the sample was then processed using the standard procedure. An additional 0.25 cc of sediment was taken and placed in a pre-weighed crucible to determine the water and organic content of the sample, as described above.

The surface soil samples from the two montane bogs did not need special pretreatment. For those samples, 1.0 cc of material was processed for pollen and sediment analysis. The other surface soil samples all contained large pieces of organic debris and/or sand and gravel, and needed to be sieved prior to processing. For these surface soil samples, I added 10-20 cc of soil to 50 ml of distilled water. The suspension was stirred for two to four minutes until the solution was

somewhat homogenized. During the stirring, large chunks of soil were mechanically crushed with a metal stirrer. The resulting mixture was sieved through a 250 um mesh screen into a plastic beaker. The screens were squirted with distilled water until most of the organic material had been washed down. The material that passed through the sieve was concentrated by repeated centrifuging for 2 minutes at about 2500 rpm. Approximately 0.6 cc of this material was then subsampled for pollen and sediment analyses as described above.

POLLEN COUNTING

The processed pollen residues were stained with safranin, suspended in silicone oil, and mounted onto microscope slides. Transects of the slides were examined under a light microscope at 400x. A "species area curve" (P. and H. Delcourt, pers. communication, 1993) was constructed for each of the vegetation types. The species area curve is an indicator of pollen type diversity in samples and was used to determine the total number of pollen grains that needed to be counted to have a sufficient sample size. This procedure suggested that a total count of 350 pollen grains exclusive of fern spores and indeterminate pollen was sufficient. The pollen types were identified to the lowest taxonomic level by using a pollen reference collection and published keys and photographs (especially Roubik and Moreno, 1991; Bartlett and Barghoon, 1973; and Horn, 1986, and references cited in those publications). The indeterminate pollen grains were classified based on the factors that rendered them unidentifiable (Delcourt and Delcourt, 1980). Fern spores were counted outside the pollen sum, and were mostly classified by morphology.

Pollen concentrations per gram dry sediment were determined by the following formula:

$$\text{Pollen concentration} = \frac{TP}{EDW} \times \frac{LA}{LC}$$

where TP = total number of pollen and spores counted, EDW = estimated dry weight of sample (in grams), LA = number of *Lycopodium* spores added, and LC = number of *Lycopodium* spores counted. The dry weight of the samples processed for pollen was estimated by multiplying the wet weight of the pollen samples by the percent dry matter in the wet sample (i.e., 1 - percent water content). Pollen concentrations could not be determined for samples not processed with *Lycopodium* spores.

MODERN POLLEN DATA ANALYSIS

Patterns in the pollen spectra among the individual sites and the vegetation types were statistically shown by using cluster analysis (Ward, 1963) and detrended correspondence analysis (Hill, 1980). The data used in the computations consisted of the pollen percentages for the major pollen types encountered in each sample. Only those pollen types that comprised 2% or greater of the total pollen in any sample were used in the analyses (Lamb, 1984).

Cluster Analysis:

Ward's Minimum Variance Hierarchial Cluster Analysis (Ward, 1963; Anderson and Davis, 1988; Burney, 1988) was used to cluster the samples. This type of analysis uses the average dissimilarity (Euclidean Distance) between the pollen percentages to construct clusters of similar sites. The Ward's Minimum Variance Analysis initially determines which two samples have the least average dissimilarity

(Euclidean distance) between their pollen percentages. These two sites will then be grouped together. Then, the site that has the least average dissimilarity in its pollen percentages to the first group of sites will be linked to the previous cluster. Again, the site with the least average dissimilarity will be linked to the cluster of the first three sites. These calculations continue until all the sites have been clustered into one group. The results of the cluster analysis are displayed on a dendrogram in which similar sites are grouped together along similar branches. The abscissa of the dendrogram represents the measure of dissimilarity between the sites (Birks and Gordon, 1985).

A cluster is a group of related sites that share a common branch on the dendrogram. These branches are divided by drawing a vertical line down the dendrogram at a specific Euclidean distance. The abscissa that are to the left of this vertical line will form the cluster branches and the sites at the ends of these branches will be classified as a cluster. The placement of the vertical line on the dendrogram is subjective; it is usually drawn at a Euclidean distance that defines the clusters in the most logical manner (Birks and Gordon, 1985).

The clusters produced in this study make sense biologically, but the data violated an assumption of the analysis. In order for cluster analysis to be used correctly, data should be homogeneous, meaning that the pollen percentages for all sites should be non-zero numbers (W. Sanders, pers. communication, 1993). My data, however, had many zeros because many pollen types did not occur at all sites, either because the taxa did not occur or because the pollen type was not preserved in the sample. Data sets with "0" values have been subjected to cluster analysis in other modern pollen rain studies (Anderson and Davis, 1988; Fine, 1978). Even though my data set had "0" values, the samples still clustered out into logical groups, as described in the following chapter.

Detrended Correspondence Analysis:

Detrended Correspondence Analysis (DCA) (Hill, 1980) was also used to show patterns in the pollen spectra among the different sites. DCA is an ordination technique that plots similar sites in close proximity and dissimilar sites farther away from each other. In DCA, ordination scores for different species are averages of the sample ordination scores and the sample ordination scores are averages of the species ordination scores. The first DCA axis is derived by arbitrarily assigning ordination scores (weighted averages) to the species data. Then sample ordination scores are calculated from the weighted averages of the species scores by the following formulae (Digby and Kempton, 1987):

$$a_i = p^{-1} \; E \; y_{ij} b_j / r_i$$

$$b_j = p^{-1} \; E \; y_{ij} a_i / c_j$$

where a_i = species scores, b_j = sample scores, p = 1, y_{ij} = transformed data, r_i = number of species, and c_j = number of samples. New species scores (a_i) are calculated by placing the derived sample ordination scores (b_j) back into the above formula. Then, new sample scores are calculated from the new species scores. Each time a new species score (a_i) is generated, it is put back into the first formula to calculate a new sample score (b_j) and vice versa. These iterations continue until the scores stabilize to generate a solution to the formula (Digby and Kempton, 1987). The first DCA axis is determined by finding the eigenvalue (the variance of sample scores accounted for by the axis) of the final sample scores (Gauch, 1980).

The second DCA axis is determined by the iteration technique described above except that the sample scores are corrected with respect to the first DCA axis. The second axis is assumed to be uncorrelated

(orthogonal) to the first axis. Axis 2 is found by dividing the first DCA axis into a number of segments, and within each segment, the axis 2 scores are adjusted to have an average of zero. This "detrending" is applied to the sample scores at each iteration until the scores stabilize to generate the final sample scores. The sample scores for the third DCA axis are calculated with respect to both the first axis and the second axis using the same iteration technique (Gauch, 1980).

In this study, a second DCA ordination was run using the same data set but excluding the first SRNP Mangrove sample (site 1), and a third ordination was run using the same data set but excluding site 1 and both lowland tropical swamp samples (sites 16 and 17). These three sites were outliers in the analysis as their pollen spectra were heavily dominated by only one pollen type. Outliers in the analysis can obscure interpretations of relationship between environmental gradients and axes because the other sites are so different from the outliers that they will be plotted closer together than they would be if the outliers were not included (Bush, 1988; Peet, 1980). By rerunning ordinations without outlying sites, the possible influences of environmental gradients on the axes are made clearer.

CHAPTER 5

RESULTS

This chapter presents the results of the sediment and pollen analyses of the surface lake and soil samples, and the results of the statistical analyses of the pollen percentage data.

SEDIMENTOLOGY, POLLEN CONCENTRATIONS AND POLLEN PRESERVATION

The percent organic matter and pollen concentrations in the 29 samples are listed in Appendix III. Water contents are not listed. This information was needed to calculate pollen concentrations on a dry weight basis, but for the lake and pond samples, it has no other significance since water freely moved into and out of the dredge during sampling. As shown in Appendix III, the organic content of the samples (dry weight basis) ranged from 5.5% at the first SRNP Mangrove site (1) to 96.0% at the Bog 68 site (24). No consistent relationships were apparent between organic content, site vegetation, or sample type (lake or pond sediment or surface soil). The pollen concentrations ranged widely, from a low of 2.4×10^5 pollen grains and spores per gram dry sediment at Palmita (6) to a high of 3.98×10^8 pollen grains and spores per gram dry sediment at Cantarrana (16). In general, pollen concentrations were higher in the lake and pond samples than in the surface soil samples. Preservation was generally good in all samples. Most pollen grains classified as indeterminate (Delcourt and Delcourt, 1980) were unidentifiable because of mechanical damage (*i.e.*, broken grains). The incidence of mechanical damage was lowest in the montane rain forest and páramo samples (with an average of 4 mechanically damaged pollen grains and spores per count of 350 pollen grains) and

highest in the mangrove, tropical dry forest, tropical wet, and montane bog samples (with an average of 10 mechanically damaged pollen grains and spores per count of 350 pollen grains).

POLLEN TYPES

Over 65 pollen types and 15 morphological classes of spores were recognized in this study. Pollen was generally identified to family or genus level. Within the order URTICALES, pollen grains of *Cecropia*, *Ficus*, and *Ulmus* were identified to genus but others were classified by pore number, following Bartlett and Barghoorn (1973) and Horn (1985a, 1993). Some researchers have separated out other genera (such as *Brosimum*, *Trema*, and *Pilea*) in neotropical pollen studies (Hansen, 1990; Leyden, 1984 and 1987; Bush, 1991; Bush and Colinvaux, 1988; Bush *et al.*, 1992). However, a study of pollen morphology within the URTICALES that I carried out as an adjunct to this thesis work (Rodgers, unpublished data) revealed that such generic (or even familial) differentiation is not possible among the Costa Rican URTICALES, at least using light microscopy. Certain tricolporate, reticulate pollen grains also proved impossible to differentiate (Roubik and Moreno, 1991; Horn, 1985a). Because many of these pollen types are found in the EUPHORBIACEAE, RUTACEAE, and ANACARDIACEAE families, undifferentiated pollen grains with a tricolporate, reticulate morphology were classified as the E/R/A pollen type (Horn, 1985a). As with the URTICALES, certain pollen types in these families could be identified, including *Acalypha*, *Alchornea*, *Dalechampia*, *Sapium* and an unknown genus (likely *Anacardium*) of ANACARDIACEAE that occurred in the SRNP Tropical Dry Forest sample (3) and the second SRNP Mangrove sample (2).

Appendix IV lists pollen and spore taxa found within each vegetation type sampled, and Appendix V provides information on the plant taxa represented.

MODERN POLLEN SPECTRA

Eleven figures illustrate the percentages of the major pollen types at the 29 sampling sites. Results are presented by vegetation type and generally arranged from lowest to highest elevation. The x-axis of each graph is used for the key pollen types, and the heights of the bars (y-axis) show the percent of the total pollen accounted for by a given pollen type. Counts for pollen types are expressed as percentages of the total pollen excluding fern spores, and indeterminate; counts for fern spores are expressed as percentages of total pollen and spores. The taxon names are abbreviated to save space. The full names of the taxa can be found in Appendix IV. The category "Oth" refers to all other pollen types found in the sample summed together. The bars for URTICALES are for URTICALES pollen exclusive of *Cecropia, Ficus* and *Ulmus*. Note that the scaling of the y axis differs for some graphs, but it is always shown with the highest value corresponding to either 25%, 50%, or 100%.

Mangrove forest (Figure 2):

The pollen rain of the first SRNP Mangrove sample (site 1) and the second SRNP Mangrove sample (site 2) differed substantially. The first SRNP Mangrove sample was dominated by *Rhizophora* pollen (79.5%), with lesser amounts of E/R/A (3.7%), *Quercus* (4.0%), *Cecropia* (1.7%), and other URTICALES (5.7%) pollen. There was very little mangrove pollen in the second SRNP Mangrove sample (site 2); *Rhizophora* accounted for only 13.7% and *Avicennia* 4.6%. The most common pollen types in the second Mangrove sample were ANACARDIACEAE (30.2%), COMPOSITAE (3.7%), *Quercus* (2.6%), GRAMINEAE (8.3%), *Cecropia* (3.4%), and URTICALES (25.4%).

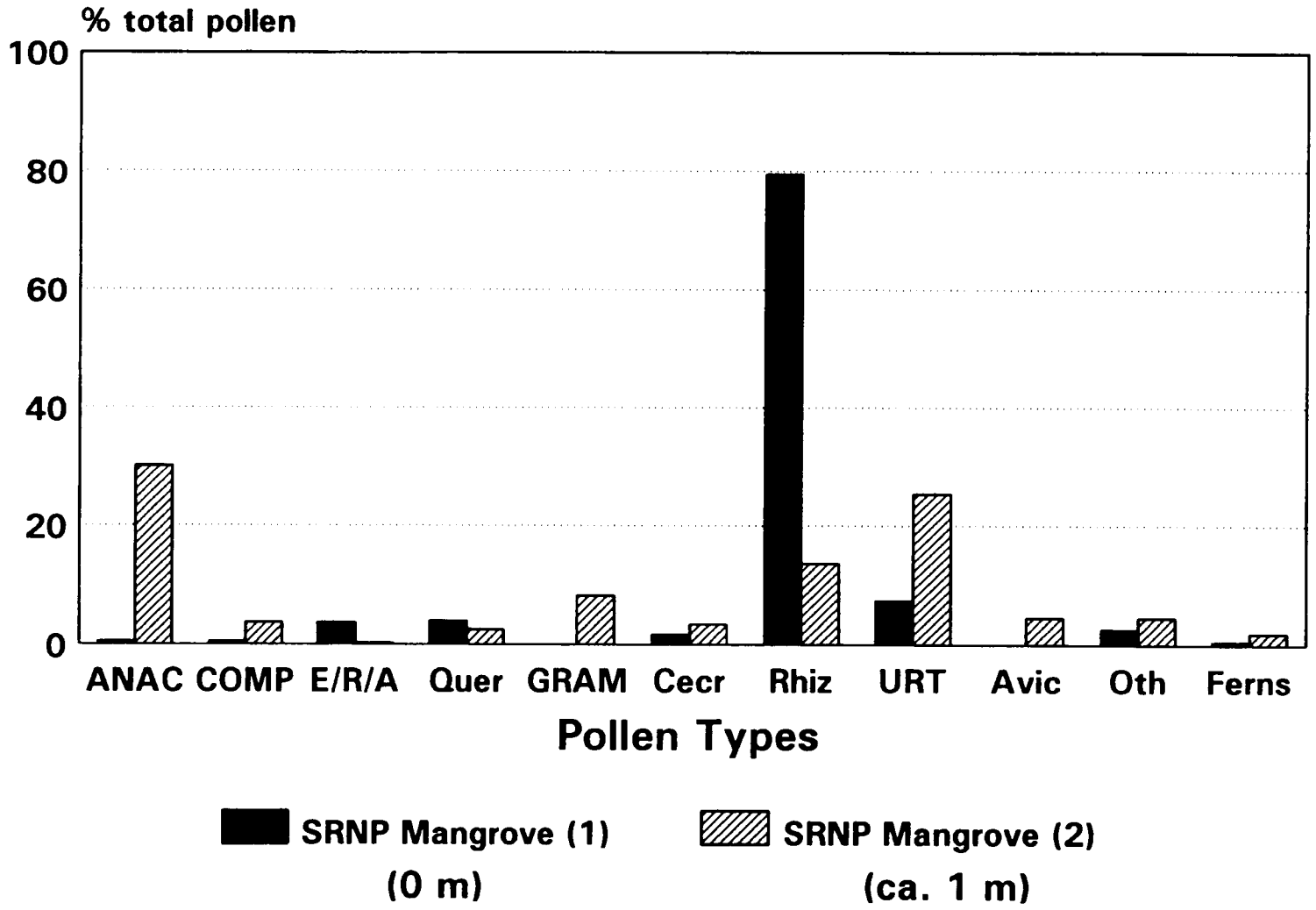

Figure 2: Pollen percentages in the mangrove samples.

Tropical Dry Forest (Figure 3):

The Tropical Dry Forest sample (3) was dominated by ANACARDIACEAE pollen (48.0%). Other important pollen types were *Bursera* (4.9%), *Quercus* (5.1%), GRAMINEAE (8.9%), *Cecropia* (5.7%), *Guazuma* (2.9%), and URTICALES (18.0%). A noteworthy rare pollen type for the tropical dry forest sample was POLYGALACEAE pollen (Appendix IV).

Derived Savanna (Figure 4):

The derived savanna samples contained abundant grass pollen, with percentages reaching 31.9% at Palmita (6), 34.2% at Escondido (5) and 74% at the SRNP Savanna site (4). Besides grass pollen, these sites also had moderate percentages of COMPOSITAE, E/R/A, *Quercus*, *Cecropia*, MYRTACEAE, and URTICALES pollen. Palmita was the only derived savanna site with *Guazuma* pollen (34.1%). Rare pollen types found only in the derived savanna samples included LACISTEMACEAE and GESNERIACEAE pollen (Appendix IV).

Tropical Moist Forest (Figure 5):

The dominant pollen type in the tropical moist forest sample [Carara (7)] was URTICALES (33.1%). Other important pollen types were ACANTHACEAE (2.7%), E/R/A (4.5%), MIMOSOIDEAE (6.6%), LEGUMINOSAE (11.7%), *Cecropia* (17.7%), *Ficus* (1.8%), MYRTACEAE (2.7%), *Iriartea* (4.2%), and *Guazuma* (2.1%). A rare pollen type found only in the Carara sample was BOMBACACEAE pollen.

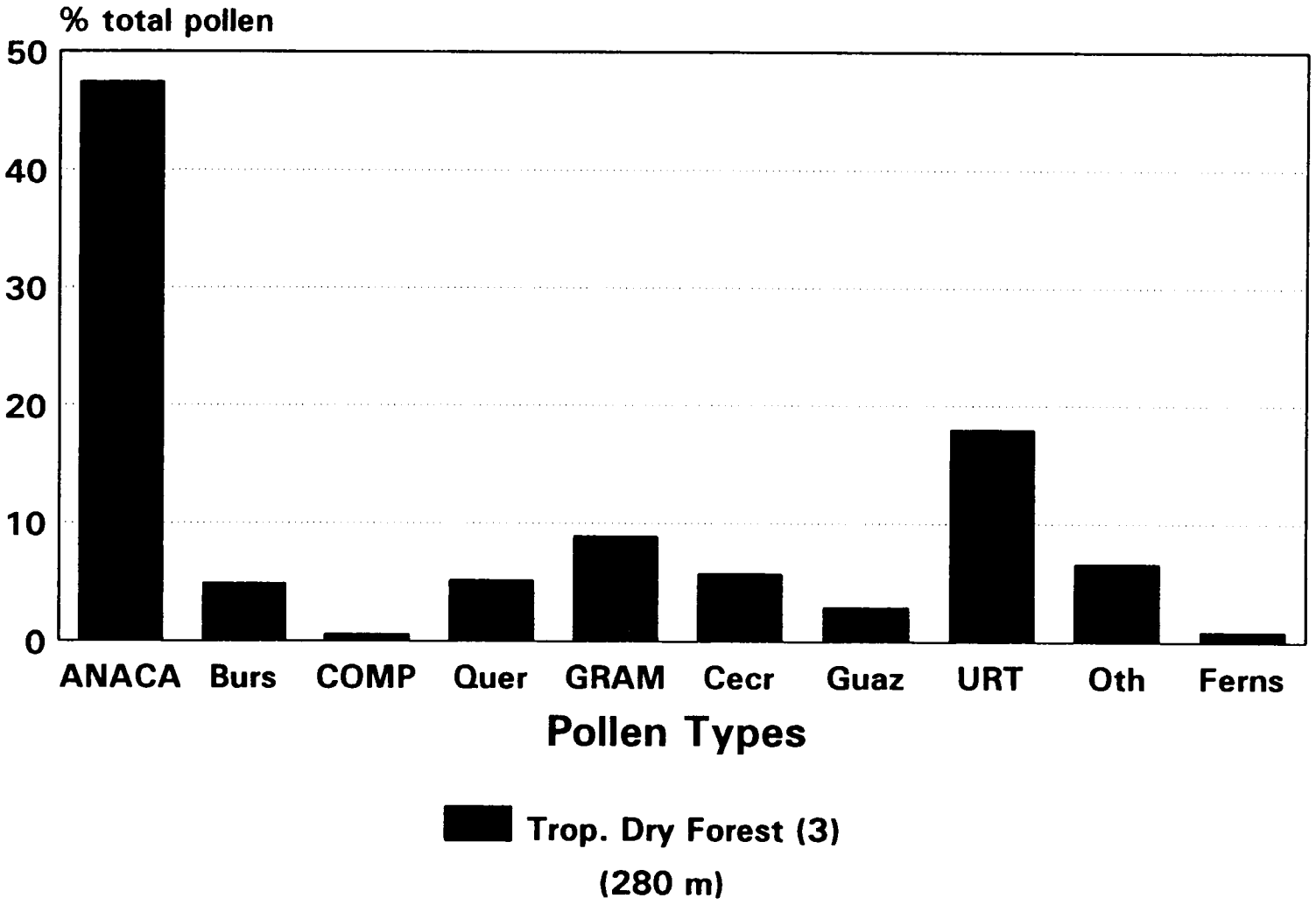

Figure 3: Pollen percentages in the tropical dry forest sample.

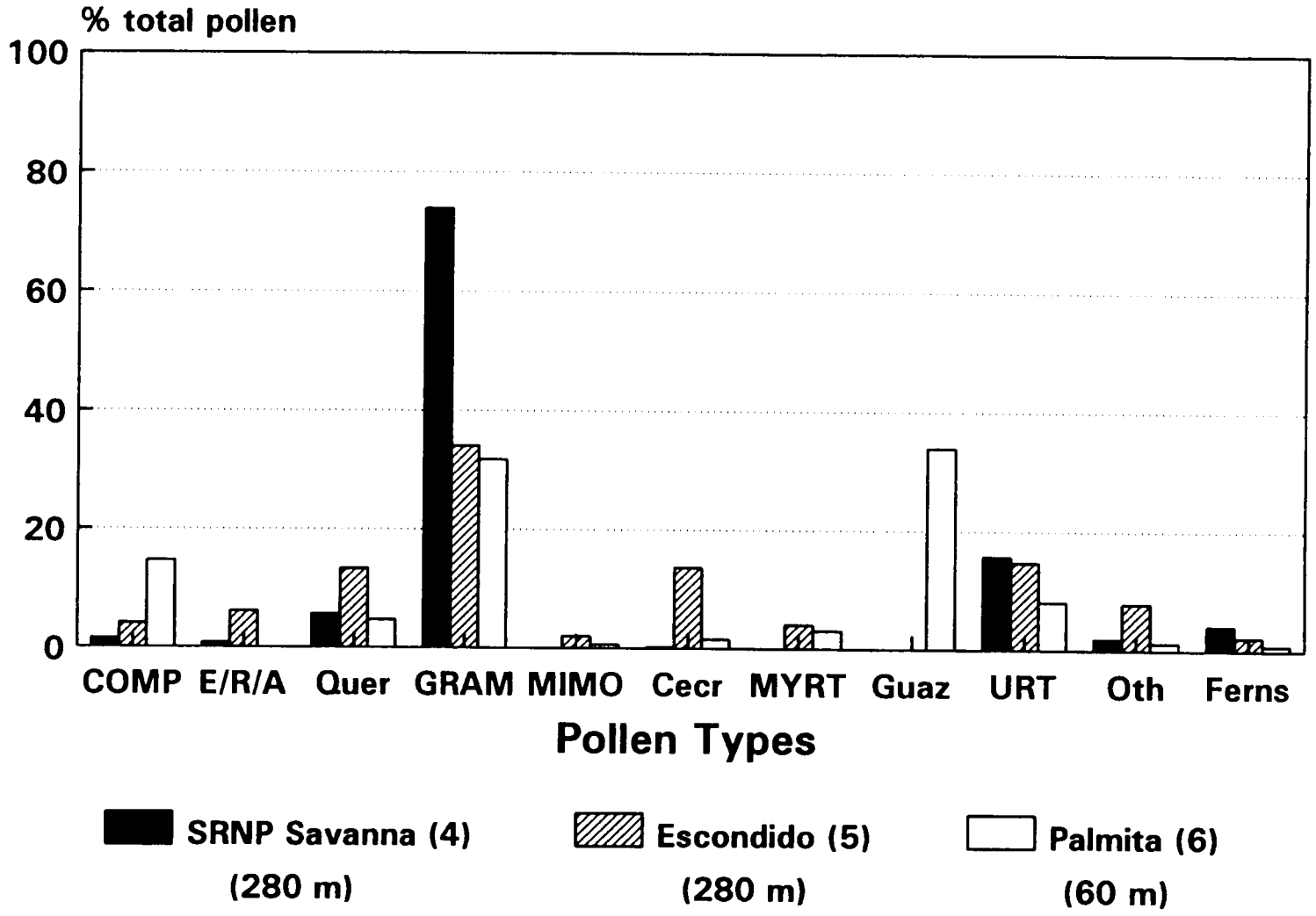

Figure 4: Pollen percentages in the derived savanna samples.

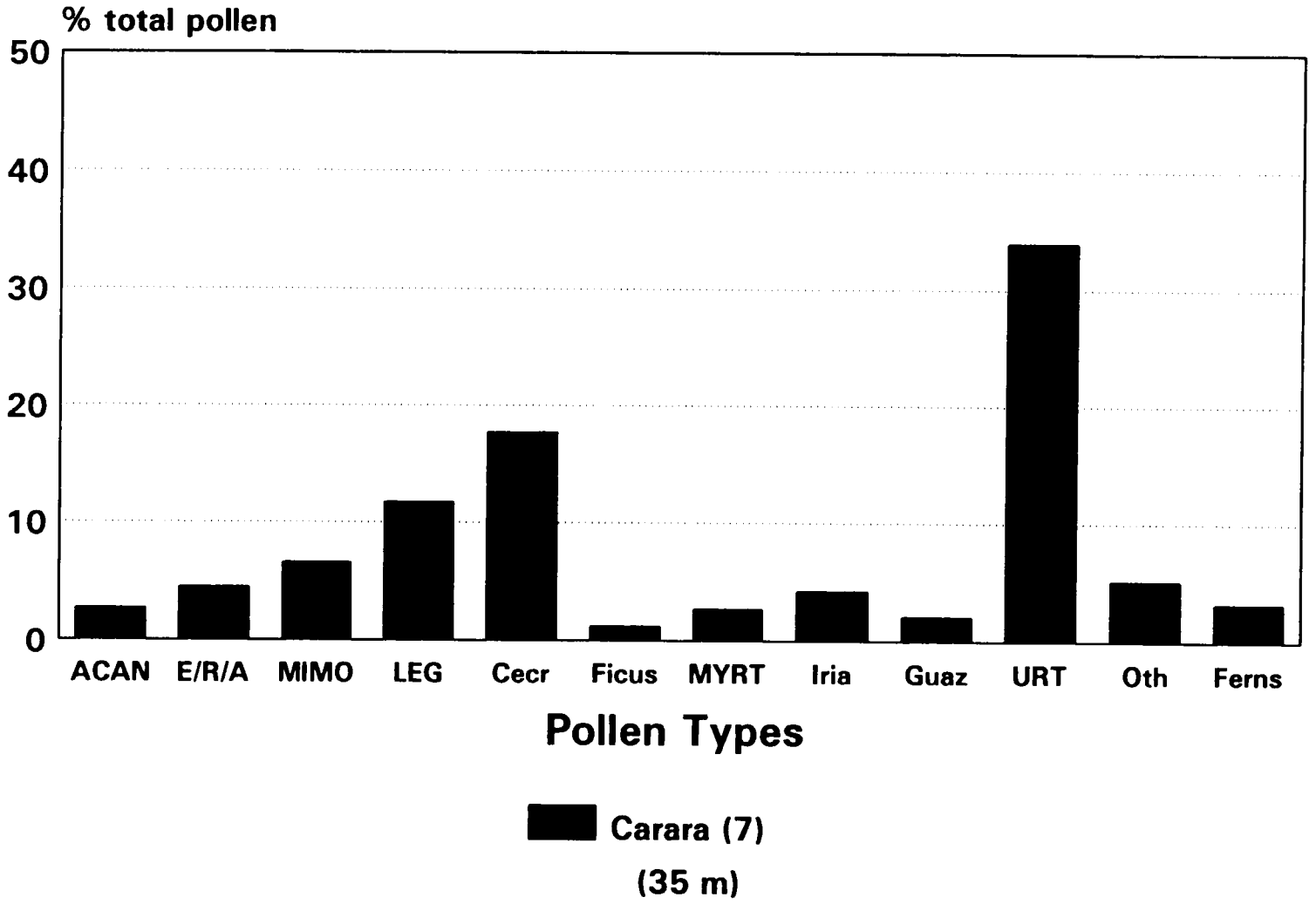

Figure 5: Pollen percentages in the tropical moist forest sample.

Tropical Wet Forest (Figures 6 and 7):

The pollen percentages for the tropical wet forest samples are shown on two figures. Figure 6 shows the three sites located below 500 m elevation, within the core tropical wet forest life zone [Río Cuarto (8), Bonilla (9), and Bonillita (10)]. Figure 7 shows the five sites located at slightly higher elevations within the premontane transition of the tropical wet life zone [González (11), Congo (12), Bosque Alegre (13), Hule (14), and María Aguilar (15)]. Samples from all wet forest sites were dominated by *Cecropia* and URTICALES pollen. On average, *Cecropia* accounted for about 20% of the pollen at these sites and URTICALES for about 30%. Also important were *Acalypha*, *Alchornea*, E/R/A, GRAMINEAE, MELASTOMATACEAE/COMBRETACEAE, MYRTACEAE, *Iriartea* and *Piper* pollen, and fern spores.

Lowland Tropical Swamp (Figure 8):

The two lowland tropical swamp samples varied in pollen composition. The Cantarrana (16) site was strongly dominated by *Cecropia* pollen (88.0%). Other important pollen types in the Cantarrana sample (expressed on the basis of a pollen sum of 350 non-*Cecropia* grains) were *Spathiphyllum* (2.9%), *Alchornea* (12.3%), *Pentaclethra* (1.4%), LEGUMINOSAE (6.8%) MELASTOMATACEAE/COMBRETACEAE (36.8%), *Iriartea* (1.7%), and URTICALES (18.2%). The Suampo sample (17) only had 8.0% *Cecropia* and was dominated by *Pentaclethra* pollen (37.4%). The other important pollen types in the Suampo sample were E/R/A (6.3%), LEGUMINOSAE (2.0%), *Iriartea* (2.0%), RHAMNACEAE (5.1%), SOLANACEAE (11.7%), and URTICALES (16.9). Fern spores were also important at the Suampo site (14.0%), much more so than at the Cantarrana site (0.57%).

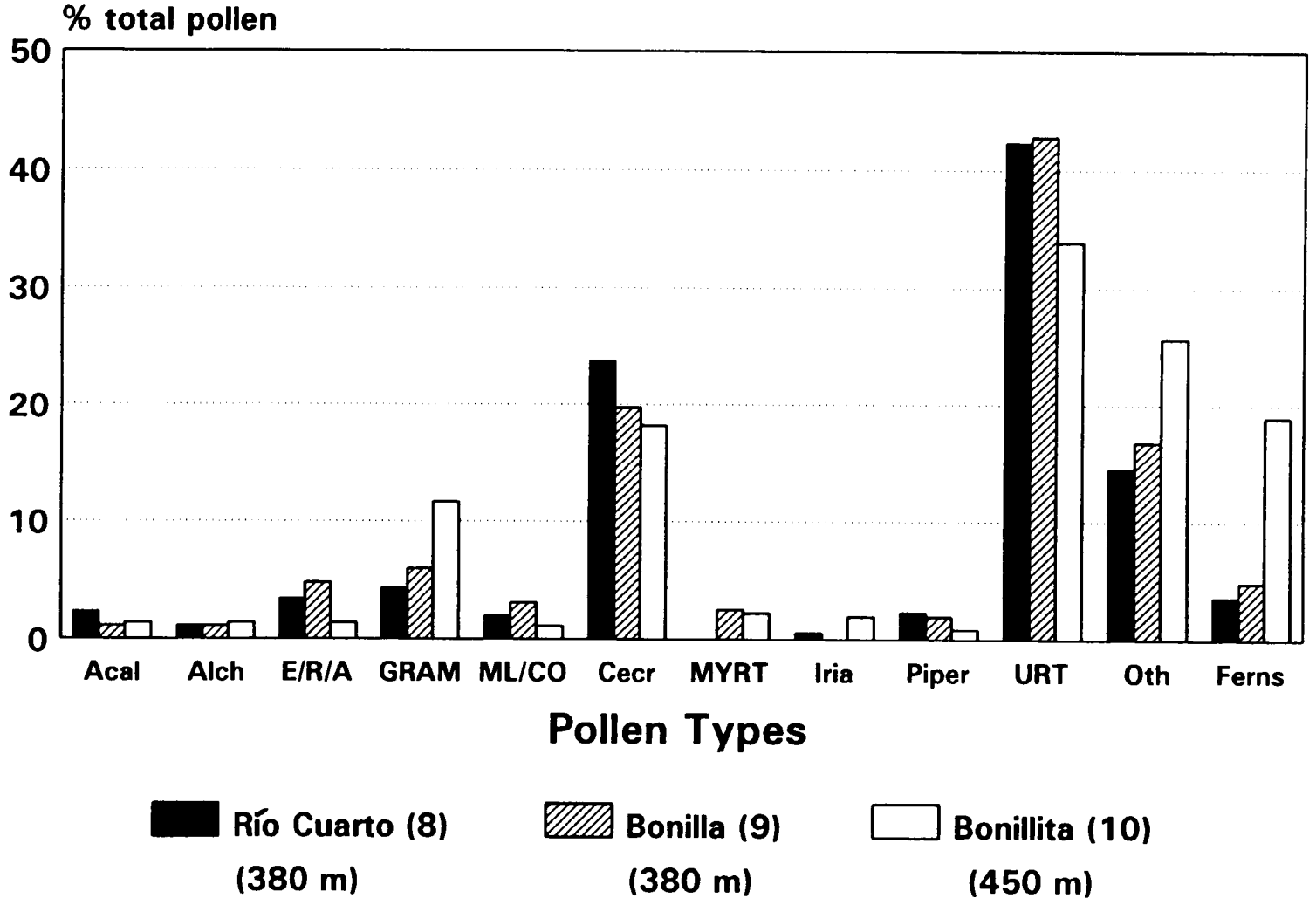

Figure 6: Pollen percentages in the tropical wet forest samples (sites below 500 m elevation).

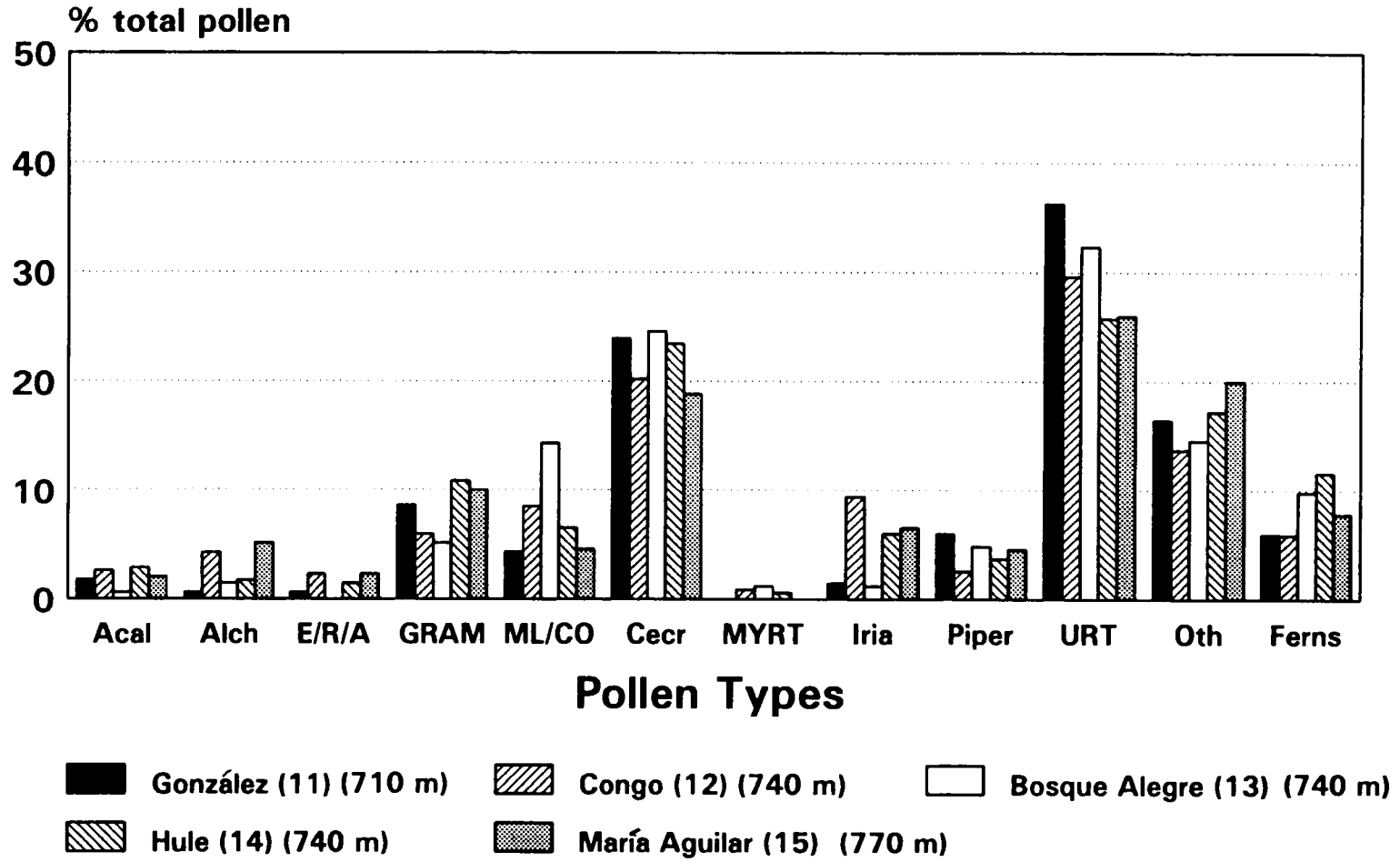

Figure 7: Pollen percentages in the tropical wet forest samples (sites above 500 m elevation).

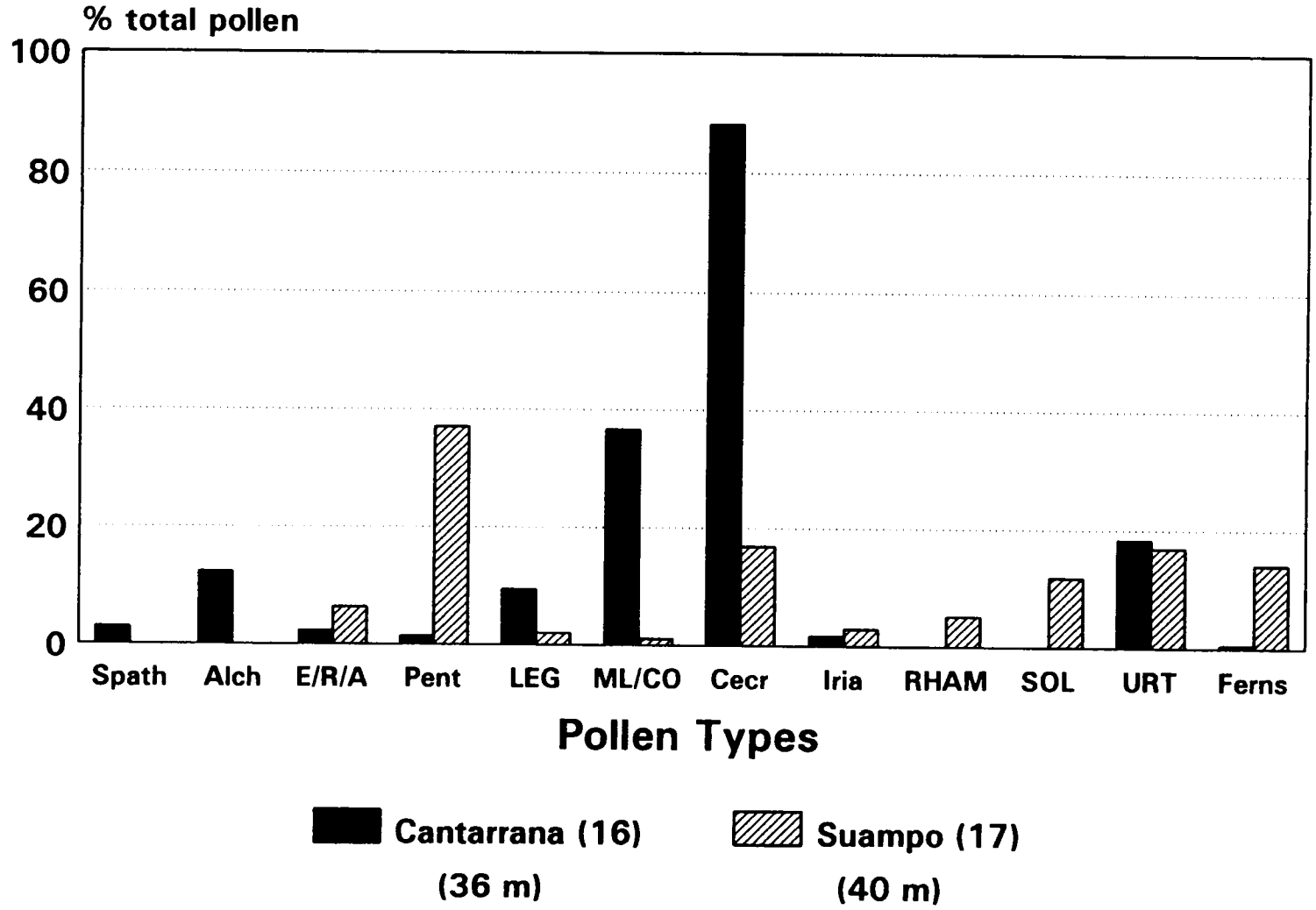

Figure 8: Pollen percentages in the lowland tropical swamp samples.

Premontane Rain Forest (Figure 9):

The premontane rain forest samples [La Palma (18), Cedeño (19), and Volcán Cacao (20)] showed considerable variation in their pollen percentages. The most common pollen types shared between these three samples were COMPOSITAE, E/R/A, GRAMINEAE, *Ficus*, MELASTOMATACEAE/COMBRETACEAE, *Mortoniodendron*, URTICALES, and fern spores. The "Other" category was also high in the premontane rain forest samples, probably as a result of the dissimilarities among these sites (*i.e.*, constraints of graphs) and high pollen type diversity.

Montane Rain Forest (Figure 10):

The most important pollen types in the montane rain forest samples [Botos (21), Barva (22), and Quebrador (23)], were *Alnus*, COMPOSITAE, *Weinmannia*, *Quercus*, GRAMINEAE, MELASTOMATACEAE/COMBRETACEAE, *Myrica*, *Myrsine*, URTICALES, and fern spores. Two rare pollen types found only in the montane rain forest samples were *Dalechampia* and *Clusia* (Appendix IV). The Quebrador sample (site 23) was dominated by *Quercus* pollen (40%), but the Botos (site 21) and Barva (site 22) samples were not strongly dominated by any one type.

Montane Bog (Figure 11):

The montane bog samples [Bog 68 (24), Bog 70 (25), and Tres De Junio (26)] had percentages of *Weinmannia*, GRAMINEAE, MELASTOMATACEAE/ COMBRETACEAE, and *Myrsine*, and URTICALES pollen that were on average similar to percentages in the montane rain forest samples. They differed in having lower percentages of *Alnus* and *Myrica*. The montane bog samples had higher percentages of COMPOSITAE, CYPERACEAE, and PODOCARPACEAE, and generally higher percentages of *Quercus* [higher than

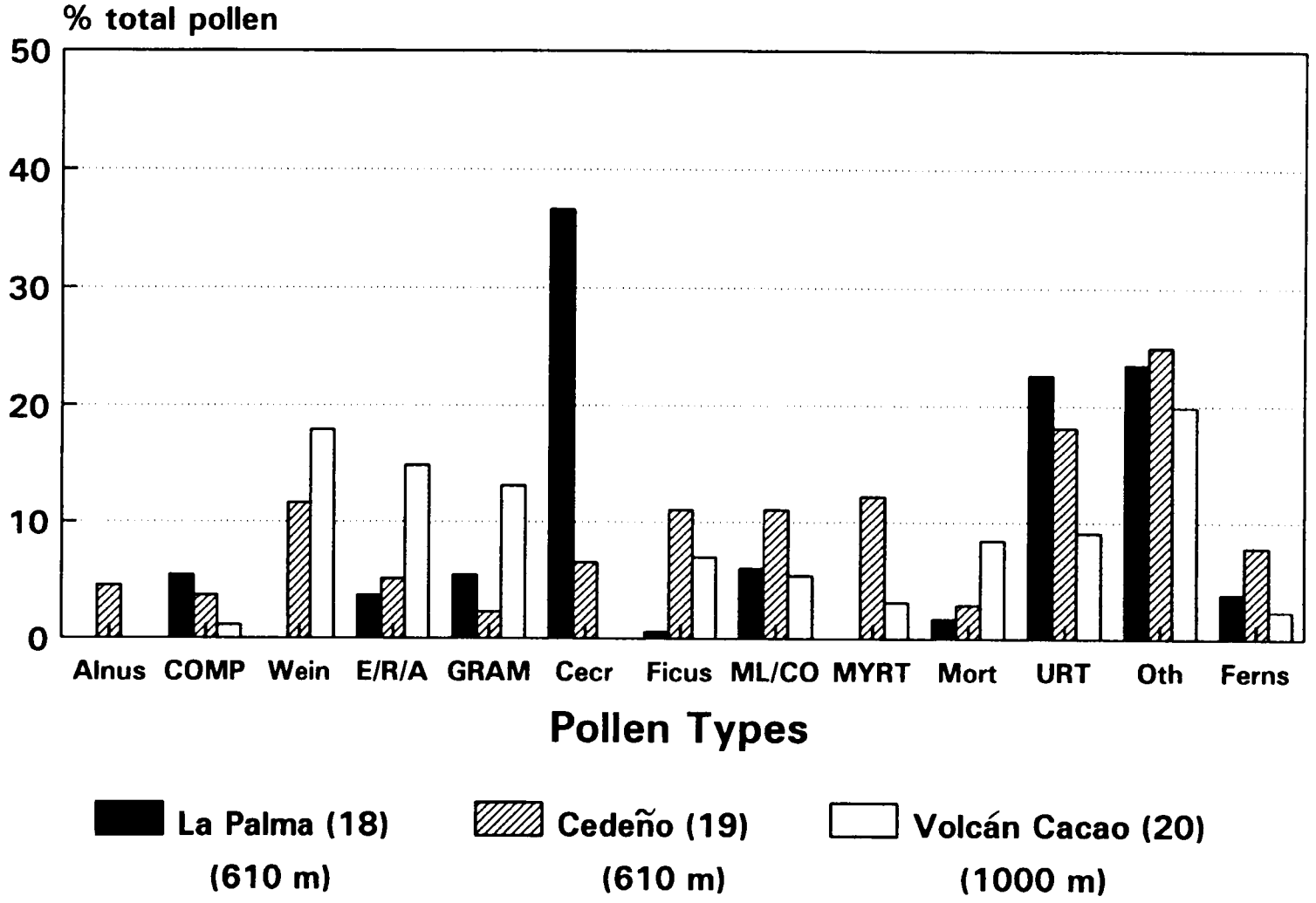

Figure 9: Pollen percentages in the premontane rain forest samples.

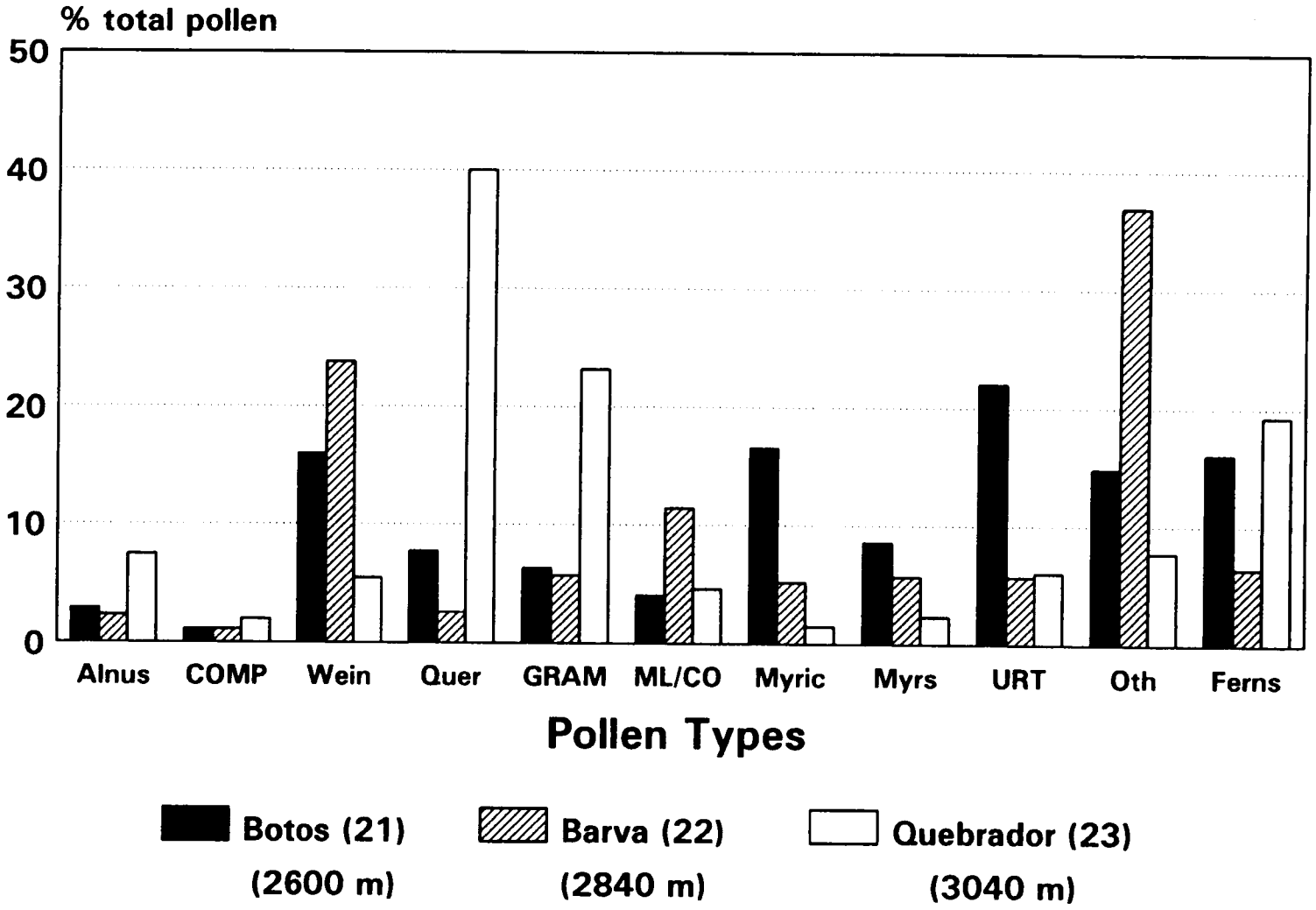

Figure 10: Pollen percentages in the montane rain forest samples.

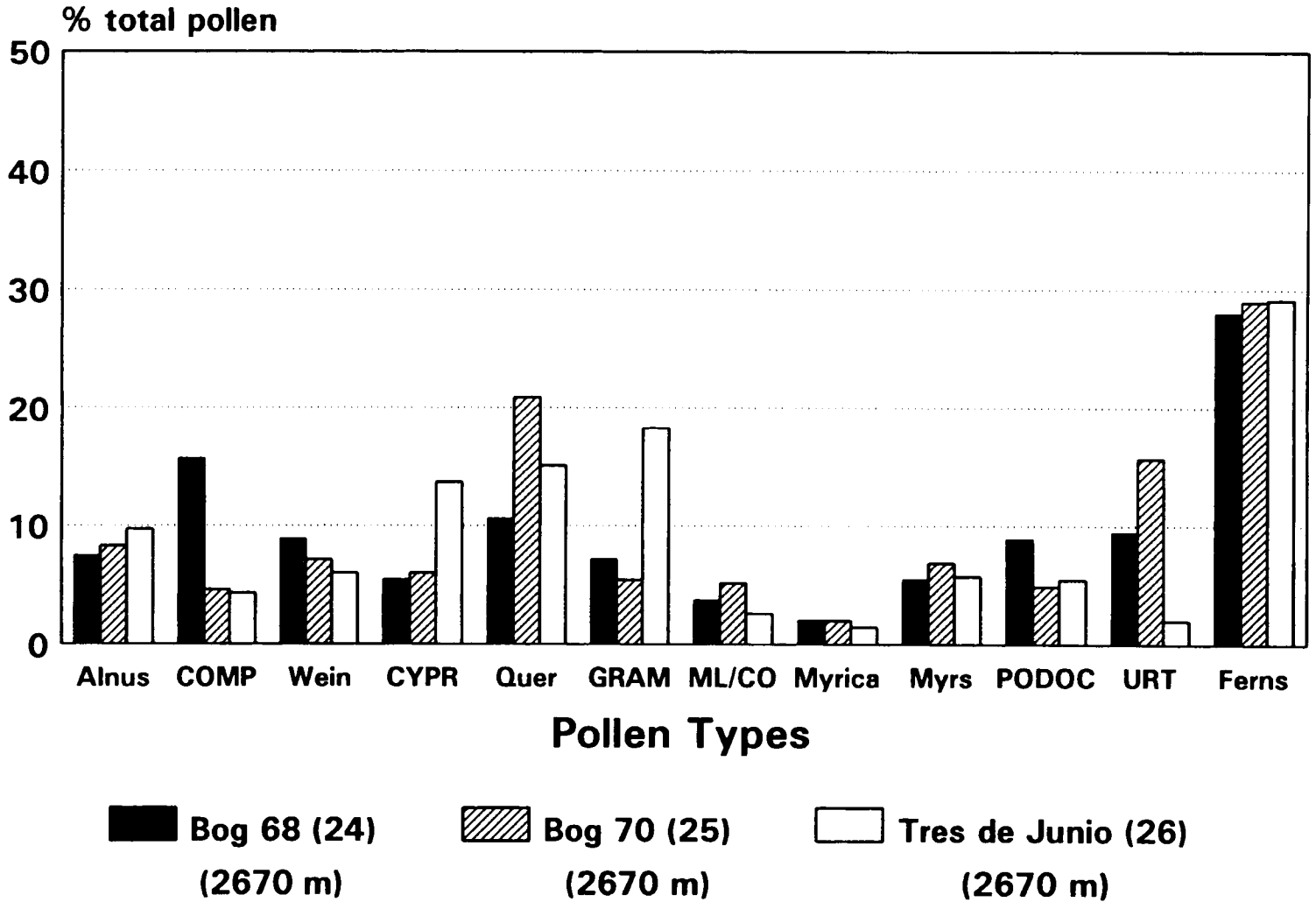

Figure 11: Pollen percentages in the montane bog samples.

Botos (21) and Barva (22) samples but not higher than the Quebrador sample (23)]. A characteristic feature of the montane bog samples was very high percentages of fern spores.

Páramo (Figure 12):

The páramo sites [Asunción (27), Morrenas (28), and Chirripó (29)] were dominated by *Quercus* and GRAMINEAE pollen. Oak pollen percentages ranged from 15% to 40% and grass pollen percentages ranged from 13% to 56%. Other important pollen types for the páramo sites were *Alnus*, COMPOSITAE, *Weinmannia*, PODOCARPACEAE, UMBELLIFERAE, *Ulmus*, and URTICALES. Fern spores were moderately abundant.

DISTRIBUTION OF KEY POLLEN TYPES

As a first attempt to examine the spatial distribution of modern pollen percentages in Costa Rica, I designated ten taxa as "key" types and looked for trends in their relative importance across different vegetation types. The ten "key" types that I considered were ANACARDIACEAE, *Alnus*, *Weinmannia*, *Quercus*, GRAMINEAE, MELASTOMATACEAE/COMBRETACEAE, *Cecropia*, *Rhizophora*, URTICALES, and fern spores. These nine pollen types and fern spores (treated as a group) each accounted for more than 7% of the total pollen in at least three sites, or for more than 40% of the pollen at one site. In the ten figures that follow, the y-axis of the graph represents the percent of the total pollen, while the x-axis represents the different vegetation type from highest to lowest elevation. The scales on the y-axis are either 25%, 50%, or 100%. Vegetation type names are abbreviated on the x-axis to save space. When more than one sample from a given vegetation type contains the key pollen type, the second and later bars are given

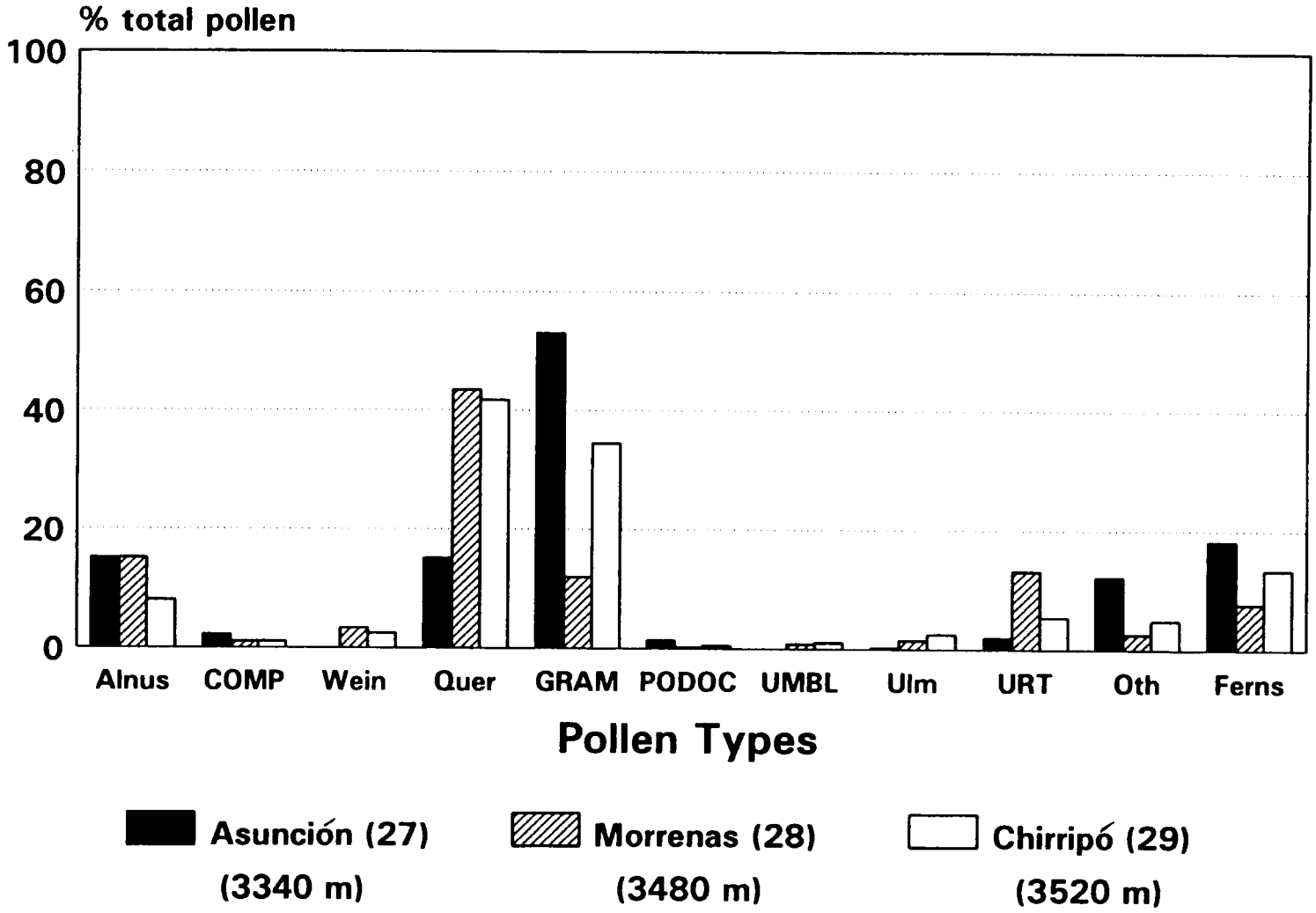

Figure 12: Pollen percentages in the páramo samples.

shading patterns. No relationship exists between samples shown with the same shading pattern.

ANACARDIACEAE pollen (Figure 13) was most common in the tropical dry forest sample (3) and the second SRNP Mangrove sample (2). ANACARDIACEAE was also found in the first SRNP mangrove sample (1), Hule (14), Cantaranna (16), Suampo (17), and La Palma (18).

Alnus pollen (Figure 14) was most important in samples from the higher elevation vegetation types (páramo, montane bog and montane rain forest). The abundance of *Alnus* pollen generally decreases with decreasing elevation. However, one premontane rain forest site at a relatively low elevation, Laguna Cedeño (19), had a significant percentage of *Alnus* pollen (4.7%).

Weinmannia (Figure 15) was another important pollen type that occurred in samples from most sites, but showed highest percentages in those from montane sites.

Quercus pollen (Figure 16) occurs in samples from most of the vegetation types. It was especially abundant and occurred in the highest percentages in the páramo, montane bog, and montane rain forest samples. *Quercus* pollen was also abundant in the SRNP Tropical Dry Forest sample (site 3), the derived savanna samples (sites 4, 5, and 6), and the mangrove samples (sites 1 and 2). The *Quercus* pollen in these samples was probably from the dry zone oak species, *Q. oleoides*. All other oak species in Costa Rica are characteristic of wetter formations at middle to high elevations (Burger, 1977).

GRAMINEAE pollen (Figure 17) was found in most samples but occurred in the highest percentages in those from the derived savanna and páramo sites.

MELASTOMATACEAE/COMBRETACEAE (Figure 18) was another important pollen type that occurred in samples from many vegetation types. Higher percentages of MELASTOMATACEAE/COMBRETACEAE were found in the wetter

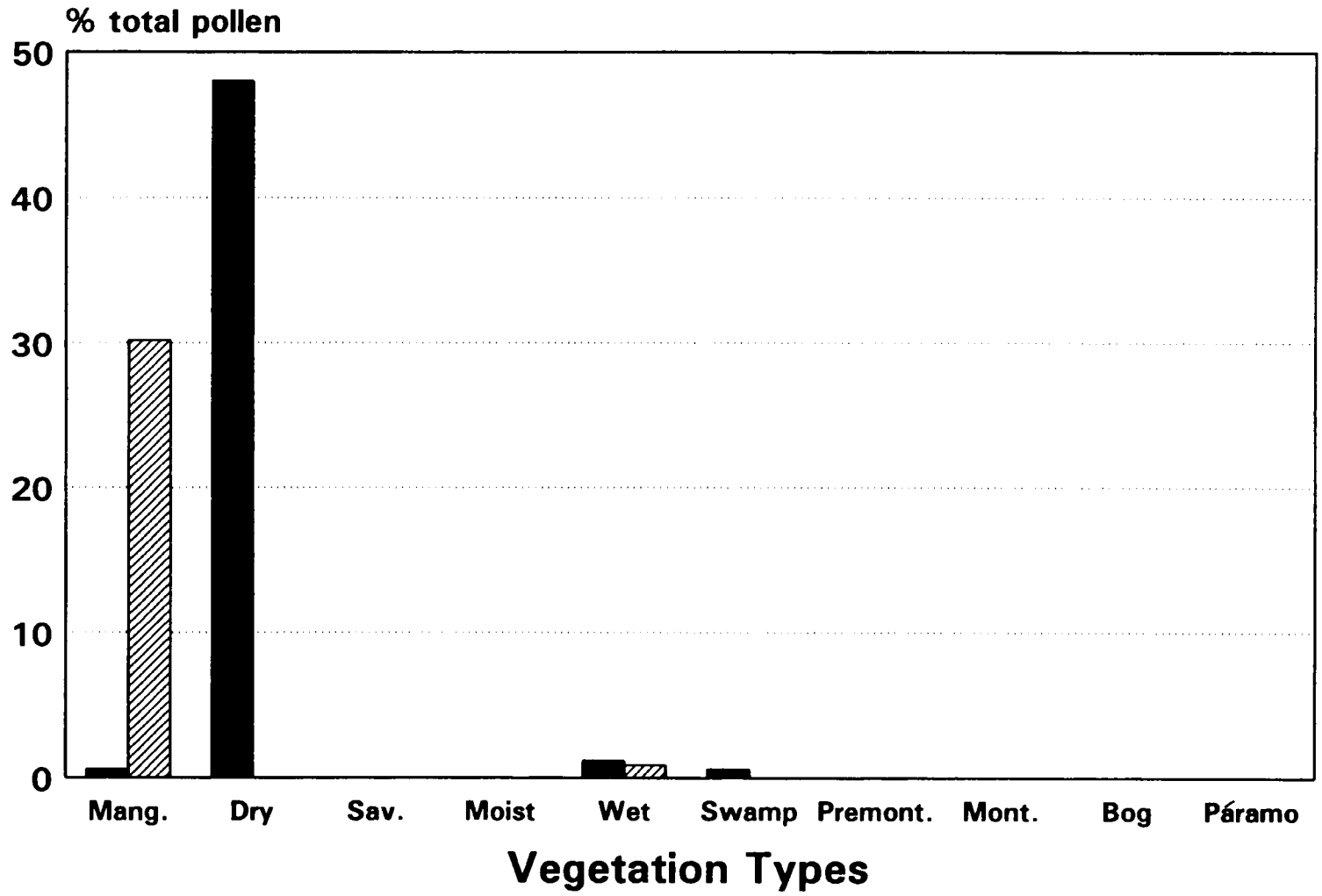

Figure 13: ANACARDIACEAE pollen percentages in different vegetation types.

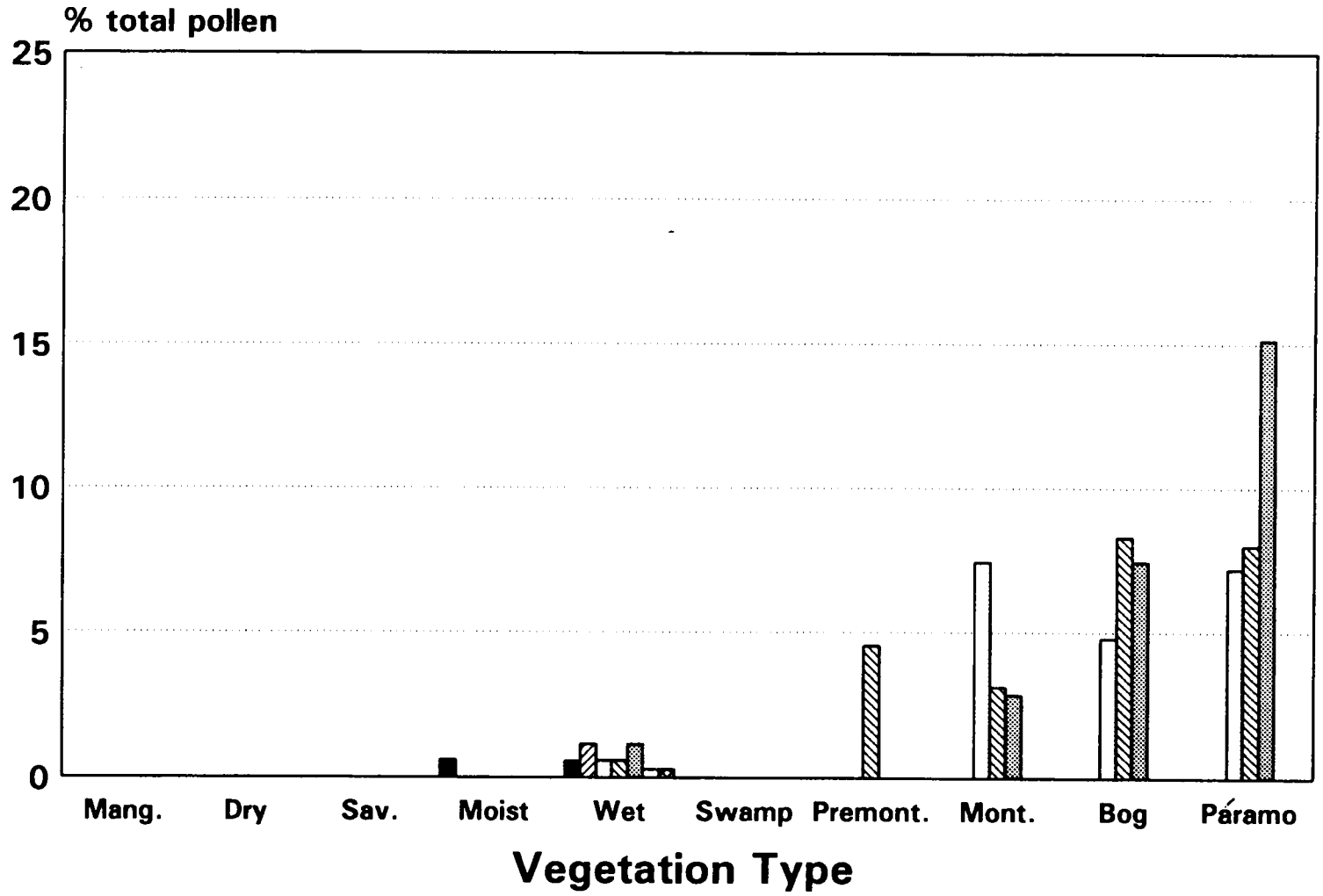

Figure 14: *Alnus* pollen percentages in different vegetation types.

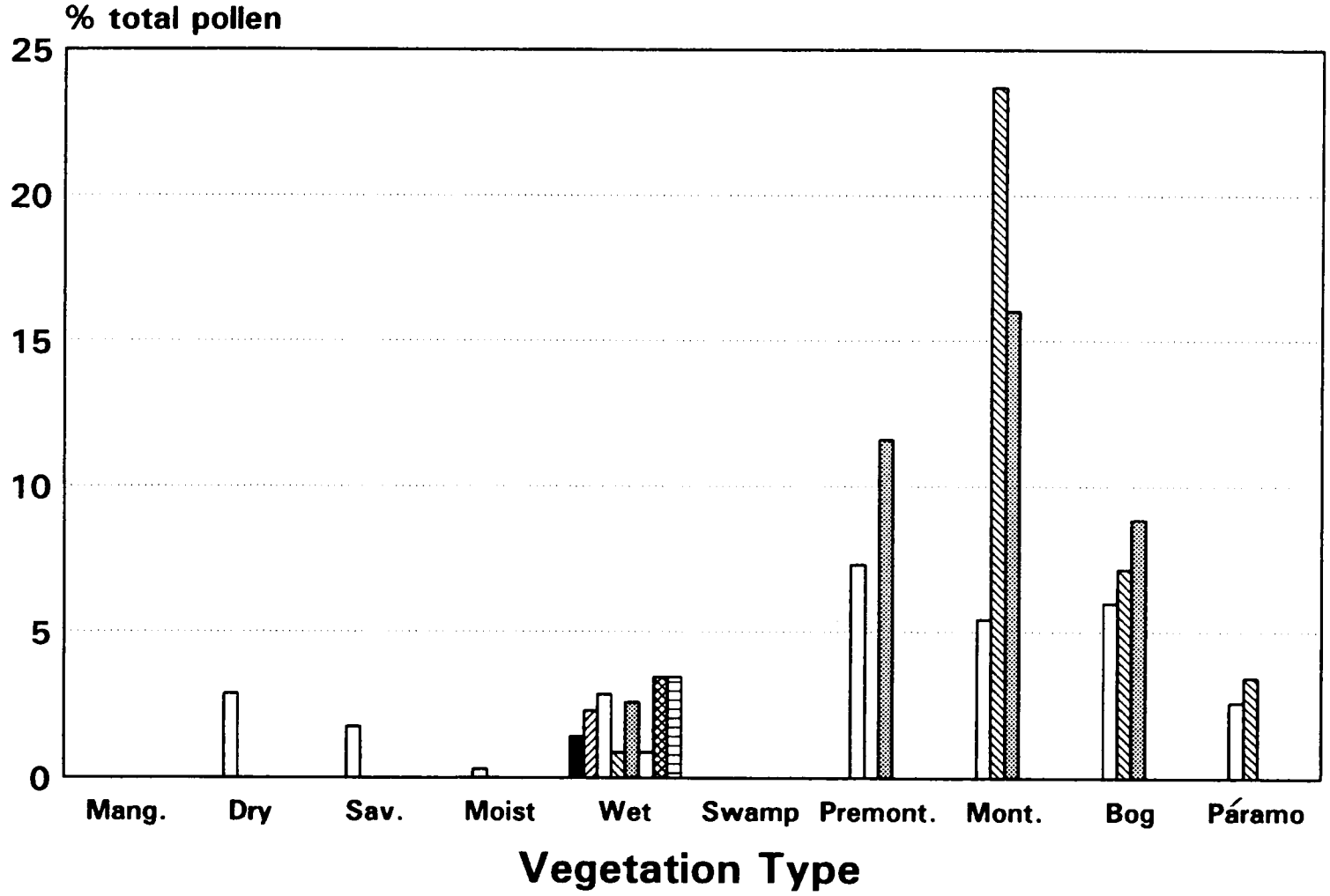

Figure 15: *Weinmannia* pollen percentages in different vegetation types.

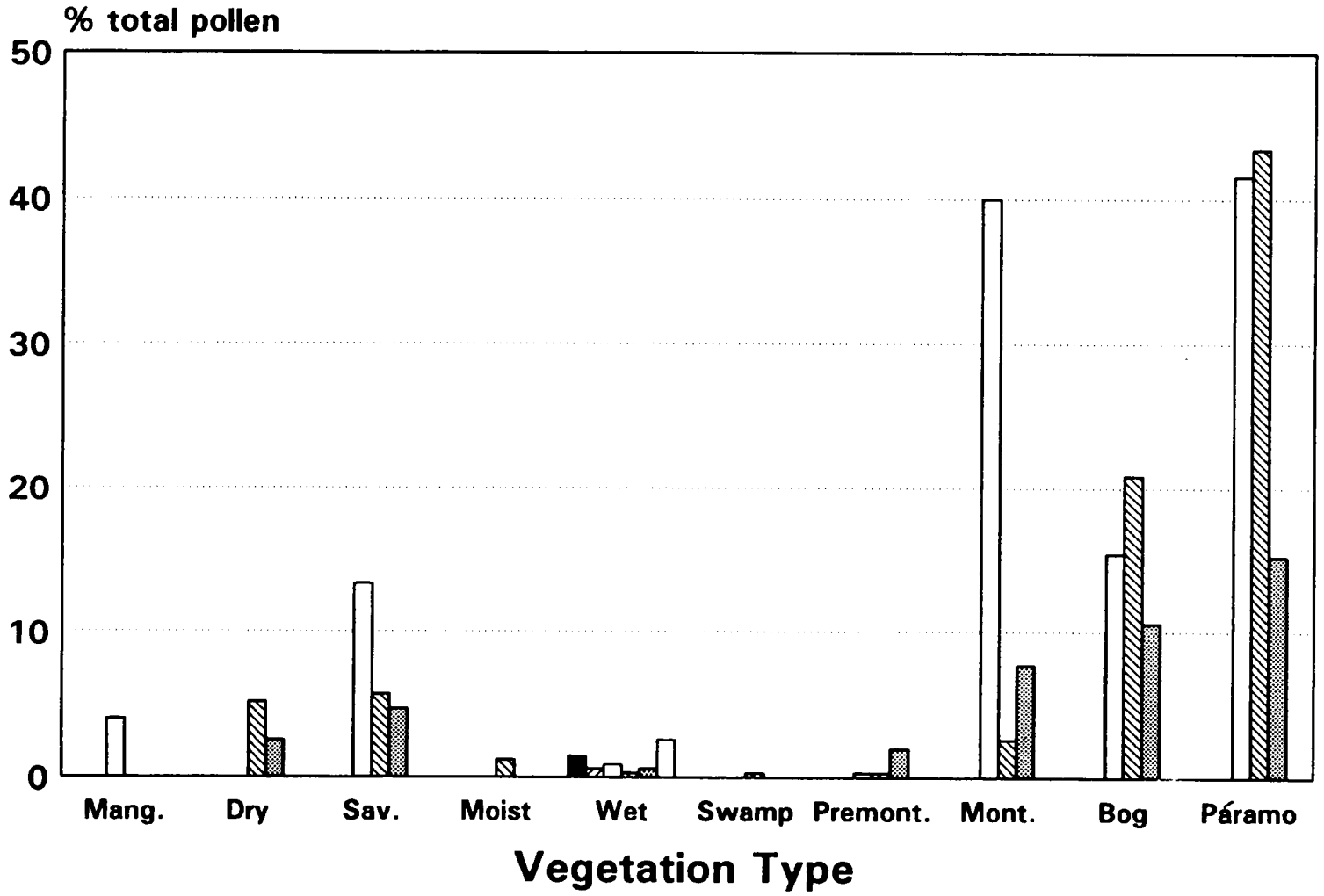

Figure 16: *Quercus* pollen percentages in different vegetation types.

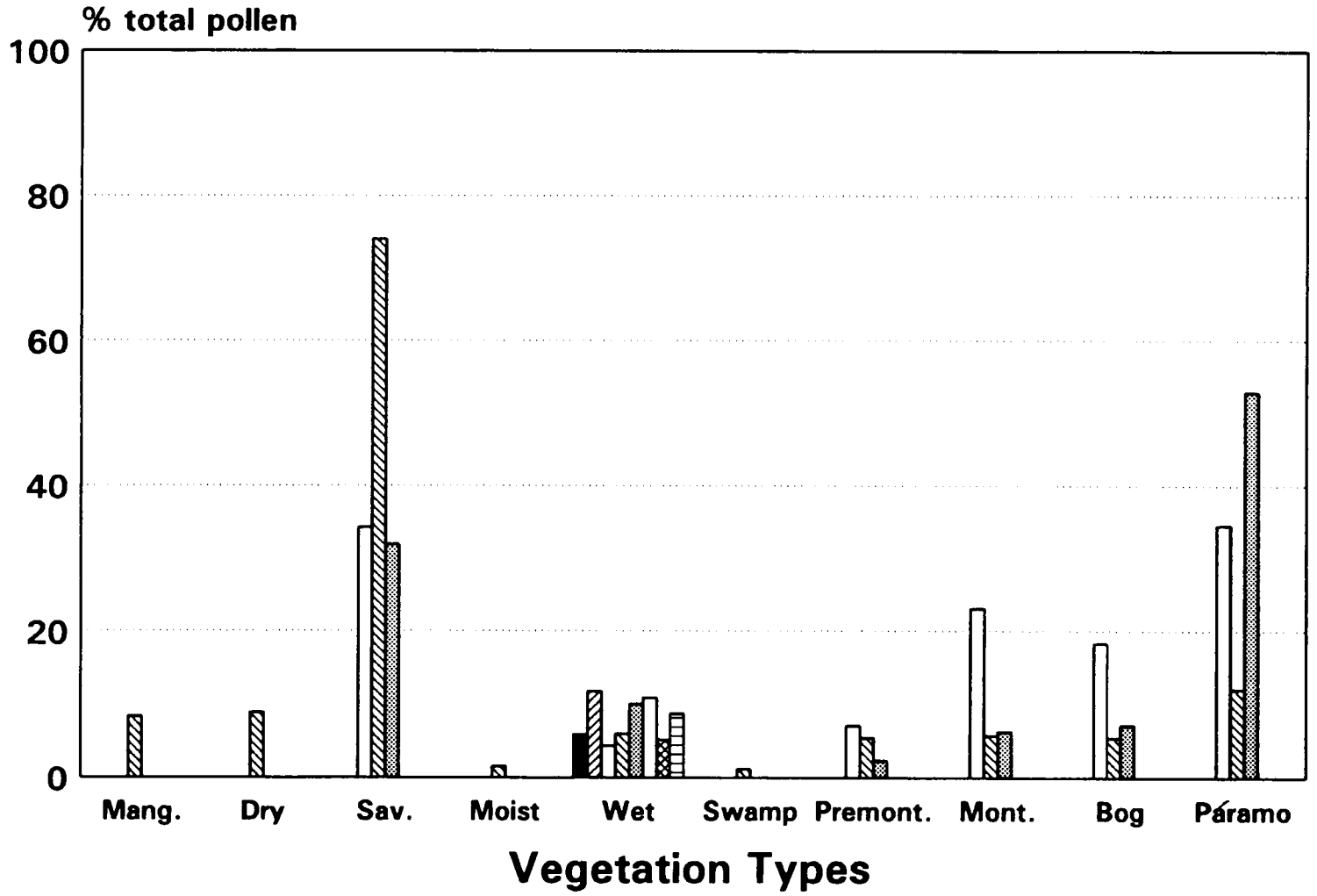

Figure 17: GRAMINEAE pollen percentages in different vegetation types.

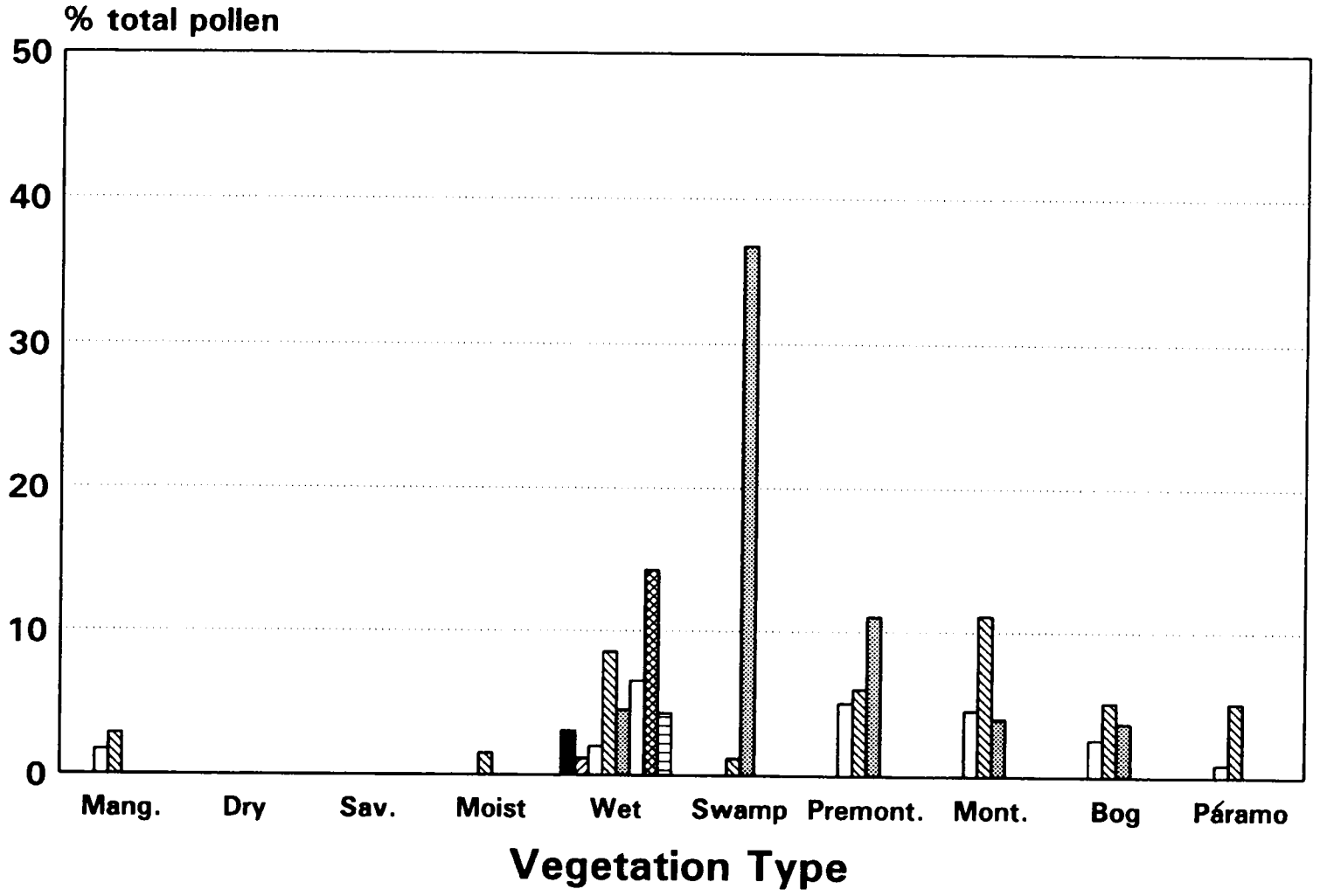

Figure 18: MELASTOMATACEAE/COMBRETACEAE pollen percentages in different vegetation types.

areas, for example the tropical wet, lowland tropical swamp, premontane rain forest, montane rain forest, and montane bog sites.

Cecropia pollen (Figure 19) was found in most of the samples, but was most important in the samples from the tropical moist forest, tropical wet forest, lowland tropical swamp, and premontane rain forest.

Rhizophora (Figure 20) pollen was only found in the first SRNP Mangrove (1) and second SRNP Mangrove (2) sites, with higher percentages in the former.

Two to five pored, undifferentiated URTICALES pollen (Figure 21) occurred in samples from most sites but the type was most abundant in samples from the tropical moist forest and tropical wet forest.

Fern spores (Figure 22) were generally found in samples from all habitats. The montane bog, montane rain forest, and páramo samples generally had the highest amounts of fern spores.

CLUSTER ANALYSIS

Six major clusters were produced from the cluster analysis, with the first SRNP Mangrove sample (site 1), Cantarrana (site 16), and Suampo (site 17) samples each forming their own separate clusters. These clusters are labeled A, B, C, D, E, and F and are shown with the sites that are included in each group in Figure 23.

Cluster A contains both the second SRNP Mangrove (2) and the SRNP Tropical Dry Forest (3) sites. Samples from these sites are similar in that they both have relatively moderate GRAMINEAE pollen (Mangrove = 8.3% and the Dry forest = 8.9%) and URTICALES pollen (Mangrove = 25.4% and Dry Forest) = 18.0%. However, the high percentage of ANACARDIACEAE pollen (Mangrove = 30.2% and the Dry forest = 48.0%) was the major factor that accounted for this cluster. Even though the mangrove sample has moderate percentage of *Rhizophora* pollen (13.7%), it is

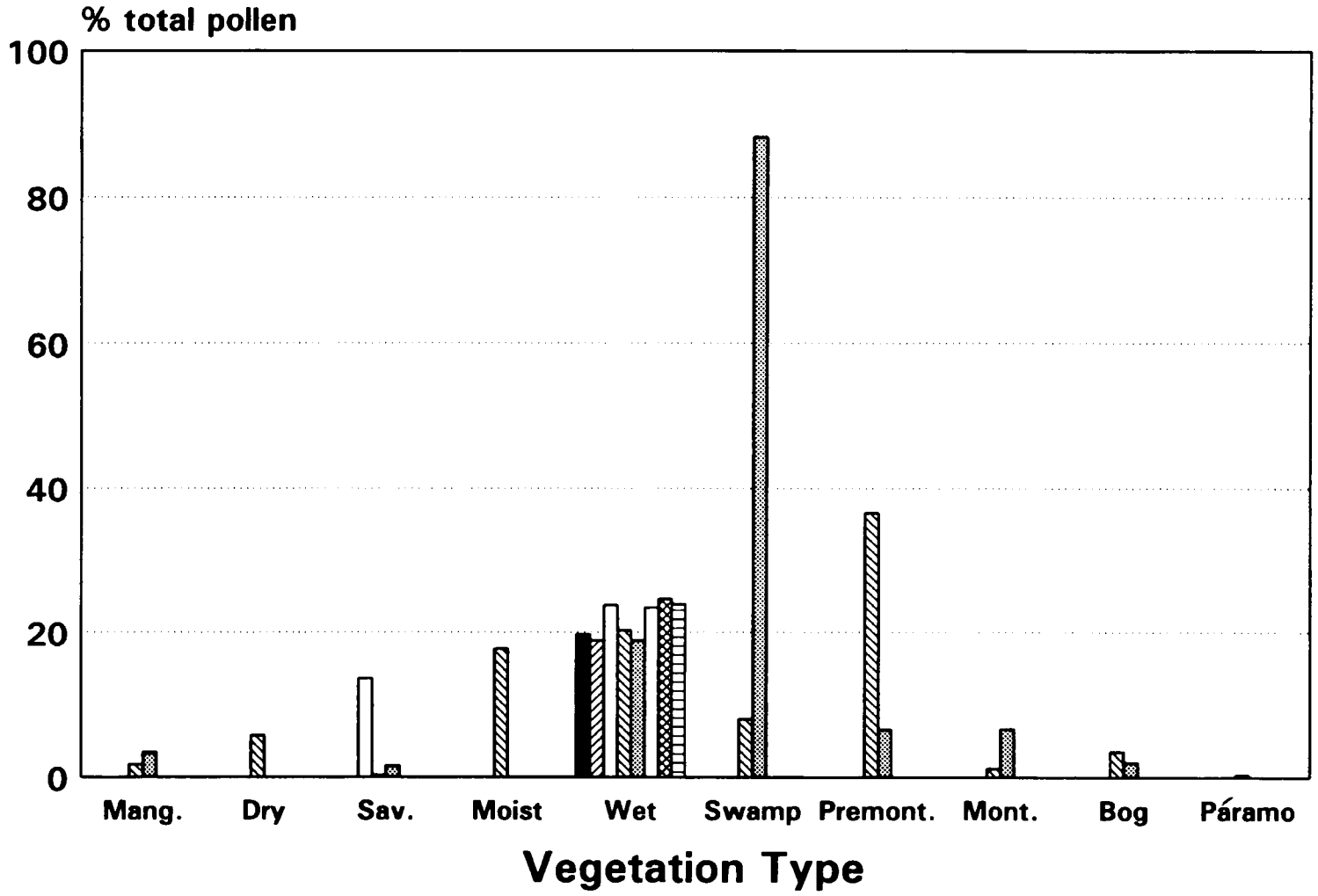

Figure 19: *Cecropia* pollen percentages in different vegetation types.

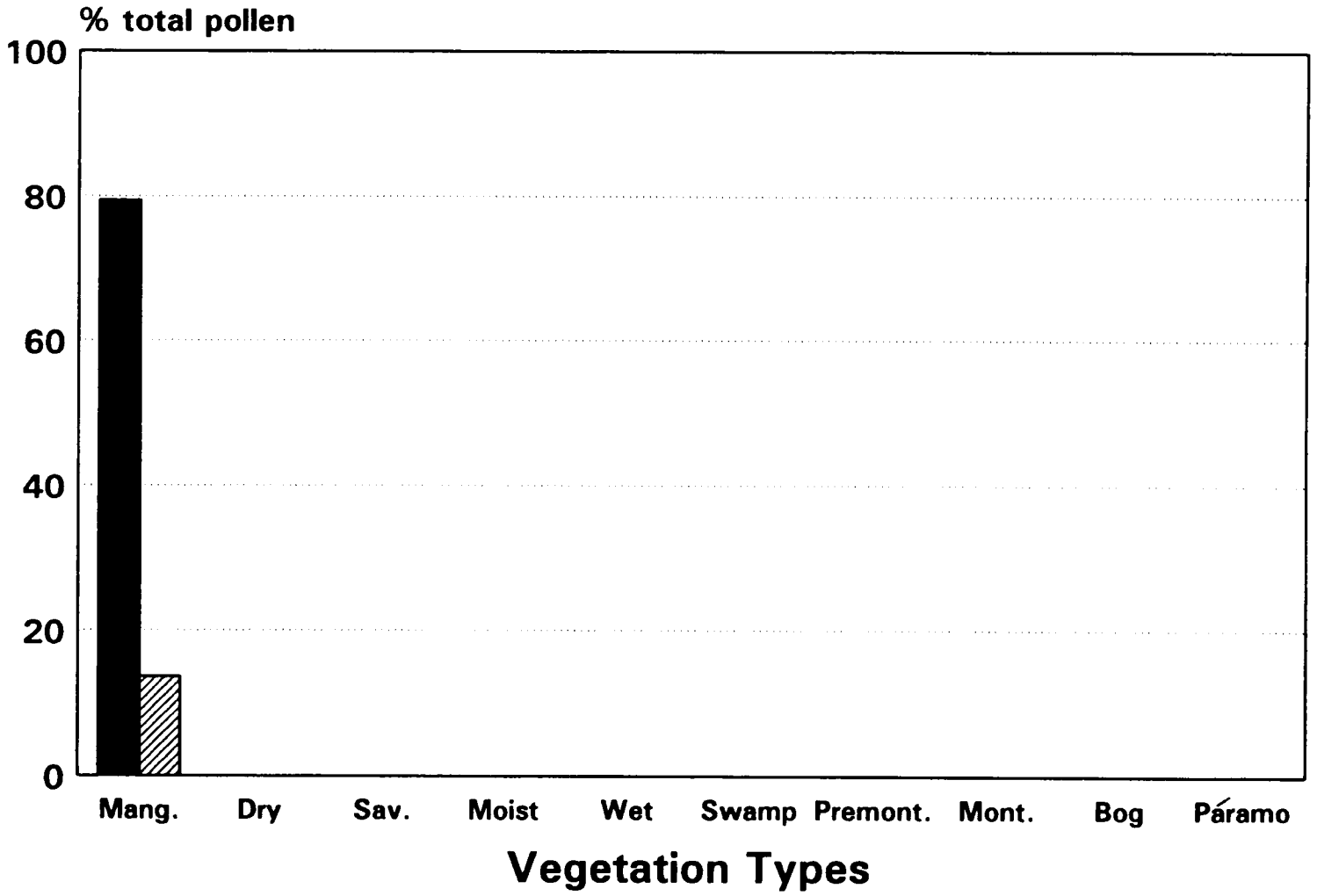

Figure 20: *Rhizophora* pollen percentages in different vegetation types.

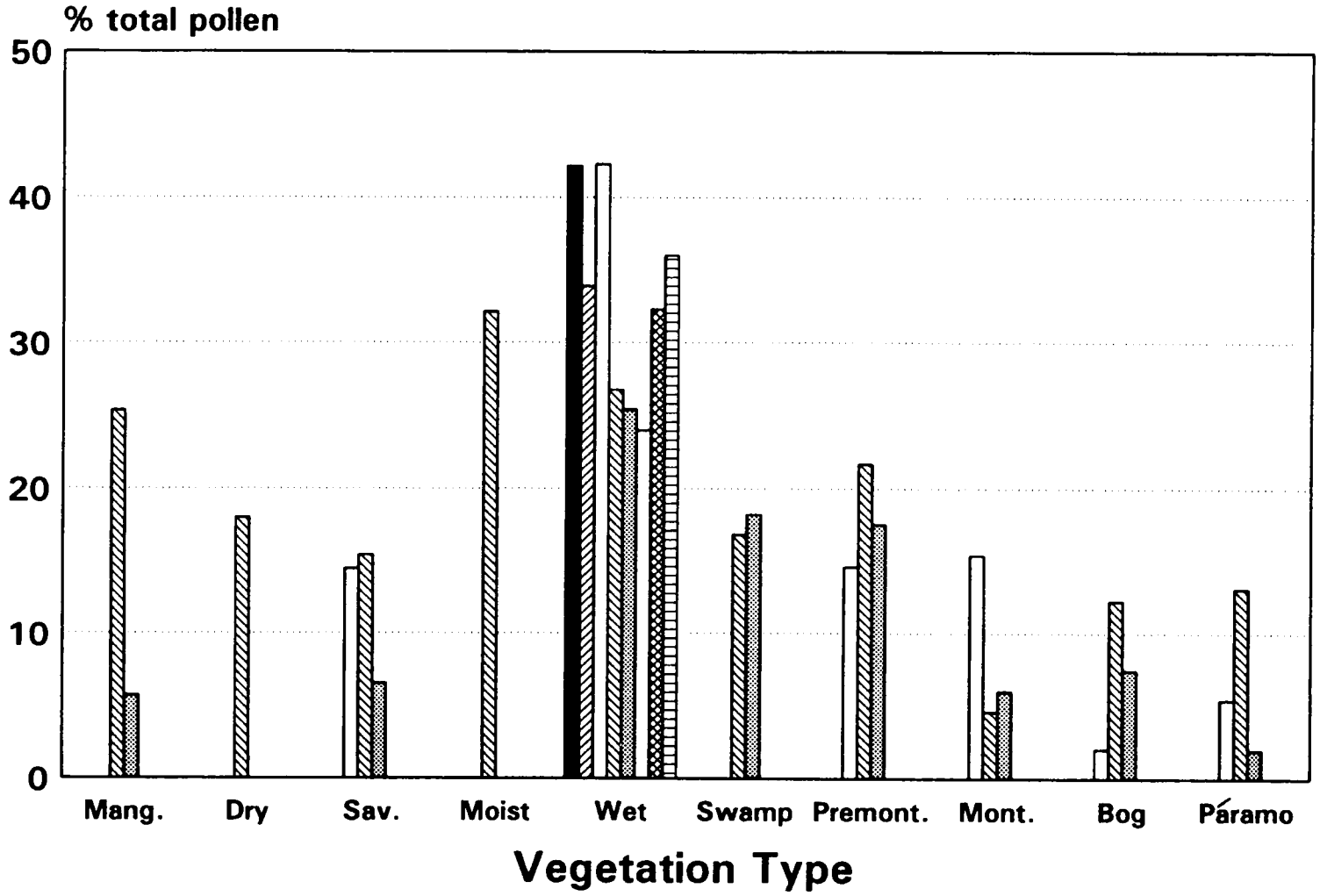

Figure 21: URTICALES (excluding *Cecropia*) pollen percentages in different vegetation types.

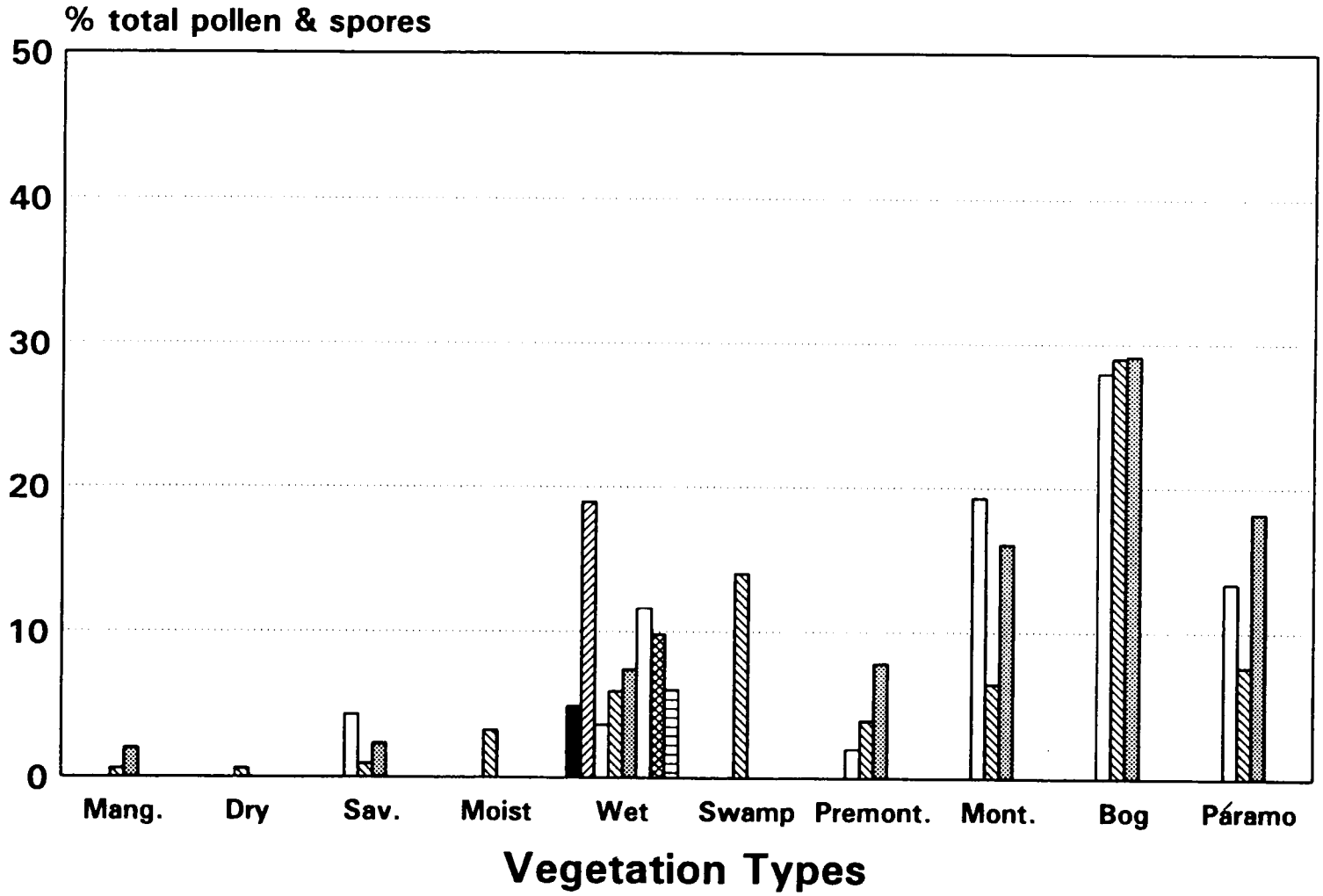

Figure 22: Fern spore percentages in different vegetation types.

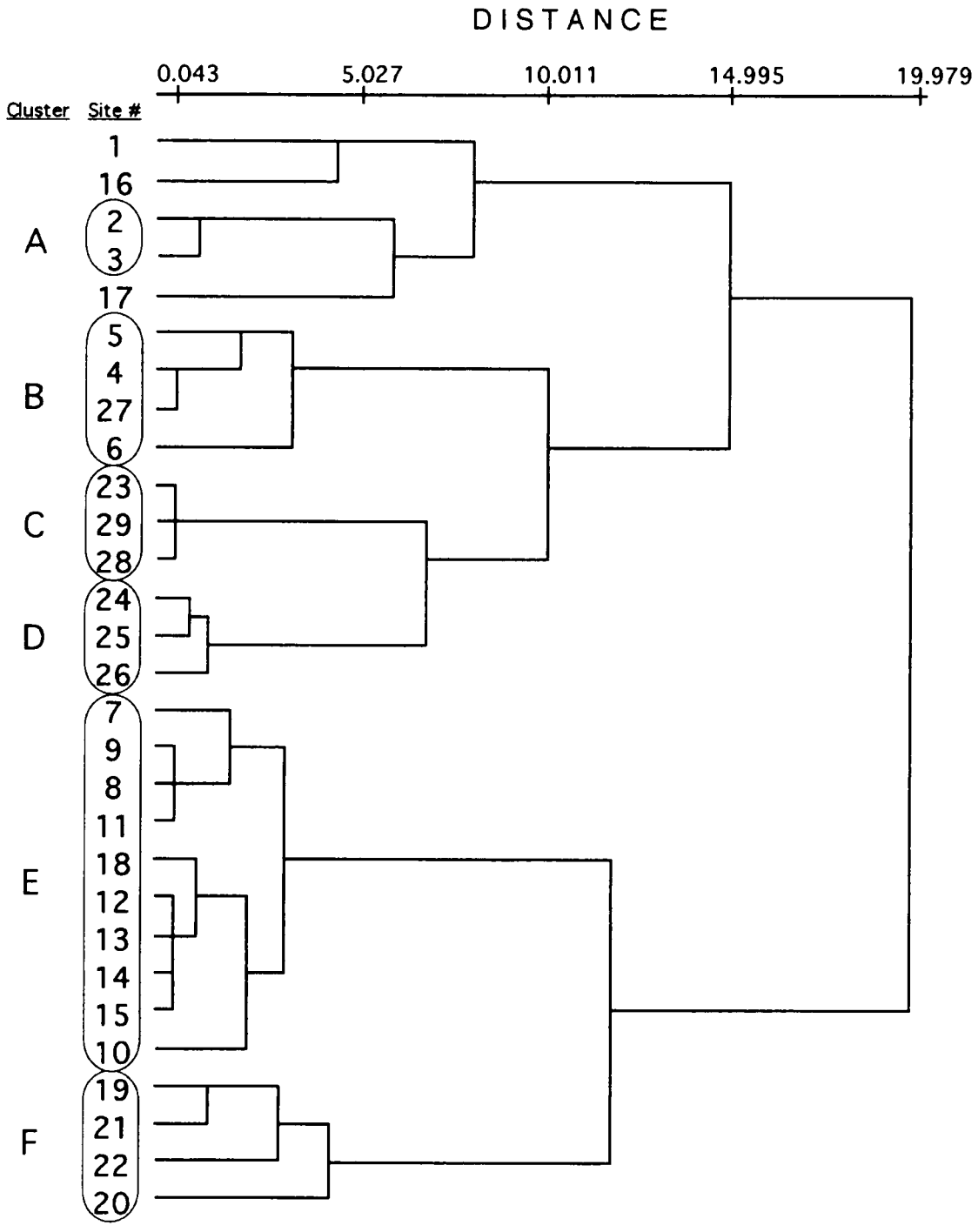

Figure 23: Dedrogram (using Ward's Mimimum Variance) showing results of groupings of sites generated from modern pollen data of the Costa Rican samples. Numbers on the dendrogram correspond to site numbers in Table 1.

statistically more closely related to the Tropical Dry Forest (3) sample than to the first SRNP Mangrove sample (site 1).

Cluster B contains the three derived savanna sites [SRNP Savanna (4), Escondido (5), and Palmita (6)] plus the Asunción (27) páramo site. The high GRAMINEAE pollen percentages (SRNP Savanna = 74.0%, Escondido = 34.2%, Palmita = 31.9%, and Asunción = 53.0%) in the samples were the dominant force that accounted for this cluster.

Cluster C contains the two páramo lake sites Morrenas (28) and Chirripó (29) and the Quebrador (23) quarry site. Similarities in pollen spectra in the samples include moderate percentages of *Alnus*, and fern spores, and moderate to high percentages of *Quercus* and GRAMINEAE pollen.

Cluster D contains the three montane bog sites [Bog 68, (24), Bog 70 (25), and Tres De Junio (26)]. Their samples share similar percentages of *Alnus*, *Weinmannia*, CYPERACEAE, *Quercus*, MELASTOMATACEAE/ COMBRETACEAE, *Myrica*, *Myrsine*, and PODOCARPACEAE pollen, and fern spores. COMPOSITAE, GRAMINEAE, and URTICALES pollen is also well represented, though not equally in all samples.

Cluster E is the largest cluster. All of the tropical wet sites, the tropical moist forest site, and one premontane rain forest site [La Palma (18)] are included in this group. The high percentages of URTICALES and *Cecropia* pollen in the samples were the dominant force that accounted for the cluster. Even though dominated by these pollen types, the sample from these sites contain a diversity of other important pollen types -- generally these are the most diverse samples in the set.

Cluster F contains the Laguna Cedeño (19), Volcán Cacao (20), Botos (21) and Barva (22) sites. Similarities in *Alnus*, *Weinmannia*, GRAMINEAE, MELASTOMATACEAE/COMBRETACEAE, and URTICALES percentages could have accounted for the grouping of these sites. Another similarity that may have influenced the grouping is that the most common pollen type at all of the sites accounted for less than 25% of the pollen sum.

Distinct Clusters include those samples that were not grouped with any of the above clusters. High pollen percentages from locally important taxa accounted for the separation of the samples from the first SRNP Mangrove sample (1), the La Selva Cantarrana (16), and the La Selva Suampo (17) sites from all other sites in the set. The mangrove sample was dominated by *Rhizophora* pollen (79.5%), the La Selva Cantarrana sample by *Cecropia* pollen (88.0%), and the La Selva Suampo sample by *Pentaclethra* pollen (37.1%). The rather heavy dominance of the pollen spectra by one local type at each site gave them high average dissimilarity coefficients and resulted in the separation of these sites into their own distinct clusters.

DCA ORDINATION

The results of the DCA ordinations are shown in Figures 24-26. To emphasize similarities and differences between the cluster and DCA analyses, I have drawn the cluster boundaries based on the cluster analysis (Figure 23). Figure 24 shows the results of the first ordination, which was run using pollen data from all sites. In this and other DCA graphs, similar sites are plotted in close proximity and dissimilar sites are plotted farther away from each other. As shown in figures 24, 25, and 26, the sites were clustered together in approximately the same groups as in the cluster analysis (Figure 23), and points can be circumscribed by reasonably tight boundaries.

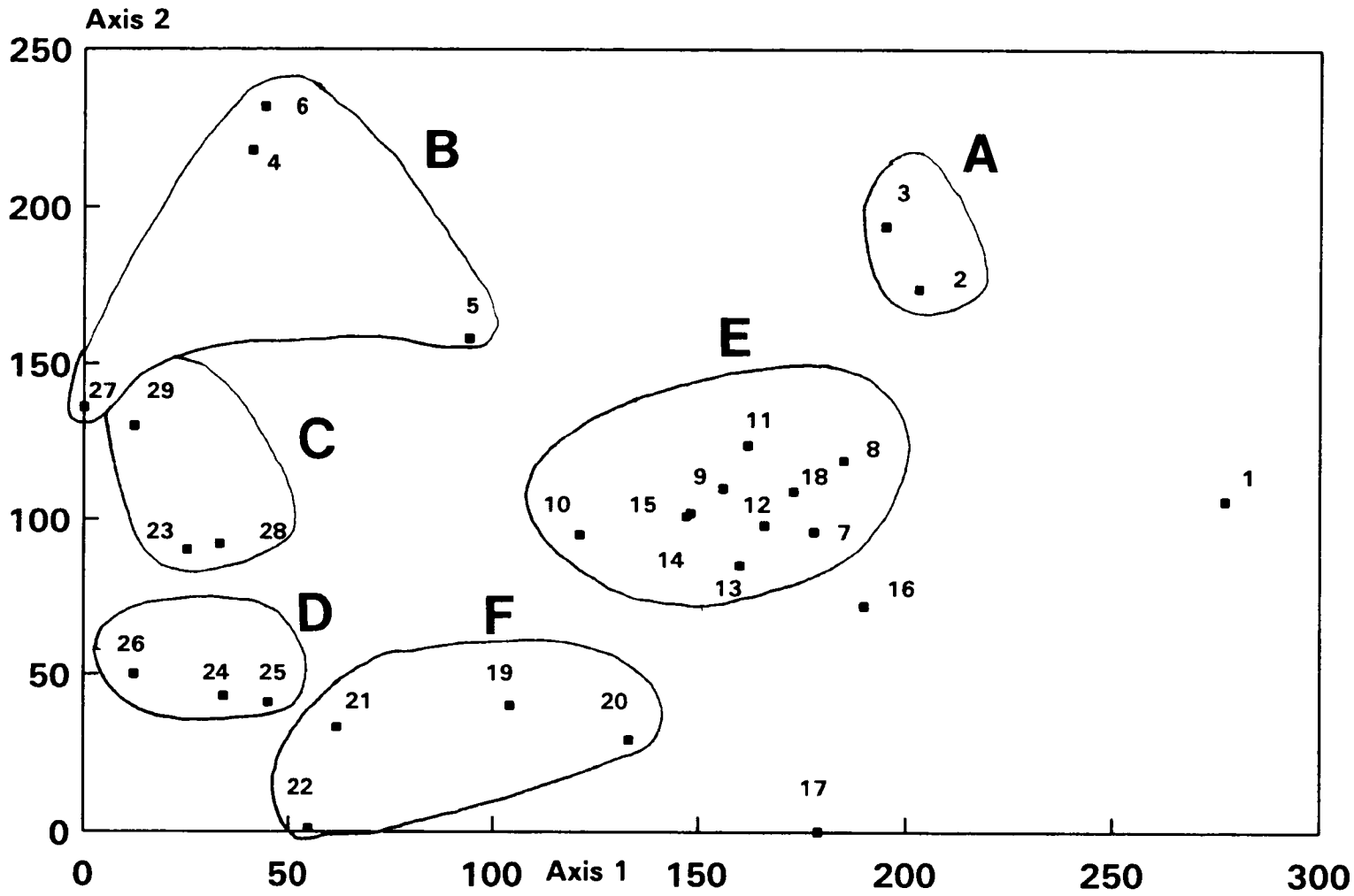

Figure 24: Results of DCA ordination of all modern pollen rain sampling sites, Costa Rica. The site groups were defined by the cluster analysis results (Figure 23).

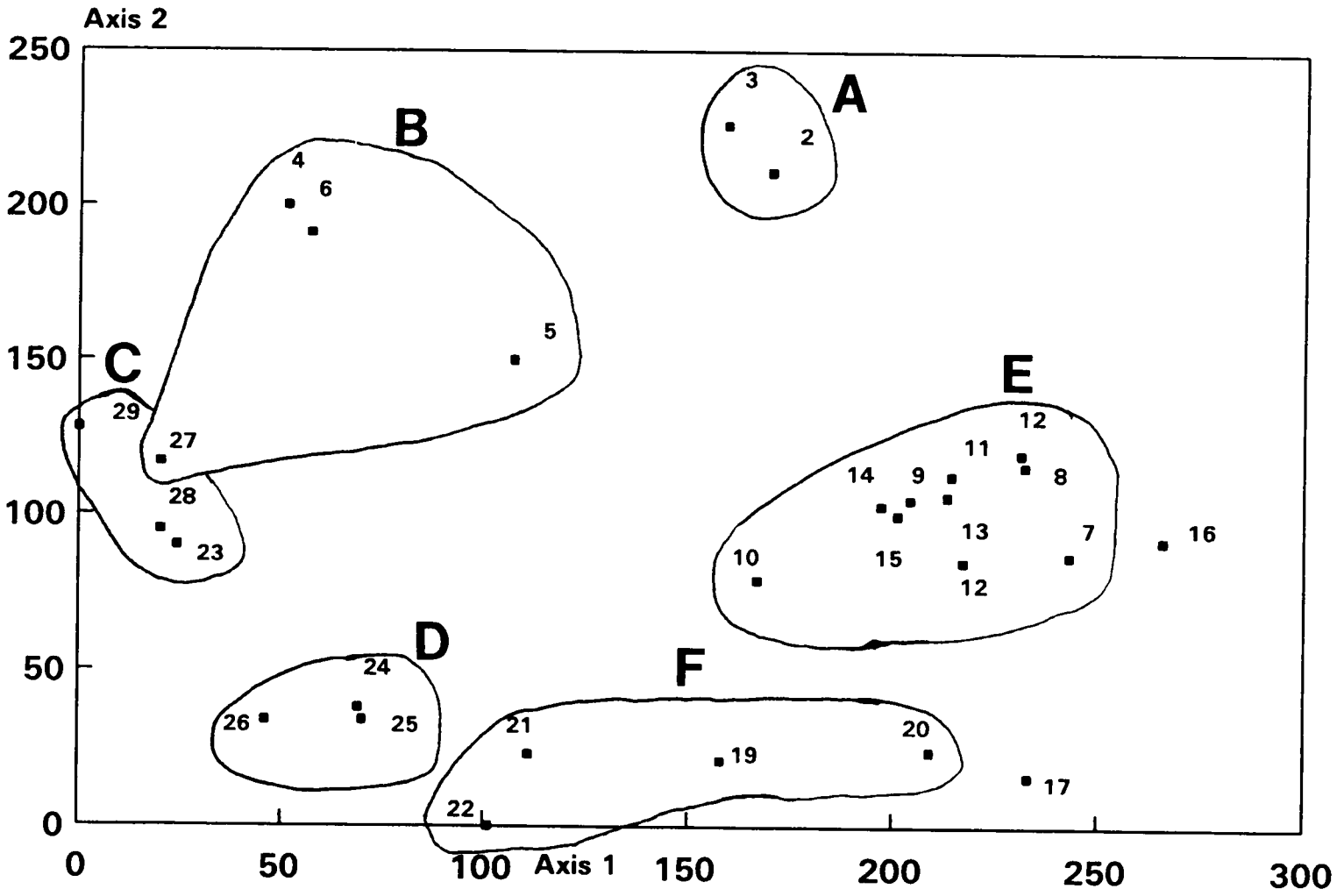

Figure 25: Results of second DCA ordination of modern pollen rain sampling sites, Costa Rica, exculding site 1. The site groups were defined by the cluster analysis results (Figure 23).

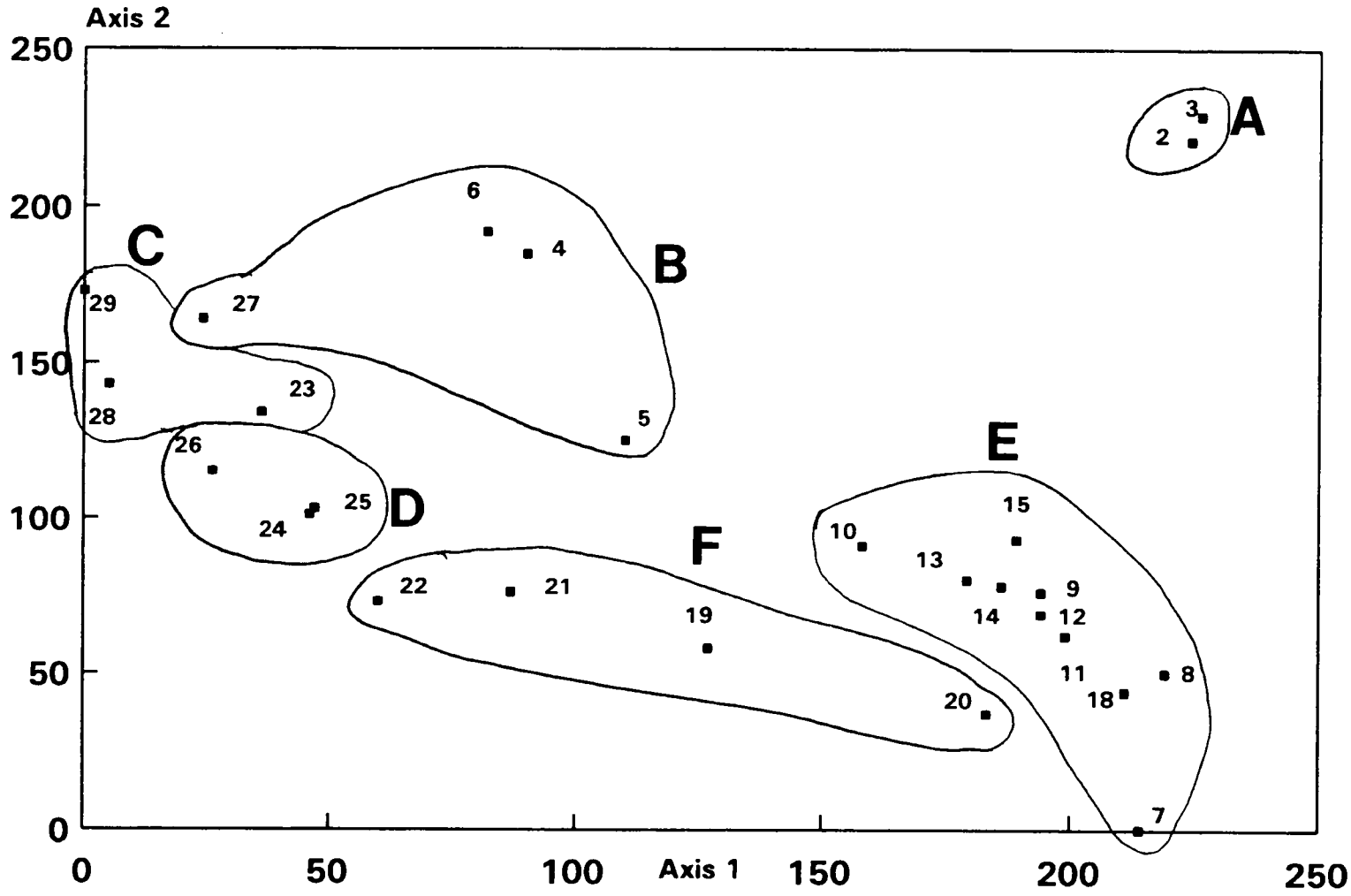

Figure 26: Results of third DCA ordination of modern pollen rain sampling sites, Costa Rica, excluding sites 1, 16, and 17. The site groups were defined by cluster analysis results (Figure 23).

But some differences exist in the grouping of sites between the DCA and the cluster analysis. In the DCA, the Asunción site (27) is plotted closer to the other páramo sites (28, 29) than to the derived savanna sites (4,5, 6). Also, there appears to be a small separation of sites within the montane rain forest cluster. The montane rain forest sites Botos (21) and Barva (22) are plotted more toward the montane bog (24, 25, 26) and páramo sites (27, 28, 29) and the premontane rain forest samples Cedeño (19) and Volcán Cacao (20) are plotted closer to the "tropical wet cluster" (Cluster E).

Figure 25 shows the results of the second ordination, run without the first SRNP Mangrove sample (1). This sample is dominated by a single type (*Rhizophora*, 79.5%), that was thought to be heavily influencing the positioning of all other sites. However, results show the grouping of the sites to have been relatively unaffected by the removal of the first SRNP Mangrove sample (site 1). The same major clusters are also evident in the second DCA ordination. The differences from the first ordination are that the Asunción site (27) is pulled a little closer to the derived savanna sites. Also, the sites within Cluster F are pulled away from each other. As in the first DCA, the true montane rain forest sites Botos (21) and Barva (22) are pulled more toward the montane bog and páramo clusters while the premontane rain forest sites Cedeño (19) and Volcán Cacao (20) are pulled more toward the "tropical wet cluster".

Figure 26 shows the results of a third ordination, in which the samples from the La Selva lowland tropical swamps [Cantarrana (16) and Suampo (17)] were excluded along with the first SRNP Mangrove (1) sample. These samples were each heavily dominated by one local pollen type, and had been placed in distinct clusters in the cluster analysis. The major differences between the third ordination and the previous two are that the premontane rain forest sites Cedeño (19) and Volcán Cacao (20) were pulled very close to the tropical wet sites. The Asunción

site (27) is again closer to the other páramo sites than to the derived savanna sites. The derived savanna sites (4, 5, 6) are pulled closer together, as are the tropical dry forest and second mangrove sites (2, 3). Finally, the Quebrador site (23), which was clustered with the páramo sites in the cluster analysis, was plotted closer to the montane bog sites.

CHAPTER 6

DISCUSSION

The results of the statistical analyses demonstrate that modern pollen spectra in different vegetation types in Costa Rica are generally distinct. The hypothesis that different vegetation types can be distinguished by their pollen rain is supported for many (but not all) vegetation types. This chapter explores the extent to which the different vegetation types sampled in this study can be differentiated by their pollen rain. Aspects of the statistical analysis are elaborated upon, and pollen data are compared to the results of modern pollen rain research in other areas in Costa Rica and elsewhere in the neotropics.

MODERN POLLEN SPECTRA IN COSTA RICA

The pollen spectra within the mangrove forest of Santa Rosa National Park [site (1) and site (2)] reflect species distributions at the sites. Site 1 was located in the nearshore zone, where *Rhizophora* dominates, and the sample contains a high percentage of *Rhizophora* pollen. The importance of *Rhizophora* plants and pollen declines inland, while that of *Avicennia* increases. Site 2, collected within a stand of *Avicennia*, showed higher *Avicennia* percentages and lower *Rhizophora* percentages. The relative importance of *Rhizophora* and *Avicennia* pollen at the two sites is also consistent with previous palynological work in mangrove swamps. According to Flenley (1979), *Rhizophora* is wind pollinated and a heavy pollen producer. The relatively small pollen grains are dispersed inland by wind and water transport. The distribution of *Avicennia* pollen has been found to be more closely related to the source area (Flenley, 1979). The low percentage of

Avicennia pollen in the sample from site 2, which was covered with a nearly monospecific stand of *Avicennia*, further suggests that this presumably insect-pollinated taxa deposits less pollen in surrounding sediments than does *Rhizophora*. As a consequence of low pollen production by *Avicennia*, the second SRNP Mangrove site (2) preserves a greater amount of pollen derived from surrounding tropical dry forest associations (see site description in Chapter 3). Pollen of the white mangrove *Laguncularia racemosa* or the mangrove swamp associate *Hibiscus tiliaceous* was not found in either sample. The small amount of MELASTOMATACEAE/COMBRETACEAE pollen in the sample could be from the button mangrove *Conocarpus erectus*, or from other members of either family that occur in surrounding plant communities.

In general, mangrove forest vegetation in Costa Rica can be differentiated from other vegetation types by the presence of *Rhizophora* and *Avicennia*, though pollen spectra from stands of *Avicennia* may underestimate the importance of this mangrove and contain more pollen from surrounding vegetation type.

The derived savanna sites all lie within grasslands, and not surprisingly the samples were dominated by GRAMINEAE pollen. Other pollen is derived from savanna herbs (*e.g.*, COMPOSITAE) and from trees growing within the grasslands or in adjacent tropical dry forests. No pollen was found in the SRNP Savanna (4) and Escondio (5) samples of the three trees common in savannas of the region (*Byrsonima crassifolia*, *Crescentia alata*, and *Curatella sp.*); these are presumably animal-pollinated taxa whose pollen is not widely transported. However, *Byrsonima* pollen has been recorded in modern and fossil pollen spectra from other neotropical savannas (Flenley, 1979).

Derived savanna vegetation can be distinguished in the pollen record. Both cluster analysis and DCA grouped the savanna/pasture sites in a distinct cluster. The specific pollen signature for derived

savanna vegetation would be very high percentages of GRAMINEAE pollen with limited amounts of tropical dry forest pollen.

The tropical dry forest sample (3) differed in its modern pollen rain from the derived savanna sites by having higher percentages of arboreal pollen types and lower percentages of GRAMINEAE pollen. As with the derived savanna sites, many tropical dry forest trees must be under-represented in the pollen record.

Cluster analysis and DCA grouped the Tropical Dry Forest site (3) with the second SRNP Mangrove site (2), whose pollen spectra were dominated by pollen from surrounding forest. Tropical dry forest can probably be distinguished as distinct from derived savanna vegetation in pollen records by higher percentages of dry forest pollen taxa and lower amounts of GRAMINEAE pollen.

The tropical moist forest sample, Carara (7) was not distinguishable from the tropical wet samples by either cluster analysis or DCA. The most abundant pollen types in this sample were found in similar amounts in the tropical wet samples. Based on the pollen spectra from Carara, it is unclear whether there is a distinct pollen signature for tropical moist forest vegetation. However, additional samples are required to adequately test this supposition.

The tropical wet forest sites can be distinguished from other vegetation types by their pollen signature. This is indicated by their clustering as one group in the cluster and DCA analyses. The high percentages of *Cecropia* and other URTICALES are consistent with the distribution of plants in this order (Burger, 1977). Though some taxa occur in dry and in montane habitats, the order as a whole is best represented in tropical lowland wet habitats (Burger, 1977). The other important pollen types *Alchornea, Acalypha,* E/R/A, MELASTOMATACEAE/ COMBRETACEAE, MYRTACEAE, *Iriartea,* and *Piper* are also well represented in wet lowland forests (Hartshorn and Poveda, 1983), though these taxa also extend into drier and cooler areas. Samples from the tropical wet

sites were also alike in having generally higher pollen diversity (as measured by the number of different taxa recorded) than samples collected in drier or cooler sites.

The two lowland tropical swamp samples differed substantially from the tropical wet samples and from each other. The high amounts of *Cecropia* and MELASTOMATACEAE/COMBRETACEAE pollen in the Cantarrana sample (site 16) are probably a result of the more open forest situation around this swamp. *Cecropia* trees growing in nearby gaps created by tree falls or along nearby streams contributed a substantial amount of pollen to the swamp, "drowning out" the signal from local vegetation. The MELASTOMATACEAE/COMBRETACEAE pollen may have been derived from herbaceous or shrubby melastomes near or within the swamp, or from a large *Terminalia oblonga* (COMBRETACEAE) located a short distance away.

While both La Selva lowland tropical swamp samples were separated into their own distinct clusters by cluster analysis, they plotted close to the large "tropical wet cluster" in DCA. The lowland tropical swamp vegetation type probably can not be separated from tropical wet forest based on pollen data. That is because open lowland tropical swamps preserve pollen blown in from surrounding forest, and because forest swamps share many taxa with better drained tropical wet forest sites.

The premontane rain forest sites [La Palma (18), Cedeño (19), and Volcán Cacao (20)] varied greatly in their pollen spectra. Cedeño (19) and Volcán Cacao (20) were clustered with the montane rain forest sites in both cluster analysis and DCA, possibly because the samples shared moderate percentages of montane pollen types. The other premontane rain forest sample, La Palma (18), was grouped with the tropical wet and tropical moist sites. This was unexpected because La Palma and Cedeño are located very close to each other on the slopes of Volcán Arenal and are both at the same elevation. Interestingly, both sites lie very close to the boundary between the tropical wet forest and premontane rain forest life zones on Tosi's (1969) life zone map. It seems that

Laguna Cedeño has pollen spectra more similar to sites in the higher premontane (and higher still montane) life zones, while Laguna Palma shows more similarities with sites in the lower tropical wet life zone. This may in part reflect localized differences in vegetation that have caused the lakes to have different source areas for pollen. More of the forest surrounding Cedeño has been cleared (in this case by both humans and volcanic activity), and the more open situation there may allow more wind-borne montane pollen types to enter the lake. The denser forest surrounding La Palma may filter out these montane pollen types, and at the same time contribute more *Cecropia* and URTICALES pollen types to the sediments.

The presence of *Alnus* pollen in the Cedeño sample (19) is interesting in that this genus has not been reported on the slopes of Arenal. Burger (1983a) provides a species account of *Alnus* in the volume *Costa Rican Natural History* that indicates that in Costa Rica A. *acuminata* is not known to occur north of Volcán Barva on the northern end of the Cordillera Central, even though the species ranges northward to Mexico. However, in the same volume, Hartshorn and Poveda (1983) provide a checklist of trees that lists A. *acuminata* as present at the Monteverde reserve in the Cordillera de Tilarán (one range northwest of the Cordillera Central; see Figure 1). The presence of *Alnus* in the Cordillera de Tilarán is confirmed by a specimen (W. Haber 9848) from the Monteverde reserve in the herbarium of the National Museum of Costa Rica (S. Horn, pers. communication, 1994). The *Alnus* pollen in the Cedeño sediments could have been derived from populations in the Cordillera de Tilarán, though pollen transport in this case would be against the prevailing northeasterly tradewinds. Long-distance transport from the slopes of volcanoes to the south is also a possibility, but again might not be favored by wind patterns, and the relatively high percentage of *Alnus* in the Cedeño samples argues for a closer source. It is possible that unreported populations of

A. acuminata exist within mature or successional forests on the slopes of Arenal. Although *Alnus* is widely planted in pastures in Costa Rica (Burger, 1977, 1983a), pastures on Arenal are likely too low in elevation to provide suitable sites for the tree. In connection with the possible occurrences of undiscovered populations of *Alnus* on Arenal, it is interesting to note that the *Alnus* pollen in the Cedeño sediments has four pores, rather than five as is more characteristic for the genus in Costa Rica.

In general, the premontane rain forest vegetation type probably cannot be separated out by its pollen spectra, based on the samples analyzed in this thesis. The variability in pollen spectra among the three premontane rain forest sites in this thesis suggest a need to collect more samples within this vegetation type.

The distinguishing characteristics of the pollen spectra from the montane rain forest sites are, not surprisingly, high percentages of pollen from montane taxa. That the Quebrador quarry site (23) did not cluster with the other montane rain forest sites [Botos (21) and Barva (22)] but rather clustered with the páramo sites seems to reflect local and regional differences in vegetation. Much more *Quercus* pollen was preserved in the Quebrador sediments, likely because of the much greater extent of oak-dominated montane rain forests in the Cordillera de Talamanca as compared to the lower and more isolated peaks of the Cordillera Central. Quebrador also showed the higher GRAMINEAE values that are associated with páramo vegetation, possibly because of transport of pollen from upslope páramo communities (absent at Botos and Barva) as well as from local pollen production by grasses growing on the rocky slopes immediately surrounding the pond.

The three montane bog sites [Bog 68 (24), Bog 70 (25), and Tres de Junio (26)] can be distinguished from the montane rain forest and other sites by their higher percentages of fern spores, and possibly also by higher values of *Alnus*, COMPOSITAE, and CYPERACEAE pollen.

Monolete, scabrate fern spores were especially abundant in the bog samples and were probably derived from the fern *Blechnum buchtienii*, which is common in these bogs (Horn, 1988). However, many other spores of varying morphology were also common in the bog samples. *Alnus acuminata* is a wind-pollinated tree that grows in pastures and forests near the bogs. That this pollen types is abundantly deposited in the bogs reflects both plant geography and the open nature of the sites, which lack a tree canopy that would filter out windborne pollen.

Páramo pollen spectra are also distinct. The high amounts of grass pollen in the páramo samples [Asunción (27), Morrenas (28), and Chirripó (29)] may be largely from *Chusquea subtessellata* which forms nearly monodominant stands in some areas (Horn, 1989b). *Vaccinium*, *Pernettia*, and *Comarostaphylos* are all common ericaceous shrubs in the páramo and in treeline associations that are transitional between páramo and oak-dominated montane rain forest; they are probably the source of the ERICACEAE pollen in these samples (Horn, 1993).

The arboreal pollen types found in the páramo samples must have been derived from montane forest growing below the páramo vegetation. As was the case for the Quebrador and bog sites, the openness of the páramo vegetation probably facilitates the infiltration of these wind-borne pollen grains.

Cluster analysis grouped the páramo sites Morrenas and Chirripó with the montane rain forest site Quebrador (24). All three sites had high percentages of *Quercus* and GRAMINEAE pollen types. Asunción, however, was not grouped by cluster analysis with the other páramo sites, but rather it was grouped with the derived savanna sites (Cluster B), presumably on the basis of the similar GRAMINEAE pollen percentages. Asunción is a very small pond that may collect pollen primarily from the bamboo-dominated vegetation immediately surrounding the site [i.e., the pond would have a very small pollen source area (Jacobson and Bradshaw, 1981)]. Perhaps it was as a consequence of its small size that Asunción

trapped proportionally less montane pollen than the larger páramo lakes, Morrenas and Chirripó. The Asunción site also trapped less pollen from forests at lower elevations (note low URTICALES percentages).

Though the Asunción and derived savanna sites were grouped together on the basis of grass and oak pollen percentages, they clearly differ in other ways. Asunción is richer in montane pollen types (*e.g.*, *Alnus*, *Weinmannia*, and *Podocarpus*) whereas the derived savanna samples were higher in tropical dry forest pollen types (*Bursera*, *Guazuma*, *Cecropia*, ANACARDIACEAE, and URTICALES). This is in keeping with the compositions of the surrounding forests.

INTERPRETATION OF DCA AXES

In DCA clustering of sampling sites, the resulting axes are often regarded as representing environmental gradients (Bush, 1991). However, the assignment of environmental gradients to the ordination axes produced in this study is not straightforward. Relationships between pollen spectra and environmental gradients are complicated by the fact that treeless, grass-dominated vegetation types occur both in cool and moist highland sites (páramo) and in hot and dry lowland sites (derived savanna) and that the genus *Quercus* shows a similar "bipolar" distribution, with one species found in lowland dry forest and all others confined to cooler and wetter montane and premontane sites.

Axis 2 seems quite clearly driven by GRAMINEAE and *Quercus* percentages and is thus not easily interpretable in terms of environmental gradients. This is most evident in Figure 26, which graphs the results of the DCA run without the three outliers. In this figure, all sites that plot lower than about the value 100 on Axis 2 have relatively low percentages of these two pollen types, while all sites plotted above the 100 value on Axis 2 have relatively high values for grass and oak pollen. If one were presented only with the DCA

diagram, with clusters labelled as to vegetation type, one might argue that Axis 2 represented a moisture gradient, with the wetter sites plotting lower on the axis. But the driving factor here seems to be the distribution in space (and in pollen samples) of two abundant taxa.

Axis 1 seems more clearly interpretable in terms of an environmental gradient. (This is again most evident on the DCA run without the outliers). Specifically, it appears to represent a temperature and elevational gradient, with percentages of URTICALES, *Cecropia*, MELASTOMATACEAE/COMBRETACEAE, and other pollen types characteristic of lowland tropical forests (both wet and dry) increasing as values increase along the axis. The montane pollen types *Alnus* and *Weinmannia*, among others, and *Quercus* and fern spores decline along this gradient, reflecting their generally decreased importance at lower and warmer elevations. But with this axis, oak and grass percentages still exert an influence, pulling the derived savanna sites closer to the montane rain forest, bog, and páramo sites than might be expected were the axis driven only by an elevationally-determined temperature gradient.

COMPARISONS WITH OTHER POLLEN RAIN STUDIES

The modern pollen data reported in this study are generally in good agreement with the limited modern pollen data previously reported from Costa Rica. The *Rhizophora* percentages from the first SRNP Mangrove site (1) are similar to the modern pollen data of Horn (1985a). Even though her sample was collected from a nearby area of the same mangrove forest, Horn found *Laguncularia* to comprise 6.7% of the total pollen. I found none of this pollen type in the sample I analyzed from the first SRNP Mangrove site (1). This difference probably reflects the clumped distribution of *Laguncularia* in the swamp (Crease *et al.*, 1982)

and the fact that my sample was collected closer to shore in an area that may have lacked *Laguncularia* (S. Horn, pers. communication, 1994).

Horn's (1985a) modern pollen data from a derived savanna in Santa Rosa National Park are also similar to the SRNP Savanna sample (site 3) analyzed in this study. Both samples were collected from the same general area and were both dominated by GRAMINEAE pollen. The major differences between the two studies were that the SRNP Savanna sample (site 3) analyzed in this thesis had higher percentages of *Quercus* pollen (8% vs. 1.6%) and lower percentages of COMPOSITAE pollen (18.9% vs. 6.5%) than the derived savanna sample analyzed by Horn (1985). These differences might reflect local differences in vegetation composition or possibly changes over time as a result of recent efforts to foster reforestation of grasslands in Santa Rosa National Park through fire exclusion and increased livestock-mediated seed dispersal (Janzen, 1986). (The sample Horn analyzed was collected in 1982, nine years earlier than the sample I analyzed was collected; both samples were collected in March.)

Horn (1993) found that pollen spectra in moss polsters from montane rain forest in the highlands of the Cordillera de Talamanca (Chirripó massif) were comprised of 50-90% oak pollen. The sample from Quebrador pond (also in the Cordillera de Talamanca) that was analyzed in this research had 40% oak pollen, but the other montane rain forest samples (Botos and Barva in the Cordillera de Central) had only 3.4% and 2.6%, respectively, oak pollen. These results are consistent with the high density of *Quercus* on the upper slopes of the Cordillera de Talamanca (Burger, 1977). That the Quebrador lake sample had lower oak percentages than the moss polsters from Chirripó may reflect the differing nature of the two pollen traps. Alternatively, it may reflect the rather substantial clearing that has taken place within oak-dominated montane rain forest immediately adjacent to the Quebrador site (Schubel, 1980; Sader and Joyce, 1988)

Previously reported modern pollen data from the Chirripó páramo (Horn, 1993) are very similar to the pollen data from the Chirripó sample (29) I analyzed in this thesis, a result that was not unexpected given that we used the same sample.

Bush (1991) has summarized and analyzed data on modern pollen deposition in 20 lakes in northern South America and one in Panama. The vegetation types of most of these sites are not directly comparable to those of this study, but there are some general similarities. Surface sediments of Lake Valencia in the tropical dry forest of northern Venezuela are dominated by CHENOPODIACEAE/AMARANTHACEAE (30%) and GRAMINEAE (20%) pollen. Other important pollen types included *Acalypha* (10%) and COMPOSITAE (5%) (Bush, 1991). The Tropical Dry Forest sample (3) analyzed in this thesis differed substantially from the Venezuelan sample in having less than 1% CHENOPODIACEAE/AMARANTHACEAE pollen and only 9.0% GRAMINEAE pollen. Also, the Tropical Dry Forest sample (3) was dominated by ANACARDIACEAE pollen (48%) while the Venezuelan sample had less than 5% of ANACARDIACEAE. However, the two sites had similar URTICALES pollen percentages (15%-18%).

Bush's "cerrado" sample from Brazil shows some similarities with the derived savanna samples included in this thesis (sites 4, 5, and 6). All samples are dominated by GRAMINEAE pollen, but the sites in this study include more arboreal pollen types such as *Quercus, Guazuma, Cecropia,* ANACARDIACEAE, and more URTICALES (which can be arboreal or herbaceous). The lower representation of arboreal pollen types in the cerrado sample might reflect the more expansive nature of the Brazilian cerrado as well as differences in tree density and species composition.

Bush also reported modern pollen data from many different tropical lowland wet forest types in the Amazon. The forest sites that were probably similar to vegetation types described in this study are his "terra firme" sites. Samples from these sites, were dominated by *Iriartea, Cecropia,* and other URTICALES pollen (Bush, 1991), as are

tropical wet forest samples from Costa Rica. Bartlett and Barghoorn (1973) also found *Cecropia* and URTICALES pollen to be consistently abundant in surface sediments collected adjacent to tropical moist forests in Gatun Lake, Panama. High percentages of *Cecropia* and other URTICALES pollen appear to be a signature of humid lowland forests (*e.g.*, tropical wet forest and tropical moist forest) in the neotropics.

Fine (1978) examined the modern pollen rain for different vegetation types of Mexico. Her mangrove forest samples were dominated by *Laguncularia* pollen, which accounted for half of the total pollen. As mentioned, I did not find this pollen type in the SRNP mangrove samples analyzed in this study (sites 1 and 2). Other differences between our data are that Fine found larger percentages of *Avicennia* and CHENOPODIACEAE/AMARANTHACEAE pollen. Even though our results differed, it is clear that neotropical mangrove vegetation has a distinct pollen signature typified by the presence (or dominance) of *Rhizophora*, *Laguncularia*, and/or *Avicennia* pollen.

Fine's nine tropical dry forest samples differed from the Tropical Dry Forest sample (3) analyzed in this study in being dominated by CHENOPODIACEAE/AMARANTHACEAE pollen; the Tropical Dry Forest sample (3) analyzed in this thesis was dominated by ANACARDIACEAE pollen. Both samples contained appreciable amounts of *Guazuma* and *Bursera* pollen, and our percentages for *Quercus* and GRAMINEAE pollen were approximately equivalent.

The modern pollen spectra from the páramo samples used in this thesis [Asunción (27), Morrenas (28), and Chirripó (29)] differ from those reported by Salgado-Labouriau (1979) for sites in the Venezuelan páramo. The Venezuelan samples were dominated by GRAMINEAE (50%) and COMPOSITAE (45%) pollen. Grabandt and Nieuwland (1985) also reported high percentages of GRAMINEAE and COMPOSITAE pollen in their modern pollen samples from the Colombian páramos. The páramo samples Morrenas (28) and Chirripó (29) had slightly lower percentages of GRAMINEAE

pollen, and all three Costa Rican páramo samples had considerably lower percentages of COMPOSITAE pollen, and much higher percentages of *Alnus*, *Weinmannia*, and *Quercus* pollen. The Costa Rican páramo sites lie 500 meters or more lower in elevation than the South American sites, in smaller areas of páramo that are closer to the upper forest limit. The higher percentages of COMPOSITAE pollen in the South American samples may reflect a greater abundance of composites in the local and regional vegetation (Grabandt and Nieuwland, 1985; Kappelle, 1991).

CHAPTER 7

CONCLUSION

The results of the pollen and statistical analyses carried out in this study are consistent with vegetation patterns. Even though a large percentage of the Costa Rican flora is zoophilous or self-pollinated, pollen is deposited at the sampling sites in sufficient abundance and diversity that characteristic pollen signatures for broad vegetation types can be determined. Within broad life zone categories, sites with similar regional vegetation have similar pollen spectra, and thus generally cluster together in the cluster and DCA analyses. Mangrove, tropical dry forest, derived savanna, tropical wet forest, montane rain forest, montane bog and páramo vegetation types can be readily differentiated from each other by their pollen rain. Where variations in pollen spectra exist among sites in similar life zones, they seem often to reflect local differences in vegetation owing to factors such as differing land use history, or to the presence of unique substrates.

There does seem to be a limit in the extent to which similar vegetation types can be distinguished by their pollen spectra. We are a far from fully understanding modern pollen distributions in the neotropics and from devising pollen-vegetation transfer functions such as those available for eastern U.S. forests (Delcourt and Delcourt, 1991). But, the work described in this thesis is an important first step in understanding pollen and plant diversity over space and time in Costa Rica.

To further advance knowledge of neotropical pollen rain, we need to collect and analyze many more samples. In Costa Rica we especially need samples from tropical dry, tropical moist, and premontane rain forest, and from lowland tropical swamps. No firm conclusions could be made about pollen rain in these forests because either only one sample

was available for the vegetation type or the samples from one particular vegetation type differed substantially. For these vegetation types, it is not known whether the available pollen samples are characteristic of the vegetation types in general or just of the vegetation of the individual sampling site.

This study should also be expanded to other vegetation types not included in this thesis research, such as premontane wet forest, premontane moist forest, lower montane wet forest, and lower montane rain forest (Hartshorn, 1983).

In enlarging the network of modern pollen sites in Costa Rica, special attention needs to be paid to sampling sediments within less disturbed areas, so as to be able to better distinguish the pollen spectra of mature as opposed to successional vegetation. This, however, is becoming more difficult as more and more of Costa Rica's forests are cleared for timber and pasture establishment. One solution, commonly used in the eastern U.S., might be to focus on pre-European, rather than "modern" pollen rain in studying the link between vegetation and pollen deposition. This approach, which would make use of sediment core samples taken at some depth below the sediment-water interface, would allow sampling of even presently highly disturbed basins. However, it would restrict sampling to natural lakes, and problems of dating the sediments seem inevitable. Few existing pollen records in the neotropics (and none in Costa Rica) have sufficient chronological control in the upper sections to permit firm identification of a specific pre-European horizon. Unlike the situation in the Eastern U. S., where European colonization is marked by a distinct *Ambrosia* rise in pollen diagrams, European settlement in Costa Rica seems to have left no clear markers in pollen diagrams. To use pre-European pollen spectra to gain a better understanding of vegetation-pollen relationships would thus require some means of isotopic dating of short cores. And focusing on this time period would still not preclude the possibility of sampling

vegetation that had been very much disturbed by human activities, in this case of those of pre-European, native inhabitants of Costa Rica.

Further use of surface soil samples would be another way to expand the network of modern pollen sampling sites in Costa Rica, though opportunities for such sampling are also lessened by recent forest conversion. Although lake and pond sediments are generally preferred for pollen analysis, the results of this study show that surface soils can also contain pollen in countable quantities. Surprisingly, subsurface soils may preserve a record of recent vegetation history, even in lowland tropical environments where pollen in soils is thought to degrade quickly (Rodgers and Horn, unpublished data). Moss polsters, used successfully in montane rain forests of the Chirripó massif by Horn (1993), also deserve further exploration as a source of information on pollen-vegetation relationships in Costa Rica.

When sampling modern sediments and soils for pollen analysis, it would be useful to also collect floristic and vegetation data, so that pollen percentages could be compared to actual species lists and to plant cover values at the sampling sites. It would be instructive to include sites in such sampling that are located along transects of varying elevation and moisture regimes. Such finer scale sampling, coupled with detailed analyses of present vegetation patterns, would contribute to a better understanding of how present and past vegetation are represented in the pollen record and, in this way, could lead to an improved resolution of the vegetation history of Costa Rica and other regions in the neotropics.

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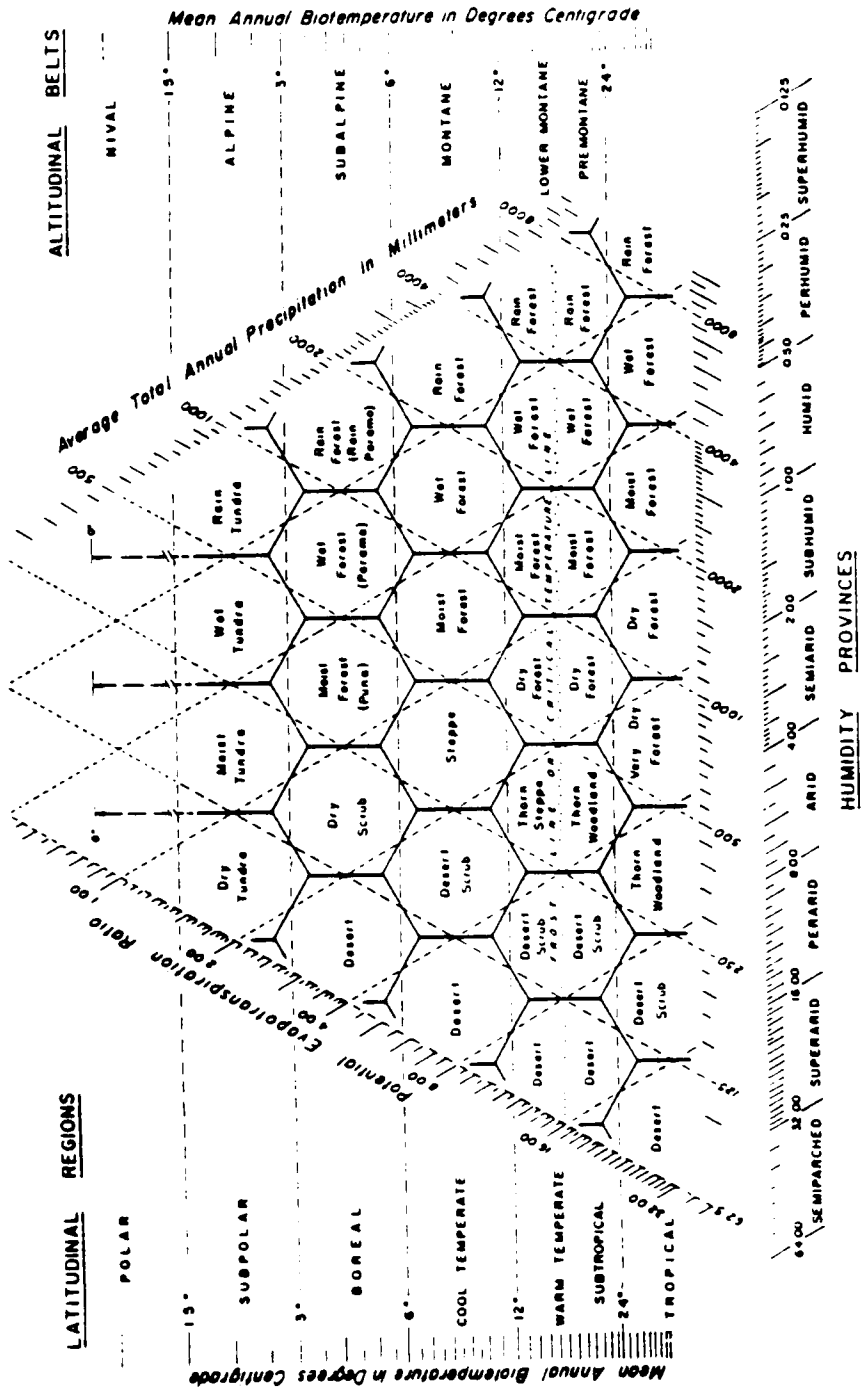
Appendixes

APPENDIX I

DIAGRAM OF HOLDRIDGE LIFE ZONES



APPENDIX II

POLLEN PROCESSING SCHEDULES

This appendix contains two pollen processing schedules. Schedule A was devised by Dr. Sally Horn for use on Costa Rican lake sediments that often tended to clump together during processing. That schedule was initially used to process all of the samples. However, ten of the samples still clumped strongly when processed with this procedure, resulting in pollen slides that could not be counted. This clumping problem required the processing of additional duplicate samples, and resulted in considerable experimentation to find the best method for doing so. Eventually I settled on the use of Schedule B below (also known as the "JR-4" method as it was the fourth modification of the standard procedure that I tested). Schedules A and B differ in that Schedule B uses many hot water washes and rinses with hot Alconox solution to break up clumped samples, and also includes a nitric acid step.

In devising the modified processing procedure, I received input from Dr. Sally Horn and students, from Dr. Donald Sullivan of the University of Denver, and from Dr. Roger Byrne of the University of California, Berkeley. None of us are yet certain as to the cause of the clumping problem that has affected many of our surface and core samples from lakes, swamps, and bogs. It is a problem most commonly associated with highly organic sediments, and may involve certain difficult to digest waxes or other substances within certain classes of organic matter. Alternatively, it may be a result of the sediment becoming electrostatically charged during processing. Another possibility is that the clumping is caused by oil released by diatom valves when they are digested in HF. It seems not to be the result of adding *Lycopodium* tablets (as long as the tablets are fully dissolved in HCl).

For completeness and in hope that the two schedules (A and B) might be useful to other researchers experiencing sediment clumping problems, I have included both processing schedules here.

SCHEDULE A:

1. Place sediment samples in pre-weighed, 15 ml polypropylene centrifuge tubes; determine weight of sample.

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 and place in hot water bath for 3 minutes. Remove from bath, centrifuge for 2 minutes at about 2500 rpm (ICE bench top model for six tubes), and decant.

4. Add distilled water, stir, and place in hot water bath for 3 minutes. Centrifuge for 2 minutes and decant. Repeat for a total of two washes.

5. Add about 10 ml 10% KOH, stir, and place in boiling bath for 5 minutes, stirring after 2.5 minutes. Remove from bath to sieve.

6. Stir samples and sieve through 125 um mesh screen, collecting liquid in a labelled beaker underneath. Wash screen by squirting it with distilled water.

7. Centrifuge down material in beaker by repeatedly pouring beaker contents into correct tube, centrifuging for 2 minutes, and decanting.

8. Add 10 ml distilled water to each tube, stir, centrifuge for 2 minutes, and decant for a total of three washes.

9. Add 8 ml of 52% HF and stir. Place tubes in boiling bath for 20 minutes, stirring after 10 minutes. HF is highly dangerous; wear gloves, goggles, and mask, and keep sashes closed on fume hood when not stirring.

10. Add 10 ml 5% KOH, stir well, place in boiling water bath for 5 minutes, centrifuge, and decant.

11. Add 10 ml distilled water, stir, centrifuge for 2 minutes, and decant for a total of three washes. Examine the tubes to see if they still contain silica. If so, repeat steps 9 - 11.

12. Add 10 ml of glacial acetic acid, stir, centrifuge for 2 minutes, and decant.

13. Make acetolysis mixture by mixing together 9 parts acetic anhydride and 1 part concentrated sulfuric acid. Add about 8 ml to each tube, stir, and place in vigorously 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. Add 10 ml 10 % KOH, stir, remove sticks, and heat in boiling bath for 2 minutes. Centrifuge for 2 minutes and decant.

16. Add 10 ml distilled water, centrifuge for 2 minutes, and decant for a total of 3 washes.

17. Add one drop 1% safranin stain to each tube. Flick each tube to begin mixing. Then add distilled water to make 10 ml. Stir, centrifuge for 2 minutes, and decant.

18. Add 10 ml Tertiary Butyl Alcohol (TBA), stir, centrifuge for 2 minutes, and decant.

19. Vibrate samples using the vortex mixer to mix the small amount of TBA left in the tubes with the microfossils. Carefully transfer the liquid to precleaned and labelled glass vials. Centrifuge for 5 minutes and decant.

20. Add 3 drops of silicone oil (2000 centistokes viscosity). Stir with a clean toothpick.

21. Place uncorked samples in a dust free cabinet to let the TBA evaporate.

22. Check samples the following day; if there is no alcohol smell, cap the samples. If the alcohol smell persists, give them more time to evaporate. If the samples look crusty or dry, add a little more silicone oil and stir before capping them.

SCHEDULE B (the "JR-4" method):

1. Place sediment sample in pre-weighed, 15 ml polypropylene centrifuge tubes; determine weight of sample.

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 and place in hot water bath for 3 minutes. Remove from bath, centrifuge for 2 minutes at about 2500 rpm, and decant.

4. Add hot distilled water, 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 the first two times. Centrifuge for 1 minute the next 2 times. Save decant from short centrifuges to check later for loss of pollen.

7. Fill tubes about 1/2 way with distilled water, stir, and pour through 125 um mesh screen, collecting liquid in a labelled beaker underneath. Wash out material remaining in test tube with more distilled water. Wash screen by squirting it with 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. HF is highly dangerous; wear gloves, goggles, and mask, and keep sashes closed on fume hood when not stirring.

10. Add 10 ml **hot Alconox solution** (5 ml Alconox to 1 l of distilled water). Stir well and let sit for 5 minutes. Stir again and then centrifuge and decant.

11. Add more than 10 ml **hot** distilled water to each tube, so top of water comes close to top of tube. Stir, centrifuge for 2 minutes, and decant. After decanting the hot water, check top of tubes for an oily residue. If present, remove carefully with a wadded up paper towel, using a clean paper towel for each sample. If there is a lot of organic matter stuck in the oily residue, save it for later examination under the microscope. The goal is to remove as much of the oil as possible without losing a lot of pollen at the same time. Also at this time, examine the samples to see if they still contain silica. If so, 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 about 8 ml **10% HNO_3** to each tube and stir well. Remove sticks and let stand for 5 minutes. Stir again and rinse down sides of tube with ethanol (adding a total of a few ml of ethanol per tube.) Centrifuge 2 minutes and decant.

13. Add hot distilled water, stir, centrifuge 2 minutes and decant.

14. Add 10 ml of glacial acetic acid, stir, centrifuge for 2 minutes.

15. 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 vigorously boiling water bath for 5 minutes. Stir after 2.5 minutes. Centrifuge for 2 minutes and decant.

16. Add 10 ml glacial acetic acid, stir, centrifuge for 2 minutes and decant.

17. Wash three times with **hot distilled water**, centrifuge and decant.

18. Add 10 ml 5% KOH, stir, remove sticks, and heat in vigorously boiling bath for 5 minutes. Stir after 2.5 minutes, then remove sticks. After 5 minutes, centrifuge for 2 minutes and decant.

19. Add 10 ml **hot distilled water**, centrifuge for 2 minutes, and decant for a total of 3 washes.

20. Use Vortex Stirrer to mix sediment, holding tubes in Vortex for about 10 seconds.

21. Add one drop 1% safranin stain to each tube. Vibrate tubes for an additional 10 seconds to begin mixing. Then add distilled water to make 10 ml. Stir and wash down sides of tubes with ethanol, centrifuge for 2 minutes, and decant.

22. Add about 2-3 ml Tertiary Butyl Alcohol (TBA), vortex for 20 seconds. Then fill tubes to 10 ml with TBA, centrifuge for 2 minutes, and decant.

23. Add 10 ml of TBA, stir, centrifuge for two minutes, and decant.

24. Vibrate samples using a vortex mixer to mix the small amount of TBA and pollen residue left in the tubes. Carefully transfer residue to precleaned and labelled glass vials.

25. Add 3 drops of silicone oil (2000 centistokes viscosity) to each vial (add more oil if residue volume is great). Stir with a clean toothpick.

26. Place uncorked samples in a dust-free cabinet to let the TBA evaporate. **STIR again after one hour, adding more silicone oil if necessary. Do not let the sample dry out; there must be enough silicone oil that the mixture stays oily when all TBA is evaporated.**

27. Check samples the following day; if there is no alcohol smell, cap the samples. If the alcohol smell persists, give them more time to evaporate before capping.

APPENDIX III

ORGANIC MATTER AND POLLEN CONCENTRATIONS IN SAMPLES

Sample	Percent organic matter in dry sample	Pollen concentrations[1]
SRNP Mangrove (1)	5.33%	1.11×10^6
SRNP Mangrove (2)	7.93%	7.95×10^6
SRNP Trop. Dry Forest (3)	15.51%	not available[2]
SRNP Savanna (4)	14.82%	1.43×10^6
Escondido (5)	11.74%	not available
Palmita (6)	9.57%	2.34×10^5
Carara (7)	13.39%	6.55×10^5
Río Cuarto (8)	23.71%	1.05×10^7
Bonilla (9)	61.54%	not available
Bonillita (10)	65.28%	1.40×10^7
González (11)	12.15%	not available
Congo (12)	50.58%	3.84×10^7
Bosque Alegre (13)	28.42%	9.11×10^6
Hule (14)	29.65%	6.99×10^6
María Aguilar (15)	21.89%	6.27×10^6
La Selva Cantarrana (16)	61.41%	3.98×10^8
La Selva Suampo (17)	53.70%	9.42×10^6
La Palma (18)	18.62%	8.20×10^6
Cedeño (19)	12.95%	2.98×10^6
Volcán Cacao (20)	12.13%	6.33×10^5

[1] pollen and spores/gm dry sediment

[2] pollen concentration could not be calculated for samples processed without the addition of *Lycopodium* control spores.

Sample	Percent organic matter in dry sample	Pollen Concentrations
Botos (21)	8.76%	3.33×10^6
Barva (22)	35.06%	2.62×10^7
Quebrador (23)	10.60%	2.86×10^6
Bog 68 (24)	96.00%	not available
Bog 70 (25)	91.53%	not available
Tres De Junio (26)	60.73%	2.36×10^6
Asunción (27)	36.74%	1.80×10^7
Morrenas (28)	50.20%	not available
Chirripó (29)	55.67%	not available

APPENDIX IV

POLLEN AND SPORE TAXA RECORDED IN SAMPLES FROM DIFFERENT VEGETATION TYPES

MANGROVE FOREST: SRNP MANGROVE (1) AND SRNP MANGROVE (2)

Pollen types

ANACARDIACEAE

Cordia (BORAGINACEAE)

Bursera (BURSERACEAE)

COMPOSITAE

E/R/A

Quercus (FAGACEAE)

GRAMINEAE

Malpighia (MALPIGHIACEAE)

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

RHAMNACEAE

Rhizophora (RHIZOPHORACEAE)

RUBIACEAE

SAPINDACEAE

SAPOTACEAE/MELIACEAE

SOLANACEAE

URTICALES

Avicennia (VERBENACEAE)

Fern Spores

Monolete echinate

Monolete reticulate

Monolete bacculate

Monolete verrucate

Trilete echinate

TROPICAL DRY FOREST: SRNP TROPICAL DRY FOREST (3)

Pollen types

AMARANTHACEAE/CHENOPODIACEAE

ANACARDIACEAE

BIGNONIACEAE

Bursera (BURSERACEAE)

COMPOSITAE

Quercus (FAGACEAE)

GRAMINEAE

Malpighia (MALPIGHIACEAE)

Cecropia (MORACEAE)

Piper

POLYGALACEAE

SAPOTACEAE/MELIACEAE

Guazuma (STERCULIACEAE)

URTICALES

Fern Spores

Monolete verrucate

Monolete echinate

DERIVED SAVANNA: SRNP SAVANNA (4), ESCONDIDO (5), AND PALMITA (6)

Pollen types

AMARANTHACEAE/CHENOPODIACEAE

ANACARDIACEAE

APOCYNACEAE

BIGNONIACEAE

Bursera (BURSERACEAE)

COMPOSITAE

Weinmannia (CUNONIACEAE)

Acalypha (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

GESNERIACEAE

GRAMINEAE

LACISTEMACEAE

MIMOSOIDEAE (LEGUMINOSAE)

Cuphea (LYTHRACEAE)

Malpighia (MALPIGHIACEAE)

Cecropia (MORACEAE)

Myrsine (MYRSINACEAE)

MRYTACEAE

Piper

SAPOTACEAE/MELIACEAE

Guazuma (STERCULIACEAE)

URTICALES

Fern Spores

Monolete psilate

Monolete bacculate

Monolete echinate

Trilete verrucate

Trilete psilate

Trilete scabrate

TROPICAL MOIST FOREST: CARARA (7)

Pollen types

AMARANTHACEAE/CHENOPODIACEAE

ACANTHACEAE

Alnus (BETULACEAE)

BOMBACACEAE

Alchornea (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

GRAMINEAE

LEGUMINOSAE

MIMOSOIDEAE (LEGUMINOSAE)

Malpighia (MALPIGHIACEAE)

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Ficus (MORACEAE)

Myrsine (MYRSINACEAE)

MYRTACEAE

Iriartea (PALMAE)

ROSACEAE

RUBIACEAE

Guazuma (STERCULIACEAE)

URTICALES

Fern Spores

Monolete psilate

Monolete verrucate

Monolete baculate

Trilete verrucate

Trilete scabrate

TROPICAL WET FOREST: RIO CUARTO (8), BONILLA (9), BONILLITA (10), GONZALEZ 911), CONGO (12), BOSQUE ALEGRE (13), HULE (14), AND MARIA AGUILAR (15)

Pollen types

Pinus (PINACEAE)

PODOCARPACEAE

AMARANTHACEAE/CHENOPODIACEAE

ANACARDIACEAE

APOCYNACEAE

Alnus (BETULACEAE)

BIGNONIACEAE

Cordia (BORAGINACEAE)

Bursera (BURSERACEAE)

Hedyosmum (CHLORANTHACEAE)

COMPOSITAE

Cucurbita (CUCURBITACEAE)

Weinmannia (CUNONIACEAE)

CYPERACEAE

ERICACEAE

Acalypha (EUPHORBIACEAE)

Alchornea (EUPHORBIACEAE)

Sapium (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

GRAMINEAE

Alfaroa (JUGLANDACEAE)

LABIATAE

MIMOSOIDEAE (LEGUMINOSAE)

LEGUMINOSAE

Cuphea (LYTHRACEAE)

Malpighia (MALPIGHIACEAE)

MALVACEAE

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Ficus (MORACEAE)

Myrica (MYRICACEAE)

Myrsine (MYRSINACEAE)

MYRTACEAE

Iriartea (PALMAE)

ONAGRACEAE

PALMAE

Iriartea (PALMAE)

Piper

POLYGALACEAE

PROTEACEAE

RHAMNACEAE

RUBIACEAE

SAPINDACEAE

SAPOTACEAE/MELIACEAE

SOLANACEAE

Ulmus (ULMACEAE)

UMBELLIFERAE

URTICALES

VOCHYSIACEAE

Fern Spores

Monolete psilate

Monolete verrucate

Monolete scabrate

Monolete echinate

Monolete reticulate

Trilete foveolate

Tilete verrucate

Trilete scabrate

Other Spores

Isoeters storkii

LOWLAND TROPICAL SWAMP: LA SELVA CANTARRANA (16) AND LA SELVA SUAMPO (17)

Pollen types

ANACARDIACEAE

APOCYNACEAE

Spathiphyllum (ARACEAE)

Bursera (BURSERACEAE)

COMPOSITAE

CYPERACEAE

Acalypha (EUPHORBIACEAE)

Alchornea (EUPHORBIACEAE)

E/R/A

GRAMINEAE

MIMOSOIDEAE (LEGUMINOSAE)

Pentaclethra (LEGUMINOSAE)

LEGUMINOSAE

Malpighia (MALPIGHIACEAE)

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Ficus (MORACEAE)

MYRTACEAE

PALMAE

Iriartea (PALMAE)

Piper

RHAMNACEAE

RUBIACEAE

SAPINDACEAE

SAPOTACEAE/MELIACEAE

SOLANACEAE

Mortoniodendron (TILIACEAE)

UMBELLIFERAE

URTICALES

Fern Spores

Monolete psilate

Monolete scabrate

Trilete bacculate

Trilete verrucate

Trilete scabrate

PREMONTANE RAIN FOREST: LA PALMA (18), CEDENO (19), AND VOLCAN CACAO (20)

Pollen types

PODOCARPACEAE

Ilex (AQUIFOLIACEAE)

AMARANTHACEAE/CHENOPODIACEAE

ANACARDIACEAE

Alnus (BETULACEAE)

Cordia (BORAGINACEAE)

COMPOSITAE

Hedyosmum (CHLORANTHACEAE)

Weinmannia (CUNONIACEAE)

CYPERACEAE

ERICACEAE

Acalypha (EUPHORBIACEAE)

Alchornea (EUPHORBIACEAE)

Sapium (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

Gunnera (HALORRHAGAACEAE)

MIMOSOIDEAE (LEGUMINOSAE)

LEGUMINOSAE

Malpighia (MALPIGHIACEAE)

MALVACEAE

MELASTOMATACEAE/COMBRETACEAE

Ficus (MORACEAE)

Myrsine (MYRSINACEAE)

Myrica (MYRICACEAE)

MYRTACEAE

ONAGRACEAE

PALMAE

Iriartea (PALMAE)

Piper

ROSACEAE

RUBIACEAE

Zanthoxylum (RUTACEAE)

SAPINDACEAE

SAPOTACEAE/MELIACEAE

SOLANACEAE

Mortoniodendron (TILIACEAE)

Ulmus (ULMACEAE)

UMBELLIFERAE

URTICALES

Fern Spores

Monolete psilate

Monolete echinate

Trilete verrucate

MONTANE RAIN FOREST: BOTOS (21), BARVA (23), AND QUEBRADOR (23)

Pollen types

PODOCARPACEAE

Ilex (AQUIFOLIACEAE)

AMARANTHACEAE/CHENOPODIACEAE

Alnus (BETULACEAE)

Hedyosmum (CHLORANTHACEAE)

Weinmannia (CUNONIACEAE)

CYPERACEAE

ERICACEAE

Acalypha (EUPHORBIACEAE)

Alchornea (EUPHORBIACEAE)

Dalechampia (EUPHORBIACEAE)

Sapium (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

GRAMINEAE

Clusia (GUTTIFERAE)

Gunnera (HALORRHAGACEAE)

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Myrsine (MYRSINACEAE)

Myrica (MYRICACEAE)

PALMAE

Iriartea (PALMAE)

SAPINDACEAE

SAPOTACEAE/MELIACEAE

Ulmus (ULMACEAE)

UMBELLIFERAE

URTICALES

Fern Spores

Monolete psilate

Monolete scabrate

Trilete reticulate

Trilete with an equatorial girdle

Trilete foveolate

Trilete psilate

Trilete verrucate

Trilete scabrate

Other Spores

Isoetes storkii

MONTANE BOGS: BOG 68 (24), BOG 70 (25), AND TRES DE JUNIO (26)

Pollen types

PODOCARPACEAE

Ilex (AQUIFOLIACEAE)

Alnus (BETULACEAE)

Hedyosmum (CHLORANTHACEAE)

COMPOSITAE

Weinmannia (CUNONIACEAE)

CYPERACEAE

ERICACEAE

Alchornea (EUPHORBIACEAE)

E/R/A

Quercus (FAGACEAE)

GRAMINEAE

Gunnera (HALORRHAGACEAE)

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Myrsine (MYRSINACEAE)

Myrica (MYRICACEAE)

SOLANACEAE

PALMAE

Ulmus (ULMACEAE)

UMBELLIFERAE

URTICALES

Fern Spores

Monolete psilate

Monolete gemmate

Monolete foveolate

Monolete verrucate

Monolete scabrate

Trilete reticulate

Trilete with an equatorial girdle

Trilete foveolate

Trilete psilate

Trilete verrucate

Trilete scabrate

Other Spores

Isoetes storkii

Lycopodium (native taxa, not the control spore)

PARAMO: ASUNCION (27), MORRENAS (28), AND CHIRRIPO (29)

Pollen types

PODOCARPACEAE

Alnus (BETULACEAE)

Hedyosmum (CHLORANTHACEAE)

COMPOSITAE

Weinmannia (CUNONIACEAE)

ERICACEAE

Alchornea (EUPHORBIACEAE)

Quercus (FAGACEAE)

GRAMINEAE

MELASTOMATACEAE/COMBRETACEAE

Cecropia (MORACEAE)

Myrsine (MYRSINACEAE)

Myrica (MYRICACEAE)

Ulmus (ULMACEAE)

UMBELLIFEAE

URTICALES

Fern Spores

Monolete psilate

Monolete verrucate

Monolete scabrate

Monolete echinate

Monolete Reticulate

Trilete with an equatorial girdle

Trilete foveolate

Trilete psilete

Trilete verrucate

Other Spores

Isoetes storkii

Lycopodium (native taxa, not the control spore)

APPENDIX V

NOTES ON PLANT TAXA REPRESENTED IN SAMPLES

This appendix describes the plant taxa represented in the modern pollen samples (APPENDIX IV). These descriptions include the number of taxa within each group that have been reported in Costa Rica and also plant size and distributional ranges. In some cases, information on pollen taxonomy is also included.

***Pinus* (PINACEAE):** The natural distribution of the genus *Pinus* only extends as far south as Nicaragua in Central America (Standley, 1937-1938), but pines have been planted in many areas of Costa Rica. Pine pollen in modern lake seiments and soils may derive from introduced pines or from long-distance transport.

PODOCARPACEAE: All North American species of the coniferous family PODOCARPACEAE were formerly referred to *Podocarpus* but a second genus, *Prumnopitys*, has recently been differentiated. In the western hemisphere, the PODOCARPACEAE ranges from southern Chile (ca. 49°S) to southern Mexico and the Caribbean (ca. 23°N) (Veillon, 1962). Five species occur in Costa Rica: *Podocarpus macrostachyus, P. guatemalensis, P. monteverdensis, P. costaricensis,* and *Prumnopitys standleyi. P. guatemalensis* occurs in lowland forests but the others are generally restricted to montane habitats (deLaubenfels, 1990).

ACANTHACEAE: There are about 38 genera of ACANTHACEAE reported in Costa Rica (Burger, 1986). Plants range in size from herbs to woody vines (*Thunbergia*) to small trees (*Trichanthera*). They live in habitats that range from dry open places (*Tetramerium*), to wet lowland forest (*Streblacanthus*), to montane rain forest (*Justicia*) (Burger, 1986).

AMARANTHACEAE: Burger (1983b) listed 11 genera of AMARANTHACEAE in Costa Rica. Plants are mostly small herbs but also grow as shrubs, climbing plants, or rarely small trees. They generally occur in cultivated grounds or waste places. Some plants, like *Bougainvillea glabra* and *Iresine spp.* are grown for ornamental purposes. The AMARANTHACEAE is closely related to the CHENOPODIACEAE. Although plant taxa can be distinguished by morphology, the pollen grains of these two families have overlapping characteristics. The CHENOPODIACEAE are poorly represented in Costa Rica with only three introduced genera (Burger, 1983b). Of these, two are grown exclusivly for food, beets (*Beta spp.*) and spinach (*Spinacia spp.*). One genus, *Chenopodium* is a genus of weedy herbs characteristic of open and disturbed areas (Burger, 1983b).

ANACARDIACEAE: There are about 10 genera of ANACARDIACEAE reported for Cost Rica (Standley, 1937-1938). Plants are mostly trees and sometimes shrubs that occur in drier areas on the Pacific Coast. However, *Mauria* grows in the central regions and ranges from 1400 to 2000 meters (Standley, 1937-1938) and *Spondias* is reported to grow in lowland tropical wet forest (Hartshorn and Poveda, 1983). *Anacardium excelsum* is reported to occur in riparian habitats in the tropical dry life zones and on slopes and alluvium in tropical and premontane life zones (Hartshorn and Gentry, 1983).

APOCYNACEAE: There are about 23 genera of APOCYNACEAE that occur in Costa Rica (Standley, 1937-1938). Plants are generally woody vines that range in habitat from tropical dry forest in the Guanacaste to tropical wet and montane wet forest of the Meseta Central. *Stemmadenia donnell-smithii* is a widespread tree that is commonly found in disturbed habitats such as riparian habitats, secondary forest, forest edges, and pastures along the Pacific slopes (Foster and McDiarmid, 1983).

***Ilex* (AQUIFOLIACEAE):** There are about 9 species of *Ilex* reported in Costa Rica (Standley, 19387-1938). These plants range in size from shrubs to trees and generally grow in wet premontane and montane forests from 1200 - 3000 meters elevation (Standley, 1937-1938). However, *I. skutchii* is reported to grow in tropical wet forest in the Atlantic lowlands (La Selva Biological Station) (Hartshorn and Poveda, 1983).

***Spathiphyllum* (ARACEAE):** There are 5 species of *Spathiphyllum* reported in Costa Rica (Standley, 1937-1938). Taxa are large perennial herbs and generally grow in lowland tropical wet forest (Standley, 1937-1938). Large areas of the Cantarrana swamp at La Selva are dominated by *Spathiphyllum* (Rodgers, personal observation).

***Alnus* (BETULACEAE):** Although *Alnus* is generally regarded as a northern temperate tree, one species (*A. acuminata*) does occur in Costa Rica. This species of *Alnus* is generally found between 1500 and 3100 m elevation, growing on landslides and in other disturbed habitats (Burger, 1983a).

BIGNONIACEAE: There are 28 genera of BIGNONIACEAE reported in Costa Rica (Standley, 1937-1938). Plants are mostly woody vines but also include shrubs and trees. They grow in forests and thickets from sea level up to 2200 meters elevation, most commonly on the drier Pacific slope and in the Central region (Standley, 1937-1938).

BOMBACACEAE: There are 7 genera of BOMBACACEAE reported in Costa Rica (Standley, 1937-1938). Most taxa are trees that range from the Pacific and Atlantic coasts up to 1600 meters elevation (Standley, 1937-1938).

***Cordia* (BORAGINACEAE):** The 14 species of *Cordia* that occur in Costa Rica range in size from shrubs to trees (Standley, 1938-1937). Most species grow in thickets of the Pacific slope, but some (*C. ferruginea* and *C. alliodora*) occur in forests of the Atlantic slopes. *C. alliodora* is especially widespread in Costa Rica and throughout Central America. It occurs naturally in many life zones up to 1500 meters elevation, and is also widely planted for timber and shade (Opler and Janzen, 1983)

***Bursera* (BURSERACEAE):** There are three species of *Bursera* reported in Costa Rica, all of which are deciduous shrubs or trees (Standley, 1937-1938). *B. tomentosa* occurs in the Guanacaste region but also is found in Venezuela and Colombia (Standley, 1937-1938). *B. simaruba* occurs from the Meseta Central down to both coasts (Standley, 1937-1938), generally in drier forests (Stevens, 1983).

***Hedyosmum* (CHLORANTHACEAE):** Six species of *Hedyosmum* occur in Costa Rica. Most of them are small, aromatic trees or shrubs. Most occur in persistently moist or wet areas (Burger, 1977), at elevations from 500 meters (*H. calloso-serratum*) up to 2800 meters (*H. mexicanum*) (Burger, 1977).

COMPOSITAE: The COMPOSITAE family is one of the largest plant families in Costa Rica. The majority of taxa are herbaceous but shrubs and small trees also occur. There are at least 102 genera represented in Costa Rica (Standley, 1937-1938). Unfortunately, the pollen of the COMPOSITAE is very similar in morphology and it is difficult to distinguish genera. Taxa occur in almost all habitats, from coastal mangrove swamps to the páramo.

***Cucurbita* (CUCURBITACEAE):** There are two species of *Cucurbita* reported in Costa Rica (Standley, 1937-1938). Both are cultivated plants that are grown in vegetable gardens. *C. ficifolia* has become naturalized in thickets and forests at mid-elevations. *C. pepo* is only found in cultivation. It no longer is found in a wild state (Standley, 1937-1938).

***Weinmannia* (CUNONIACEAE):** Two species of *Weinmannia* are reported to occur in Costa Rica (Hartshorn and Poveda, 1983). *W. pinnata* occurs in wet forest of the colder regions from 1200 to 3000 meters elevation. It is the most common tree of the upper slopes of the central volcanoes (Standley, 1937-1938). *W. wercklei* is common in forest of the Meseta Central (1400 - 2200 meters elevation) and on the Pacific slope (1100 - 1250 meters elevation) (Standley, 1937-1938).

CYPERACEAE: Standley (1937-1938) reported 17 genera of CYPERACEAE in Costa Rica. These plants are all herbaceous and generally occur in or near wet places. Genera in this family range from sea level up to 3000 meters elevation.

ERICACEAE: There are 12 genera of ERICACEAE reported in Costa Rica (Standley, 1937-1938). These plants range from shrubs to small trees and occur between 1100-3400 meters elevation.

***Acalypha* (EUPHORBIACEAE):** There are 16 species of *Acalypha* reported in Costa Rica (Standley, 1937-1938). The plants range in size from small, herbaceous taxa (*A. arvensis*) to shrubs or small trees (*A. diversifolia*). *Acalypha* grows in habitats ranging from waste places to mature wet forest, from sea level on both coasts up to 2300 meters elevation.

***Alchornea* (EUPHORBIACEAE):** Two species of *Alchornea* occur in Costa Rica (Hartshorn and Poveda, 1983). Thy are shrubs or small trees that occur in habitats ranging from lowland wet forest up to montane forest.

***Dalechampia* (EUPHORBIACEAE):** Five species of *Dalechampia* are reported to occur in Costa Rica (Standley, 1937-1938). These taxa are all herbaceous vines. Most of the species are common in forests and thickets of the Pacific slopes.

***Sapium* (EUPHORBIACEAE):** There are 5 species of *Sapium* reported in Costa Rica (Hartshorn and Poveda, 1983). Taxa are all trees that range in habitat from forests of the Pacific Slopes to the Meseta Central region (from sea level to 1800 m) (Standley, 1937-1938) to the Atlantic lowlands (Hartshorn and Poveda, 1983).

***Quercus* (FAGACEAE):** Burger (1977) reported twelve species of oaks in Costa Rica. Most occur in premontane and montane forests at an elevation above 600 m, but one species, *Q. oleoides* occurs in the tropical dry forest (Burger, 1983b). Oaks form dominant stands on slopes in the Cordillera de Talamanca from 2500 - 3000 m (Burger, 1977).

GESNERIACEAE: Standley (1937-1938) reported 21 genera of GESNERIACEAE in Costa Rica. Taxa are mostly epiphytic herbs or shrubs.

GRAMINEAE: Over 100 genera of grasses occur in Costa Rica (Burger, 1978). The grasses encompass many different species that occupy most life zones, both disturbed and undisturbed, in Costa Rica.

***Clusia* (GUTTIFERAE):** Species in the genus *Clusia* range in size from trees to shrubs and are often epiphytic during their younger stages of development (Standley, 1937-1938). There are 11 species of *Clusia* reported in Costa Rica. These trees range from the Guanacaste region to forest of the Atlantic slopes. They range in elevation from 300 to 2000 meters (Standley, 1937-1938).

***Gunnera* (HALORRHAGACEAE):** *Gunnera* are very large, perennial herbs with some of the largest leaves of all flowering plants. *G. insignis* and *G. wendlandii* grow in montane wet forests of the central volcanoes ranging in elevation from 1500 to 2400 meters elevation (Standley, 1937-1938). A third species, *G. talamancensis*, is sympatric with *G. insignis* in montane rain forests of the Cordillera de Talamanca (Weber, 1959)

***Isoetes* (ISOETACEAE):** *Isoetes* are seedless, vascular plants that occur in areas that are inundated with water for most of the year (Tyron and Tyron, 1982). *I. storkii* is known to occur in Costa Rica in Laguna Botos (Macey, 1975), in glaciated lakes of the Chirripó massif (Horn, 1989a), and in montane bogs (Gómez, 1986).

***Alfaroa* (JUGLANDACEAE):** Taxa in the genus *Alfaroa* genus are large, wind-pollinated trees that predominately occur in premontane rain forest vegetation types (Stone, 1983). Four species are reported in Costa Rica. *A. costaricensis*, *A. guanacastensis*, and *A. menningii* occur in both primary forest and in pastures of the mid elevations (600 m - 2000 m) (Burger, 1977). *A. willionsii* is a sterile hybrid of *A. costaricensis* that occurs in forests of Monteverde, the Cordillera Tilaran, and the Cordillera de Talamanca (Burger, 1977).

LABIATAE: There are 13 genera of the LABIATAE reported in Costa Rica (Standley, 1937-1938). Taxa are mostly herbs but include some shrubs or small trees. They range in habitat from savannas and other grassy places of the Pacific slope to fields and thickets of the Meseta Central and montane regions, extending up to 3000 meters elevation.

LACISTEMACEAE: The family LACISTEMACEAE is represented in Costa Rica by two genera, *Lacistema* and *Lonzania* (Hartshorn and Poveda, 1983). These plants are shrubs or small trees that grows in forests and thickets of the Pacific and Atlantic coasts (Standley, 1937-1938).

LEGUMINOSAE: The LEGUMINOSAE is another very large plant family. Taxa range from herbs to tall trees and occur in a wide range of habitats. The pollen types that were included in this group were from the CAESALPINOIDEAE and PAPILIONOIDEAE subfamilies. The CAESALPINODIEAE is represented by at least 15 genera and the PAPILIONOIDEAE is represented by at least 55 genera.

MIMOSOIDEAE: The MIMOSOIDEAE subfamily can be distinguished as a separate pollen type from other legumes. This taxon is represented by 16 genera in Costa Rica, including *Acacia* (Standley, 1937-1938).

***Pentaclethra* (LEGUMINOSAE):** The only species in the New World is *Pentaclethra macroloba*. This is a large tree that is abundant in tropical wet forest of the Atlantic slopes (Standley, 1937-1938). This species typically grows on infertile soils without a dry season, and in swamps (Hartshorn, 1983).

***Cuphea* (LYTHRACEAE):** *Cuphea* is a small herbaceous plant that ranges from the Atlantic slopes to the Pacific, and grows in a wide range of habitats from pastures to forests (Standley, 1937-1938).

***Malpighia* (MALPIGHIACEAE):** *Malpighia* can occur as either a shrub or small tree. There are two species in Costa Rica. *M. glabra* grows in thickets and hedges of the Meseta Central to the Pacific Coast. *M. mexicana* is a small tree that grows in the Meseta Central (Standley, 1937-1938).

MALVACEAE: There are 15 genera of MALVACEAE reported in Costa Rica (Standley, 1937-1938). Taxa in this family range in size from herbs to small trees. They grow in a range of habitats from dry areas of Guanacaste (*Malachra* and *Malvastrum*) to forests of the Pacific slopes (*Palvonia*) and range in elevation up to 2100 meters (Standley, 1937-1938).

MELASTOMATACEAE/COMBRETACEAE: Pollen grains produced by these two families have overlapping morphological characteristics and it is extremely difficult to separate them to genera or family. There are 25 genera of MELASTOMATACEAE reported in Costa Rica. The majority of the taxa are herbs or shrubs, but they can occur as small trees. They range from lowland forests of the Pacific and Atlantic coasts to the highest peaks of the country (Standley, 1937-1938; Kapelle *et al.*, 1991). Standley (1937-1938) reported five genera of COMBRETACEAE in Costa Rica. Taxa are trees or shrubs that range in habitat from the wet forest of the Atlantic lowland forest to mangrove swamps.

***Cecropia* (MORACEAE):** Five species of *Cecropia* are reported in Costa Rica (Burger, 1977). All five are tall trees that are important components of tropical forest. They grow in disturbed sites in the lowlands but are also found in mature forest. Most species range in elevation from sea level to 1500 meters. However, *C. polyphlebia* is known to occur in wet montane forests at elevations from 1400 m to 2400 m (Burger, 1977).

***Ficus* (MORACEAE):** There are about 40 species of *Ficus* reported in Costa Rica (Burger, 1977). Taxa include trees and shrubs that range in habitat from tropical wet forests of the Atlantic slope (*F. brevibracteata*) to montane rain forests of the central highlands (*F. crassiuscula*). Species also occur in seasonally parched forests of the Pacific slopes (*F. ovalis*) (Burger, 1977). The pollination mechanism of *Ficus* raises questions as to how the pollen type can end up in lake sediments; Horn and Ramirez (1990) discuss possible scenarios.

***Myrsine* (MYRSINACEAE):** Species in *Myrsine* (= *Rapanea*) are shrubs and small trees commonly associated with forests of the Meseta Central from 1000 to 1800 m elevation. *M. pittieri* grows along the slopes of the central volcanoes up to 3000 meters elevation (Standley, 1937-1938). However, at least one species (*M. floridana*) occurs in lowland forest.

***Myrica* (MYRICACEAE):** Burger (1977) reported 4 species of *Myrica* in Costa Rica. Taxa are shrubs to small trees that are common in forests from 800-2800 m elevation (Burger, 1977).

MYRTACEAE: There are 7 genera of MYRTACEAE reported in Costa Rica. Most of these are shrubs or small trees that occur in the middle elevations from 1000 to 2000 meters elevation (Standley, 1937-1938). Some or much of the MYRTACEAE pollen may be from *Psidium*, a shrub or small tree that is very common in the tropics. It grows up to an elevation of 1400 meters.

ONAGRACEAE: Standley (1937-1938) reported six genera of ONAGRACEAE in Costa Rica. Taxa range in size from herbs to small trees and grow in habitats ranging from forests and pastures of elevated regions (*Fuchsia*), to swampy and wet places in the lowlands (*Jussiaea*), to meadows of the central highlands (*Oenothera*) (Standley, 1937-1938).

PALMAE: The Palm family is represented by about 26 genera in Costa Rica (Standley, 1937-1938). Palms grow in a wide range of forest habitats from tropical moist forest to montane rain forests. They can extend up to 2000 meters elevation (Standley, 1937-1938).

***Iriartea* (PALMAE):** Standley (1937-1938) reported one species of *Iriartea* (*I. gigantea*) for Costa Rica. Hartshorn and Poveda (1983) list the species as occuring in tropical wet forest at the La Selva Biological Station and in Corocovado National Park along the southern Pacific coast. Chazdon (1988) lists *I. deltoideae* (= *I. gigantea*) as occuring from 35 to 1000 m at the La Selva Station and within adjacent tropical wet and premontane rain forest of Braulio Carillo National Park. *Iriartea* is commonly exploited for heart of palm.

***Piper* (PIPERACEAE):** Species in the genus *Piper* range from herbs to small trees and they occur throughout the moister regions of Costa Rica up to an elevation of 2600 meters (Burger, 1971).

POLYGALACEAE: Standley (1937-1938) reported three genera of POLYGALACEAE in Costa Rica, most of which are herbaceous. *Monninas* grows in montane forests of the Meseta Central from 1500 to 2800 meters and *M. crepini* grows in the higher páramo regions. *Polygala* grows in grassy places of the Pacific slopes from sea level to the Meseta Central. *Securidaca* is common in forests and thickets of the coast and extends up to 600 meters elevation.

PROTEACEAE: Three genera of PROTEACEAE occur in Costa Rica and they are generally trees or shrubs (Burger, 1983c). *Guevilleras* are small trees that are often planted in gardens and along streets and avenues. Species in *Panopsis* are trees that grow in very wet forest on the Atlantic slopes (1000-2200 m elevation). Species in *Roupala* range from

trees of very wet forest (*R. glaberrima*) to shrubs in seasonally dry forest on the Pacific slopes between 40-1200 m elevation (*R. montana*) (Burger, 1983c).

RHAMNACEAE: There are seven genera of RHAMNACEAE that are reported in Costa Rica, the majority of which are trees and occasionally shrubs that grow in thickets on the Pacific slope up to the central mountains (Standley, 1937-1938). *Colubrina spinosa* is a frequent understory tree at the La Selva Biological Station in the Atlantic lowlands of Costa Rica (Hartshorn and Poveda, 1983).

***Rhizophora* (RHIZOPHORACEAE):** *Rhizophora* or red mangrove is a shrub or small tree that grows in protected areas along both coasts. Two species are reported; *Rhizophora mangle* grows on both the Atlantic and Pacific coasts while *R. harrisonii* (also known as *R. brevistyla*) only grows on the Pacific coast (Simberloff, 1983).

ROSACEAE (including CHRYSOBALANACEAE): Standley (1937-1938) reported 17 genera of ROSACEAE in Costa Rica. Taxa include herbs, shrubs, and trees and occur in habitats such as páramo (*Acaena*), montane forest (*Alchemilla*), beaches on both coast (*Chrysobalanus*), and dry forest of the Pacific lowland (*Licania*) (Standley, 1937-1938). Trees in the genera *Couepia*, *Hirtella*, and *Licania* occur in the tropical wet forest of the La Selva Biological Station (Hartshorn and Poveda, 1983).

RUBIACEAE: The RUBIACEAE is well represented in the tropics. There are 80 or more genera reported for Costa Rica alone (Burger, 1993). Taxa include herbs, shrubs, and trees. Habitats include dry forest (*Anisomeris*) lowland tropical wet forest (*Psychotria*), and montane wet forest and páramo to 3000 meters elevation (*Arcytophyllum*)

(Kappelle *et al.*, 1991). Coffee is a rubiaceous plant that is widely cultivated throughout the mid elevations of Costa Rica.

***Zanthoxylum* (RUTACEAE):** Ten species of *Zanthoxylum* are reported in Costa Rica (Standley, 1937-1938). Taxa are mostly trees, but some are shrubs. They occur in habitats that range from thickets and forests at Guanacaste (*Z. insulare*) to forest of the central region (*Z. procerum*). They are also reported to occur in the tropical wet forest at the La Selva Biological Station (Hartshorn and Poveda, 1983).

SAPINDACEAE: There are at least 14 genera of SAPINDACEAE in Costa Rica (Standley, 1937-1938). Most are trees or shrubs that range in habitat from thickets and open forests of the Pacific slopes (*Allopylus*) to forests of the Meseta Central (*Serjania*). *Matayba* occurs in the Atlantic lowland forest of La Selva Biological Station (Hartshorn and Poveda, 1983). Two genera (*Cardiospermum* and *Paullinia*) are large woody or herbaceous vines that grow in thickets of the Pacific slopes and Gaunacaste forests, extending up to 1550 meters elevation (Standley, 1937-1938).

SAPOTACEAE/MELIACEAE: Pollen grains from the SAPOTACEAE and MELIACEAE families have overlapping characteristics and are difficult to separate. Standley (1937-1938) lists 8 genera of SAPOTACEAE for Costa Rica; all are woody and most are trees. Taxa are common in dry forest of the Pacific lowlands, but *Bumelia austin-smithii* grows in forest of the central highlands (extending up to 2000 meters) and *Manilkara spectabilis* grows in the Atlantic lowlands. There are at least 6 genera of MELIACEAE reported in Costa Rica. Most of the taxa are either trees or shrubs. They range in habitat from tropical wet forests and premontane rain forest of the Atlantic slopes to dry forests of the Pacific coast (Standley, 1937-1938).

SOLANACEAE: There are at least 22 genera of SOLANACEAE in Costa Rica (Standley, 1937-1938). Taxa range from herbs to shrubs to trees. They can range in habitat from disturbed sites in the Meseta Central to forest on both the Atlantic and Pacific slopes.

STERCULIACEAE: There are 7 genera of STERCULIACEAE listed for Costa Rica (Standley, 1937-1938). Taxa range in size from herbs to trees and range in habitat from thickets in the Meseta Central down to both the Pacific and Atlantic coasts.

***Guazuma* (STERCULIACEAE):** Only one species of *Guazuma* is reported for Costa Rica, *G. ulmifolia* (Janzen, 1983b). *G. ulmifolia* is a common tree that occurs in tropical dry forest and pastures from Mexico to Panama. This deciduous tree is suggested to be wind-pollinated (Janzen, 1983b).

***Mortoniodendron* (TILIACEAE):** Two species of *Mortoniodendron*, *M. anisophyllum* and *M. membranaceum*, are reported in Costa Rica; both species are common in tropical wet forest but they can also occur in tropical moist forest (Holdridge *et al.*, 1971).

***Celtis* (ULMACEAE):** Only two species of *Celtis* are reported in Costa Rica. *C. iguanaea* can be a climbing vine, shrub, or tall tree. This species grows in wet or seasonally dry forests on both the Caribbean and Pacific slopes, ranging in elevation from sea level up to 1200 meters (Burger, 1977).

***Ulmus* (ULMACEAE):** Only one species of *Ulmus* (*U. mexicana*) is reported in Costa Rica (Burger, 1977). This tree grows in forest between 900 and 1900 meters elevation (Burger, 1977).

UMBELLIFERAE: Standley (1937-1938) reported 13 genera of UMBELLIFERAE in Costa Rica. Most of the taxa are herbs but shrubs and small trees are also included. Plants in this family mostly grow in open and/or disturbed sites (pastures) in the lowlands and in the Meseta Central (*Apium*), but some grow in wet montane forest (*Hydrocotyle*).

URTICALES: Three families make up the URTICALES, the MORACEAE, the ULMACEAE, and the URTICACEAE. Aside from *Celtis, Cecropia, Ficus, Dorstenia,* and *Ulmus,* taxa in the URTICALES produce pollen that cannot be readily differentiated. URTICALES pollen that could not be assigned to a genus was classified by pore number.

The taxa within the URTICALES are well represented in Costa Rica and throughout the neotropics. Plants range from small herbs to very large trees and grow in a very wide range of habitats. There are at least 21 genera of MORACEAE reported for Costa Rica; most plants are tall trees that grow in tropical lowland and premontane wet forests (Burger, 1977). There are only five genera of ULMACEAE reported in Costa Rica; most taxa are tall trees that range from lowland tropical wet forest to montane wet forests (Burger, 1977). There are 9 genera of URTICACEAE reported in Costa Rica (Burger, 1977). Taxa are characteristically herbaceous or shrubby but some are tall trees. They grow in a range of habitats from seasonally dry forest to very wet forest (Burger, 1977).

***Avicennia germinans* (VERBENACEAE):** *Avicennia germinans* (black mangrove) occurs in mangrove swamps and on saline flats that are inudated by high tides on both coast of Costa Rica (Standley, 1937-1938; Simberloff, 1983).

VOCHYSIACEAE: Taxa of the VOCHYSIACEAE are large trees that occur in lowland wet forest (Standley, 1937-1938). Hartshorn and Poveda (1983) report two genera of VOCHYSIACEAE, *Vochysta* and *Qualea*, both of which occur in the lowland wet forests of Corcovado National Park and La Selva Biological Station.

VITA

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