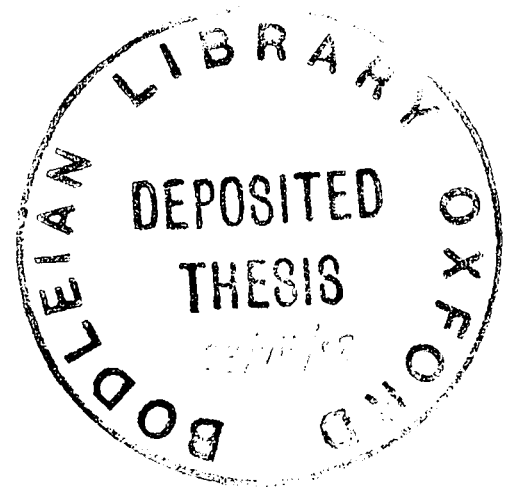
Long-term forest dynamics in high-altitude mountains of West-Central Mexico: The human and climate dimension in the Holocene

Thesis submitted for the degree of Doctor of Philosophy at the University of Oxford, Oxford, UK

Trinity Term, 2007



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Abstract

This thesis presents the results of a study to examine long-term forest dynamics in the high-altitude mountains of West-Central Mexico. Vegetation dynamics on temporal scales ranging from 10^2 to 10^3 years were reconstructed in order to provide essential information on the temporal variability of ecological patterns and processes in these forests; information that is of direct relevance for their current and future conservation and management strategies.

Vegetation and palaeoecological methods undertaken included fossil and modern pollen analysis, vegetation surveys, microfossil charcoal analysis, magnetic susceptibility, inorganic and organic geochemistry, radiocarbon and ^{210}Pb dating. These were used to evaluate the long-term dynamics of three forest types; Pine Forest, Cloud Forest and Transitional Forest on timescales spanning the past 4260, 1340 and 1230 years respectively.

The main drivers of change were climate and disturbance events induced by climate fluctuations, for example increased fire frequency. The reconstructed records indicate that the sequences from the Cloud Forest and the Transitional Forest spanned two wet and one dry climatic interval while the Pine Forest sequence spanned two dry and two wet periods. The impact of these climatic fluctuations was significant on all three forest types and resulted in variations in forest diversity, taxonomic turnover and successional change. The climate change episodes observed in these records seem to be the local manifestation of climatic events that were occurring throughout Mexico at these intervals in time. Human influences were evident in the three forests through the appearance of cultural taxa, particularly during the driest period (~ 1200 yr BP). There is little evidence from these records, however, to suggest a widespread clearance of the landscape for agriculture

Results from this study support the current conservation and management recommendations for Cloud Forest to exclude timber extraction, grazing and agricultural activities from this forest type. In the Pine Forest, human interventions such small-scale agriculture, prescribed burning and silvicultural actions are in agreement with the long-term pine ecology and as such, total exclusion of human activities is not necessary. For the Transitional Forest, results from this study suggest that there needs to be the establishment of adequate plans to reduce frequent fires to arrest the development of prone-to-fire taxa.

I dedicate this work to the memory of my father, Juan Alberto† and to my lively daughter Paula.

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Blanca Lorena Figueroa Rangel, July 2007, Oxford

CONTENTS

1. GENERAL INTRODUCTION

1.1 Introduction

A long-term perspective in conservation and ecosystem management can provide an important understanding of the range and temporal variability in current ecological patterns and processes (Swetnam et al., 1999). This perception also can help to anticipate future conditions of ecosystems, in particular in response to climate change and human interventions. It has long been recognised that environmental disturbance regimes as well as the biotic and vegetation responses of ecosystems are different depending on the scale under study with the temporal and spatial scale corresponding accordingly. Decadal to centurial intervals are considered in the microscale (10^0-10^3 years in the temporal scale and 10^0-10^8 m^2 in the spatial scale) domain with vegetation responses from the herbaceous, tree, shrub and stand level to the forest type level. Biotic responses in this scale include succession, replacement and competition while the environmental disturbance regimes encompass human activities and climatic fluctuations (Delcourt et al., 1983).

One of the most valuable disciplines in assessing long-term forest dynamic is palaeoecology because pollen records, alongside dating techniques, sediment geochemistry and charcoal analysis provide information on vegetational change involving many taxa, within multiple spatial and temporal scales. Such records can also provide information on the past environmental conditions underlying the responses in vegetation.

The Temperate and Subtropical forests in Mexico are situated in the mountainous zones of the Sierra Madre Occidental, Sierra Madre del Sur, Sierra Madre Oriental, Central Mexico and some areas in the South (Fig. 1.1). Long-term studies at the microscale level are the most

relevant to understand and to manage these forests as the longevity of the arboreal component spans one to three centuries and in such a forested environment the impact of environmental changes can take several decades to become apparent (MacDonald, 1992).

A high biodiversity spot located in the Sierra Madre del Sur in West-Central Mexico, namely the Sierra de Manantlan Biosphere Reserve, was selected as an appropriate system for the study of three high-altitude forests; pine forest, cloud forest and a transitional forest (*Pinus-Carpinus-Quercus*)(Fig. 1.1). This thesis examines the long-term dynamics of these three mountainous ecosystems covering the Late Holocene (4262, 1388 and 1231 cal yr BP respectively) to present times at altitudes from 1820 to 2570 m asl with a particular emphasis on the climate and human dimensions.

To date paleoenvironmental studies in Mexico have been focused in Central and Southern Mexico (Almeida-Lenero et al., 2005; Beach et al., 2006; Goman and Byrne, 1998; Hodell et al., 2005a; Hodell et al., 2001; Hodell et al., 2005b; Hodell et al., 1995; Islebe and Sanchez, 2002; Lozano-Garcia and Ortega-Guerrero, 1998; Lozano-Garcia and Xelhuantzi-Lopez, 1997; Lozano-Garcia et al., 1993; Lozano-Garcia et al., 2005; Lozano-Garcia and Vazquez-Selem, 2005; Ludlow-Wiechers et al., 2005; Metcalfe, 1995; Metcalfe et al., 1991; O'Hara, 1993; O'Hara et al., 1993; Sluyter and Dominguez, 2006; Wahl et al., 2006; Xelhuantzi-Lopez, 1994a; Xelhuantzi-Lopez, 1994b). In addition a few studies has been conducted in the Baja California Peninsula (Lozano-Garcia et al., 2002; Rhode, 2002), in the Central-East region (Conserva and Byrne, 2002) and in the North (Metcalfe et al., 2002)(Fig. 1.2).

These previous works have focused on the study of environmental change through vegetation reconstructions, soil erosion changes, climate change and human-related activities such as forest clearance and agriculture.

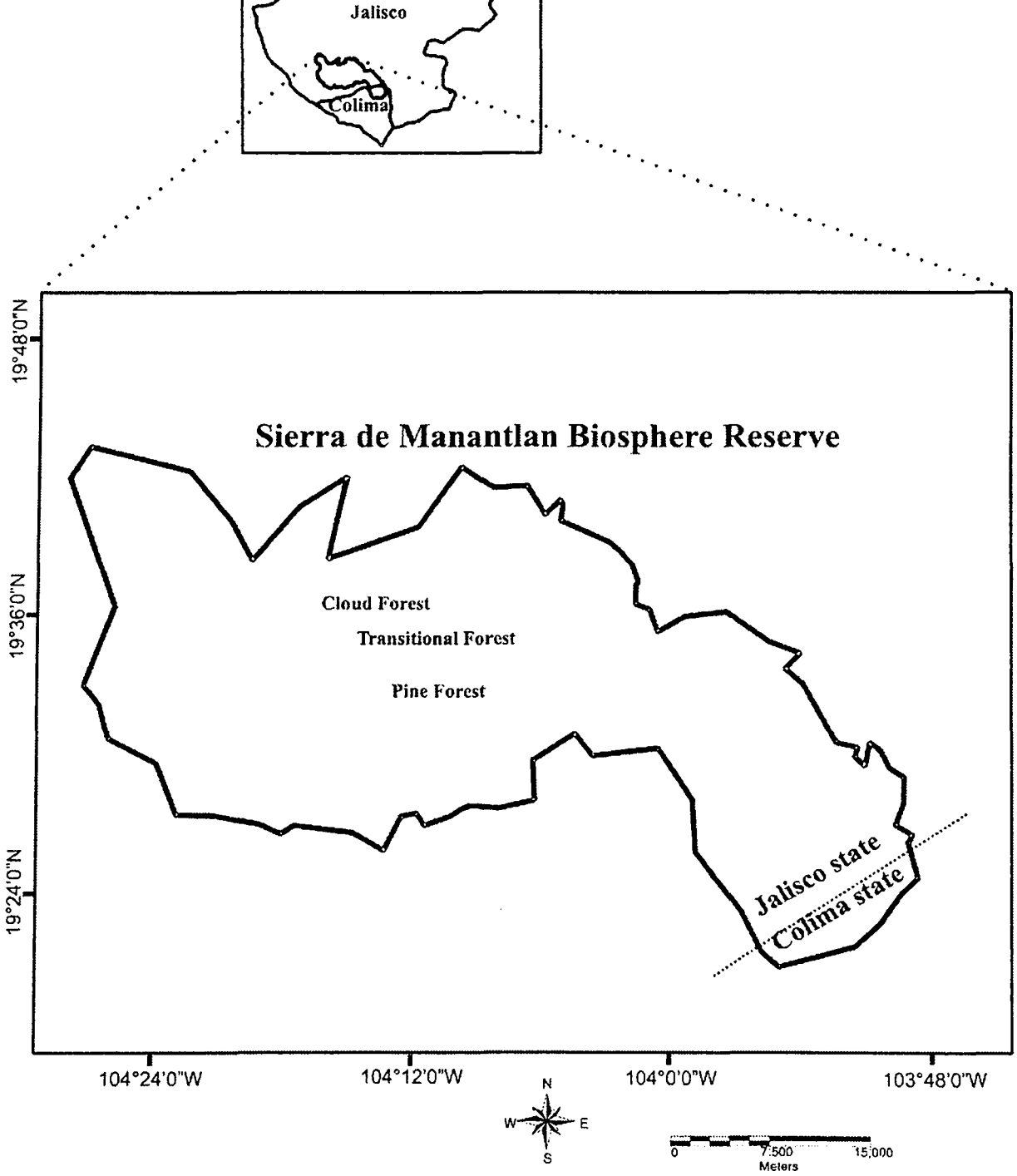


Fig. 1.1. Geographical location of the Sierra de Manantlan Biosphere Reserve in West-Central Mexico with the study sites corresponding to pine-dominated forest, transitional forest and cloud forest.

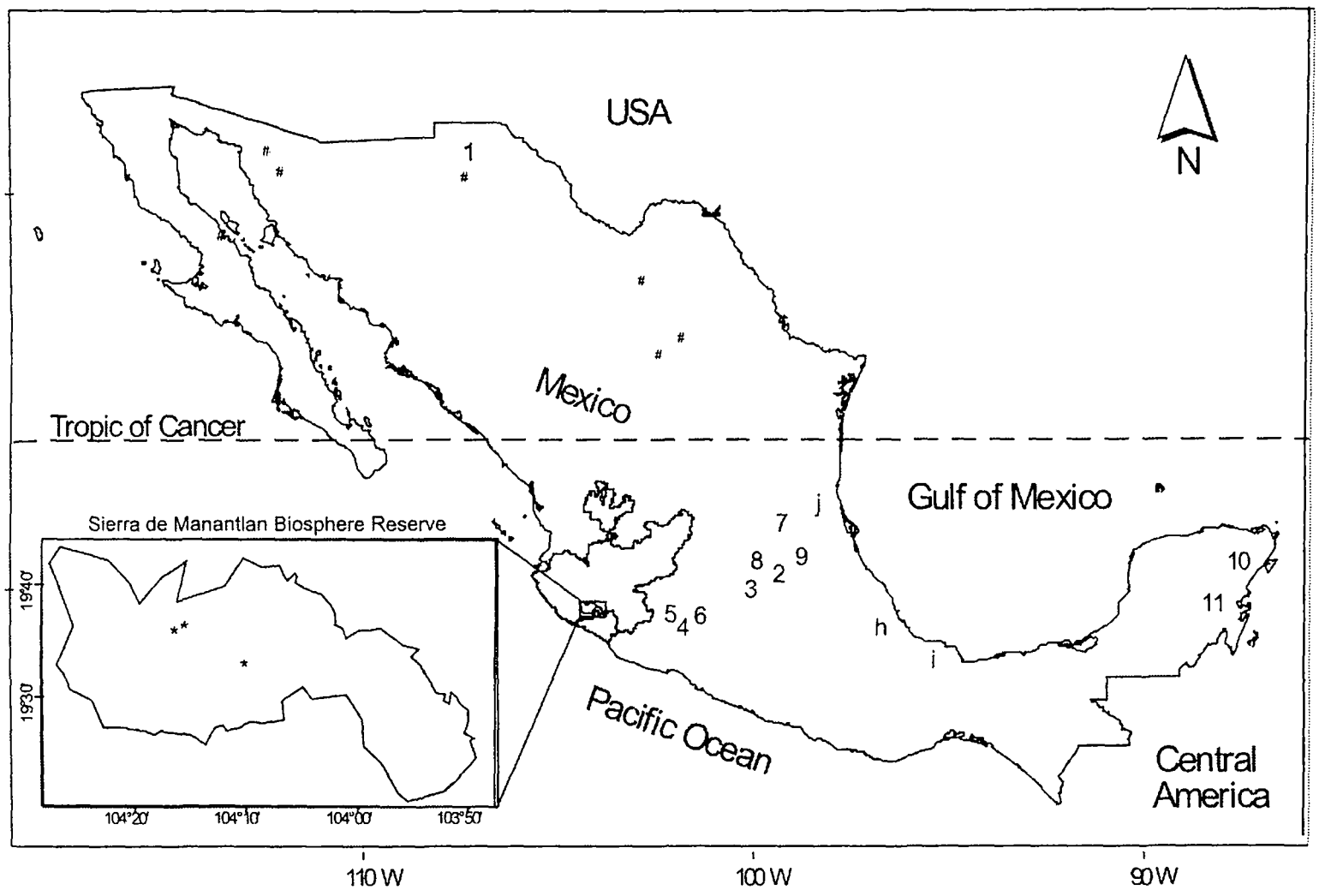


Fig. 1.2. Palaeoecological studies in different regions of Mexico. Numbers and letters represent sites in different regions that will be referred in chapter 2. # represent sites not mentioned in the introduction.* represents study sites located in the Sierra de Manantlan Biosphere Reserve, West-central Mexico.

In contrast there has never been any palaeoecological studies carried out in West-Central Mexico. The present project therefore provides novel information for this geographical region in terms of its long-term forest dynamics and the relative influence of past climate and humans in creating the present day landscape. The selected study area, the Sierra de Manantlan Biosphere Reserve, is an important convergent zone in terms of geography, climate and vegetation (Fig 1.1, 1.3, & 1.4) with physical, biological and cultural characteristics as follows:

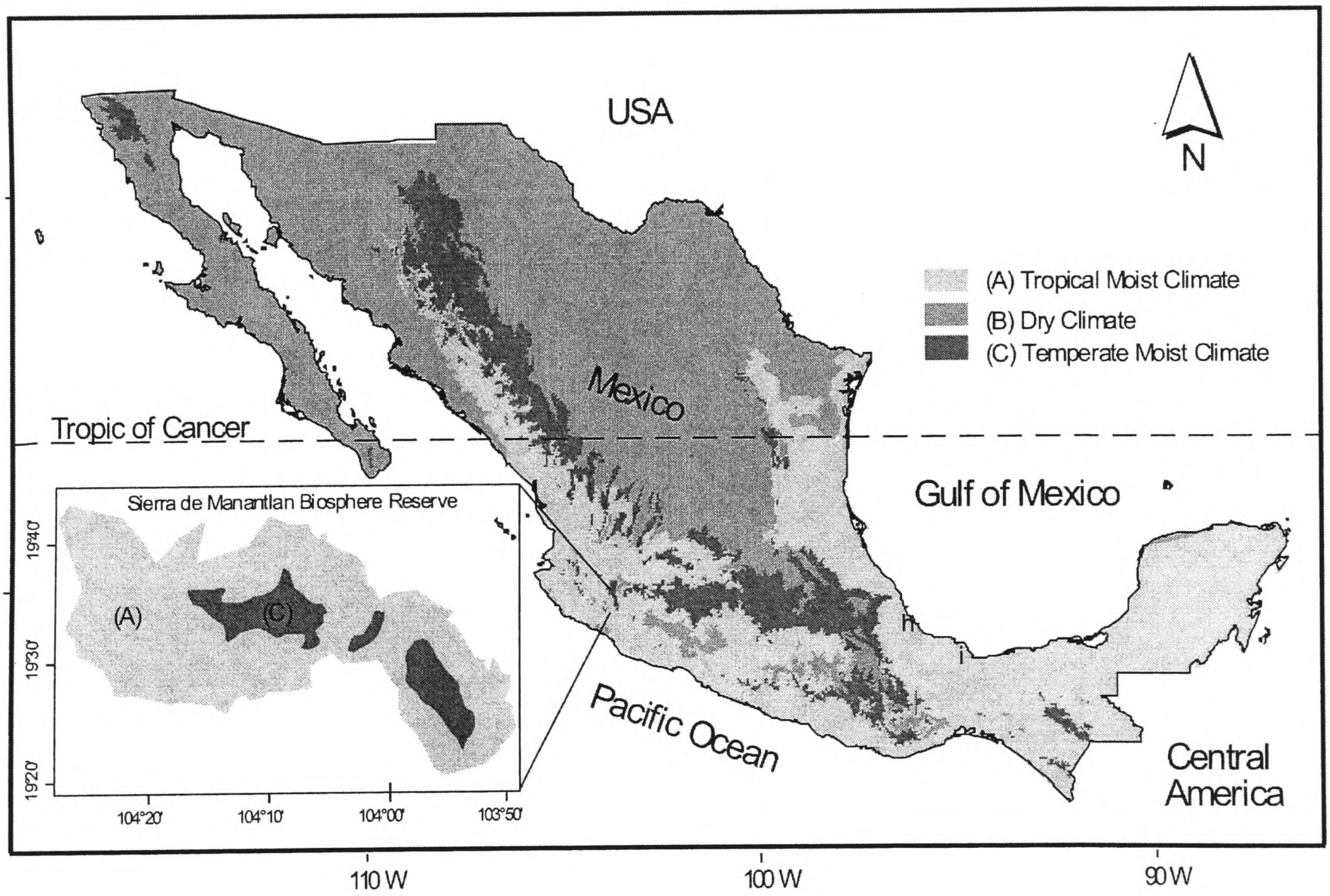


Fig. 1.3. Climate types in Mexico and the Sierra de Manantlan according to Köppen modified by (García, 1987).

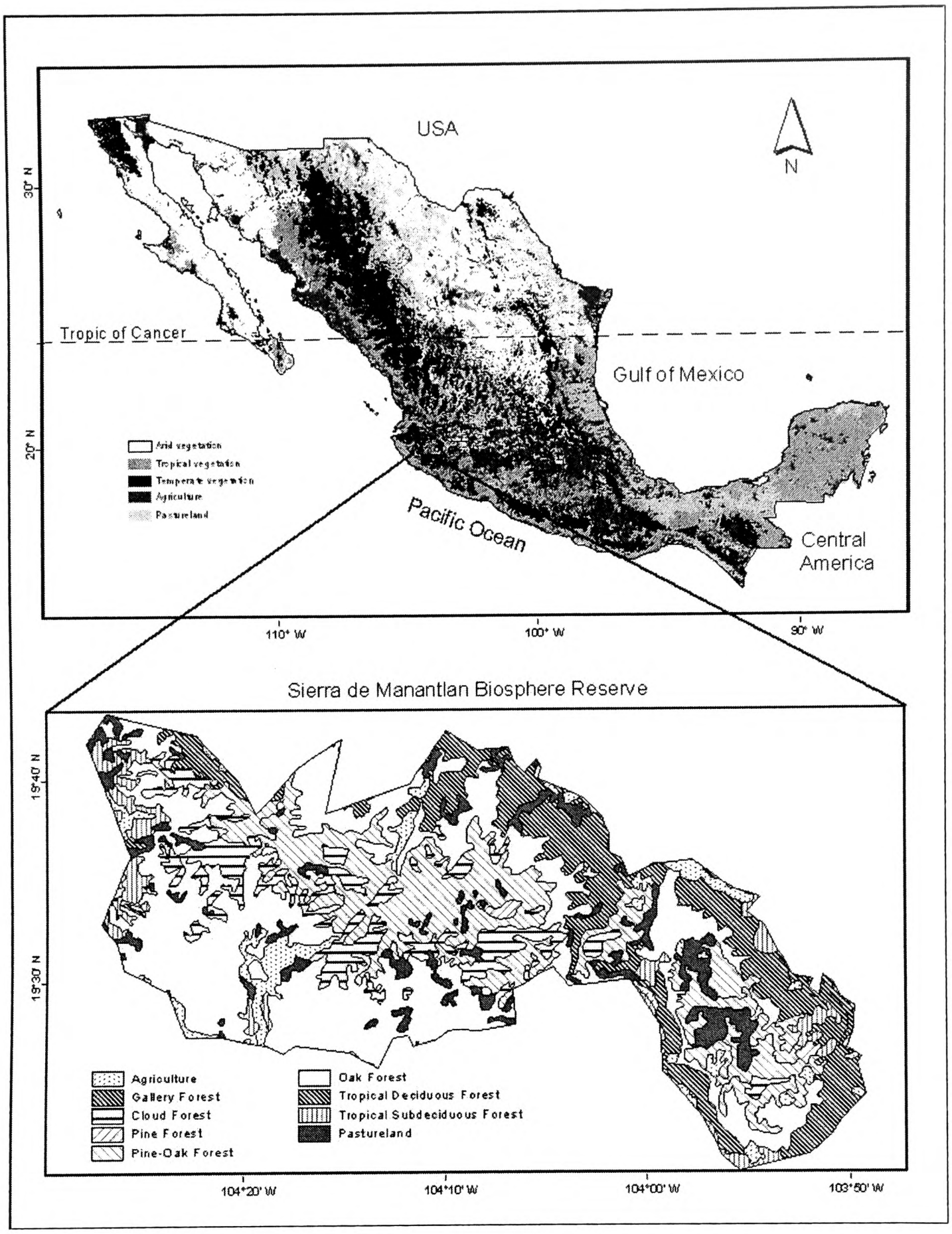


Fig. 1.4. Vegetation types in Mexico and the Sierra de Manantlan.

1.2. The Study Area: The Sierra de Manantlan Biosphere Reserve

1.2.1. Physical settings

The Sierra de Manantlan emerged in the late Cretaceous as part of the Sierra Madre del Sur. Underlying causes of its emergence was subduction volcanism that occurred in Central Mexico and assembled two major volcanic arcs: the Sierra Madre Occidental silicic volcanic province and the roughly east-west trending Trans-Mexican Volcanic Belt (Rossotti et al., 2002). The Sierra de Manantlan is situated in the south-east of the State of Jalisco and in the north-east of the State of Colima in West-Central Mexico between 19°26'-19°42'N and 103°51'-104°27'W (Fig. 1.1). The area comprises 139,577 ha and contains a diverse physiography manifested in a broad altitudinal range of 400 to 2,860 m asl and irregular topographies with slopes ranging from 15 to 45%. Plateaux, slopes and alluvial terraces are derived from igneous extrusive rocks from the Tertiary and Quaternary (Quintero A. and Martinez R., 1993).

Climate of the region has been classified according to Köppen (García, 1987) into two groups; A (tropical) and C (temperate) with six subgroups A, A(C), (A)Ca, (A)Cb, Ca and Cb (Martínez-Rivera et al., 1991 (Fig. 1.3). Mean annual temperatures fluctuate between 16 to 22°C. The driest area has mean annual precipitation lower than 800 mm but in the highlands it ranges between 1000 and 1500mm [Martínez-Rivera, 1991 #150). Rainfall season corresponds to summer, mainly from June to October, while the dry season takes place from March to May.

The area is located among three river basins *Ayuquila-Armeria, Marabasco* y *Purificacion* with 34 permanent watercourses. The Sierra de Manantlan provides a good source of water for all lowland valleys even during the dry season due to the constant cloudiness as the canopy forest captures humidity.

There are 13 soil types in the region according to FAO classification; Lithosols, Regosols, Fluvisols, Rendzinas, Acrisols, Gleysols, Phaeozems, Luvisols, Kastanozems, Andosols, Cambisols, Chernozems and Vertisols (Martinez Rivera and Ramirez, 1998).

1.2.2. Biological settings

The vast territory of the Sierra de Manantlan (139,577 ha) is a diverse landscape in terms of climate, geology, soils and physiography, as well as in a myriad of natural and human disturbances. These characteristics have played an important role in shaping ecosystems, communities and populations within the biosphere reserve and this has resulted in a highly diverse fauna and flora. Faunal species present include over 20 amphibians, 60 reptiles, 336 birds (representing 30% of all bird species in Mexico), 110 mammals (25% of all mammals in Mexico), 16 species of fishes and 180 families of insects (SEMARNAP, 2000). Floristic richness in flora consists of more than 2900 species of vascular plants with 50% endemic to Mexico (Vazquez-Garcia et al., 1995). Vegetation types consist of 13 categories (Jardel, 1992; Rzedowskii, 1994; Vazquez-Garcia et al., 1995) that have been arranged for simplicity into nine groups for map elaboration. Therefore names in parenthesis are according to categories in Fig. 1.4 as follows:

Temperate and Subtropical Forests

1. Fir forest. This forest is located in altitudes > 2500 m asl comprising *Abies religiosa var religiosa* and *A. religiosa var emarginata* in the canopy (Figueroa-Rangel, 1991). This forest is included in the pine forest category in Fig. 1.4.
2. Pine forest. This forest type is located at altitudes > 2500 m asl with *Pinus pseudostrobus* and *Pinus douglasiana* intermixed with *Quercus laurina, Quercus crassipes, Abies religiosa* and *Alnus jorullensis*. In the understory the following herbaceous families prevail: Asteraceae, Poaceae, Fabaceae, Lamiaceae, Solanaceae and Schropulariaceae (Cuevas-Guzmán, 1994). This category also occurs intermixed with others forest types such us pine-oak forest and cloud forest and not solely as mapped on Fig. 1.4.
3. Pine-oak forest. This forest is located at 1500-2500 m asl with 60-90% of *Pinus* species (*Pinus douglasiana*) and 10-40% of *Quercus* species (*Quercus praineana* and *Quercus scytophylla*) in the canopy. *Pinus oocarpa, Pinus herrerae* and *Arbutus xalapensis* are in less abundance. The shrub layer includes *Acacia pennatula, Vaccinum stenophyllum, Myrica cerifera* and *Ternstroemia lineata.* Herbs include Asteraceae, Poaceae, Euphorbiaceae, Solanaceae, Rosaceae and Scrophulariacae (Cuevas-Guzmán, 1994).
4. *Cupressus* forest. This is vegetation with patchy distribution in altitudes corresponding to Fir and Pine-Oak forest. This is a monodominant type with *Cupressus lusitanica* (SEMARNAP, 2000).
5. Cloud forest. This forest comprises both temperate (*Carpinus tropicalis, Cornus disciflora, Pinus douglasiana, Quercus xalapensis, Quercus candicans, Quercus castanea, Quercus xalapensis, Tilia americana var mexicana, Juglans major,* etc.) and

tropical *Cinnamomum pachypodum, Clethra vicentina, Clusia salvinii, Dendropanax arboreus, Inga hintonii, Persea hintonii*, etc.) elements with patches at 1700-2300 m asl (Munoz-Mendoza, 1992; Santiago-Perez and Jardel Pelaez, 1993).

6. Oak forest (sub-deciduous). This forest is located at altitudes > 1500 m asl with *Quercus crassipes, Q. candicans, Q. acutifolia* and *Q. laurina* associated to *Pinus leiophylla, Prunus serotina* and *Alnus jorullensis* (Olvera-Vargas et al., 2006).

Tropical Forests

7. Oak forest (deciduous). This forest is located at 400-1500 m asl mainly characterised by the *Quercus resinosa-Quercus magnoliifolia* association with *Quercus castanea* in some locations.
8. Gallery forest. This forest type is located along rivers and permanent watercourses. Dominant species include *Salix bomplandiana, Astianthus viminalis and Ficus sp.* (Vazquez-Garcia et al., 1995).
9. Tropical deciduous forest. This forest is located at 600-1300m asl with *Lysiloma acapulcensis, Jacaratia mexicana, Amphyterigium adstringens, Ceiba aesculifolia, Pseudobombax ellipticum, Bursera sp.*(Vazquez-Garcia et al., 1995).
10. Tropical sub-deciduous forest. This forest type is at 400-1200 m asl with species such as *Brosimum alicastrum, Bursera simaruba, Cedrela odorata, Enterolobium cyclocarpum, Ficus sp., Hura polyandra, Sideroxylon cartilagineum, Tabebuia palmeri, Trichilia americana, Trophis racemosa.* (Vazquez-Garcia et al., 1995).

Human-induced vegetation

11. Agriculture. This type includes crops such as maize and beans.
12. Pastureland. This vegetation is intended for grazing with *Panicum* sp. as the dominant grass.
13. Scrubland/Slope agriculture/Pastureland. This is a combination of types 11 and 12 with the wild maize or *teosinte* (*Zea diploperennis*) in some locations.

1.2.3. Cultural settings

The Sierra de Manantlan was established Biosphere Reserve by government decree in 1987 due to the discovery of *Zea diploperennis*, a perennial wild relative of maize (Guzman M., 1978a; Guzman M., 1978b; Iltis et al., 1979). At present the region is recognized as an area of economically valuable germoplasm for maize hybridisation. Further ecological studies indicated that Manantlan is also a high biodiversity spot with a high number of endemic species, and a significant economic forestry potential. Management strategies for this biosphere reserve include the division of the region in two different zones; the *Core Zone* appointed as an area of rigorous protection where no human interferences is allowed and the *Buffer Zone* where most of the people live and use natural resources (SEMARNAP, 2000). At present the Sierra de Manantlan Biosphere Reserve is home to 79 human settlements with 97% population inhabiting below 1500 m asl. Only in the east of the reserve (Cerro Grande) some people live above 2000 m asl. To subsist people produce maize and beans, raise poultry and cattle and do backyard gardening, hunting and gathering.

Autlan, one of the nearest biggest prehistoric settlements to the study area, was occupied before the Spanish Conquest (1521 A.D.). Pre-Hispanic tools corresponding to the *Autlan, Mylpa* and *Cofradia* ceramic complexes that seem to correlate with the Aztec I, II III and IV periods from Central Mexico (Kelly, 1945) date to ~1200 to 1500 A.D. Similar archaeological studies in Colima, a Mexican state (north-east) where the reserve is located (Fig. 1,1), reported human occupation from 3400±200 yr BP (Kelly, 1980). The main prehispanic groups developed in this region were Toltecs (900-1200 A.D.) and Chichimecs (1200-1400 A.D.)(Kelly, 1945) (Fig. 1.5).

Forest clearance for timber extractions, as well as for agriculture and grazing purposes, have been the more common human disturbances in Manantlan's recent past. Logging operations from foreign and national lumber companies started early in the 1900's. These activities (mainly extracting timber from old growth forests) were interrupted by the Mexican Revolution (A.D. 1910-1921) and by the Cristero War (A.D. 1926-1929), to be restarted in the 1940's (Guzman M., 1985). Late in the 1970's lumber companies stopped logging activities in parts of the Sierra de Manantlan.

Small-scale fires occur every year in Manantlan, mostly as a result of uncontrolled burning from the *coamil* agricultural system (a slash-and-burn land management technique used locally). Fire frequency ranges from 4.8 to 17 years (Jardel, 1991) favouring species with vegetative regeneration (*Quercus* sp., *Arbutus xalapensis, Alnus jorullensis, Rubus adenotrichos* and *Pteridium aquilinum*) mainly in Pine-Oak forest. Fires also damage the

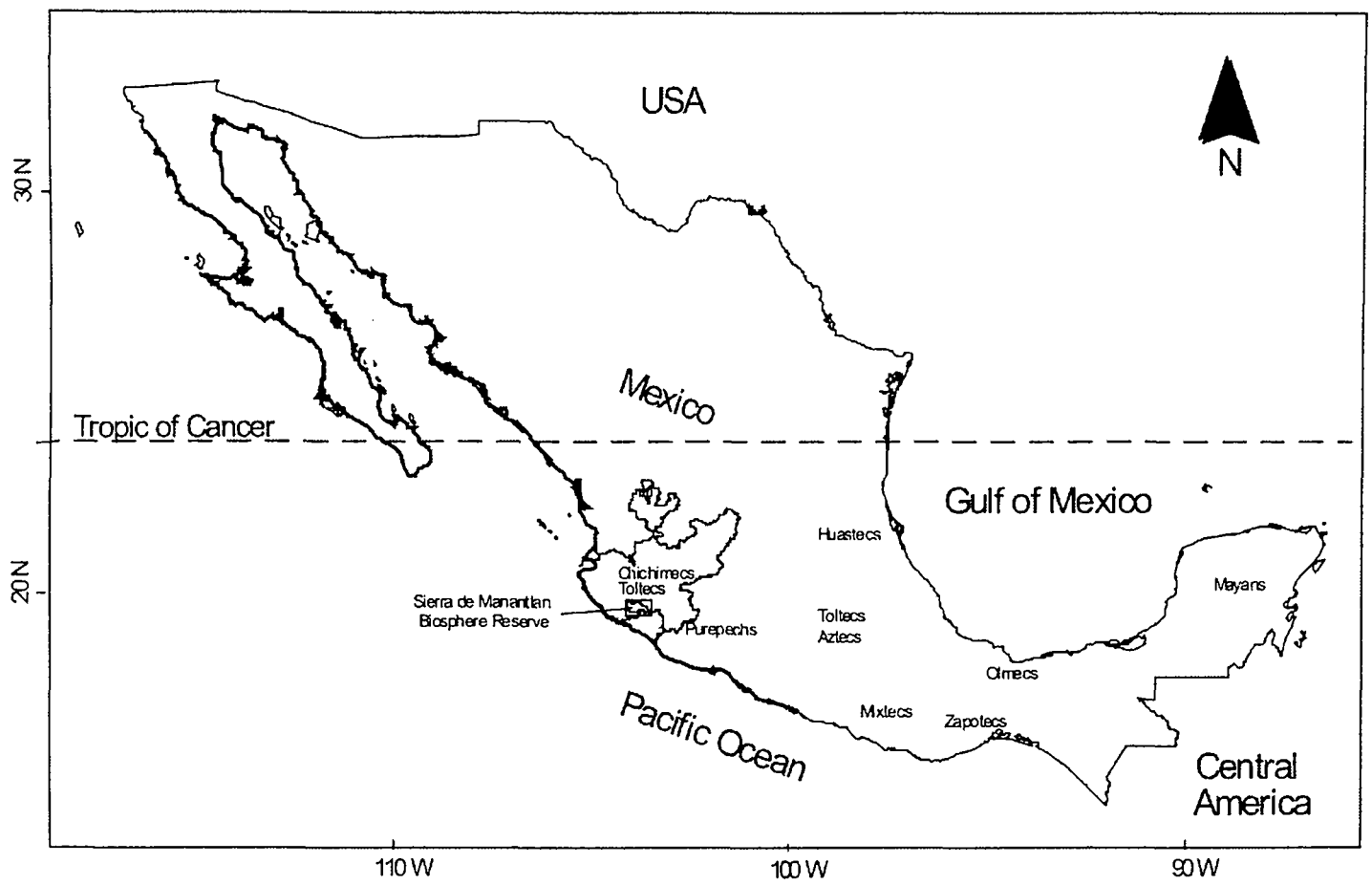


Fig. 1.5. Pre-Hispanic civilizations in Mexico.

understory vegetation in pine forest favouring the establishment of oak and cloud forest species (Saldana and Jardel, 1992).

A number of long-term ecological studies have been carried out in the Sierra de Manantlan using permanent plots in the forests (Figueroa-Rangel and Olvera Vargas, 2000a; Figueroa-Rangel and Olvera Vargas, 2000b; Olvera-Vargas and Figueroa-Rangel, 1998; Olvera-Vargas and Figueroa-Rangel, 2000) and in *Zea diploperennis* populations (Sanchez-Velasquez et al., 2002) but these studies span less than 20 years. Consequently there are no detailed records from the forest dynamics before the establishment of the reserve (1987). It is not possible to discern either if the present taxa composition and structure of the forests is a transitional or a final stage or, alternatively, whether it is the result of a particular management practice in the past. These are, however, fundamental questions for the design of present and future forest management alternatives. Therefore the present study aimed to address these questions in a broad time scale (10^2 to 10^3 years) encompassing the longevity of the trees present in the three different forests, as well as the periods of important climate change and human disturbance events occurred during the last 4000 years in Mexico.

1.3. Aims of the research

In order to accomplish the need for longer-term studies in West-Central Mexico, the present research focuses in the Sierra de Manantlan Biosphere Reserve. The research aims to reconstruct the predominant ecological mechanisms (e.g. secondary succession, changes in diversity and taxa turnover) that have occurred on timescales from 10^2 to 10^3 years and

resulted in the development of the present day pine forests at 2510-2570 m asl, transitional forests dominated by *Pinus-Carpinus-Quercus* at 1880-2100 m asl, and the cloud forests at 1820-1890 m asl.

1.4. Research Questions

The following research questions will be addressed:

1. Are the modern pollen assemblages different among pine, cloud and the transitional forest?
2. Is the modern pollen abundance related to the actual forest structure in the three forest types?
3. Is there temporal environmental variability among the three forests expressed by microfossil charcoal, carbonates, magnetic susceptibility and organic matter?
4. Which forest is undertaking the biggest change in vegetation, including temporal taxa turnover, changes in abundance and in diversity?
    a. Are the cycles of abundance in the different taxa coincident among the three forest types?
5. Are there evident periods of climate change?
    a. Do dry intervals increase fire occurrence?
    b. Is the increase in fire related to the increases in pine?
6. Which periods are related to human disturbances in each of the three forests?
    a. Which taxa are associated to human disturbances?

7. How will the information obtained in this study assist or alter the conservation and management strategies already taken in each of the three forest types?

1.5. Outline of the thesis

This thesis is arranged in seven sections; the present general introduction, a literature review, four papers and general conclusions as follows:

Chapter 1. General Introduction

Chapter 2. Literature Review

Chapter 3. Paper 1, *Can modern pollen reflect the diversity and structural complexity of high-altitude vegetation in West-Central Mexico?* This paper presents results of a study to analyse the modern pollen signature of the three forest types. The aims were 1) to investigate the difference in pollen representation by forest type, 2) its relationship to forest structure and 3) the concordance between forest types and pollen assemblages?

Chapter 4. Paper 2, *4000-years of pine-dominated forest dynamics in the uplands of West-Central Mexico: conserving a human or natural legacy?* This paper presents the reconstruction of the pine-dominated forest over the past ~4200 years. The aims were 1) to investigate if fire favoured the expansion of pine over other tree species; 2) if this forest is an anthropogenically-derived vegetation type, 3) what specific management techniques were

essential to its long-term preservation and 4) to discern if pines are a human or a natural legacy

Chapter 5. Paper 3, *Successional stages in a transitional montane forest in the Mexican Neotropic during Late Holocene.* This paper involves the reconstruction of a transitional forest dominated by *Pinus-Carpinus-Quercus* over the last ~1200 years. The aims were 1) to discover if past stages developed into pine, pine-oak and/or cloud forests; 2) which were the main drivers for those forest conversions, human-induced or climate-induced disturbances; 3) if the current conservation and/or management strategies undertaken in the transitional forest are in accordance with its long-term dynamics

Chapter 6. Paper 4, *Dynamics of a cloud forest in the Mexican Neotropic during the Holocene* This paper reconstructs the cloud forest dynamics through a sequence spanning the last ~1400 years covering a crucial time when important climatic events impacted the Mexican territory. The aims were 1) to determine if human disturbance and climate change affected the temporal taxa turnover in the cloud forest assemblage and 2) if the current conservation strategies undertaken in the cloud forest are in accordance with its long-term dynamics.

Chapter 7. General Conclusions

2. Literature Review

2.1 Introduction

The study of long-term dynamics in high-altitude forests in Mexico requires knowledge of a number of different subjects. First, it involves an appreciation of the physical environs where the forests are located such as characterization of physiographical and climatic features. Second, it requires information on temporal patterns of plant distribution and the ecological processes underlying those patterns. Third, the factors causing changes on the temporal patterns of plant species need to be understood. Concerning the scale of the present study (the last 4200 years), the main aspects implicated in vegetation change in Mexico are climate change (Metcalfe et al., 2000) and human disturbances (Lentz, 2000; Williams, 2003). Each of these factors will be considered in turn:

2.2. The physical environs

Mexico is a vast territory with highly diverse physical environs. In terms of physiography these include a complex and heterogeneous topography and the extensive mountain range (Rzedowskii, 1994). In terms of geographical features it is important for its position alongside the Tropic of Cancer and its narrow continental extension constantly influenced by ocean forces (Metcalfe et al., 2000). Half of the country contains mountainous zones over 900 m asl. The most important areas with that altitude are Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur and Central Mexico (Fig. 1.1.).

This remarkable physical heterogeneity has resulted in a variety of climate and vegetation types. According to Köppen classification modified by (García, 1987), four types (A, B, C and E) out of the five climatic types in the world, are reported for Mexico. In general, the three first are the most conspicuous. Type E (Polar climate) corresponds to a reduce extension in mountains over 4000 m asl (Figure 1.3). Type A is a Tropical Moist Climate characterized by an average temperature above 18 degrees Celsius all the year round. Type B is a Dry Climate with deficient precipitation during most of the year and Type C is a Temperate Moist Mid-latitude Climate with mild winters and precipitation during summer. Type A prevails in most of the Yucatan Peninsula and in the Pacific slope extending from 24°N to the south. Type B predominates in most of North of Mexico. Type C, specifically *Cw*, characterizes mountains over 800 to 1000 m asl mainly located in centre and south of Mexico, north and central Mexico, Sierra Madre Oriental and Occidental and Sierra Madre del Sur where the present research sites were located (Figure 1.3).

For long it has been assumed that climate rules the geographical distribution of plants (Woodward, 1996). Such assumption has resulted in the pragmatic use of vegetation classification based on climatic zones in different parts of the world (Holdridge, 1967; Köppen, 1918) as well as in Mexico (García, 1989; Miranda and Hernandez X., 1963; Rzedowskii, 1994). As different climate types converge in Mexico, vegetation is also diverse ranging from tropical rainforests (climate type A) in low altitudes of Chiapas, Yucatan, Veracruz and Guerrero in south Mexico, to the Sonoran and Chihuahuan deserts (climate type B) in the north and to the cool temperate forests (climate type C) in the mountains of central and south Mexico as well as in the Sierra Madre Occidental and Oriental (Figure 1.4).

Following the above mentioned assumption "climate-vegetation", important studies conducted in Mexico have discerned climate change through changes in vegetation and changes in taxa distribution and abundance from reconstructed pollen records. A discussion follows in a subsequent section.

2.3. Temporal patterns of forest dynamics and the ecological processes underlying these patterns

Through vegetation reconstruction of tropical forests in the world it has been possible to reveal ecological processes occurring at time scales from $1x10^2$ to $5x10^3$ years (Berrio et al., 2002; Bush, 2005; Bush and Colinvaux, 1994; Donders et al., 2006; Metcalfe et al., 2007). All of these studies have revealed temporal heterogeneity through time implying that different environmental conditions exist at temporally discrete intervals in the same locality, either in a periodic or a non-periodic manner (Tokeshi, 1999). These induce heterogeneous responses among the taxa. Climate and disturbance provide broad-scale filters for long-term dynamics (Walker and del Moral, 2003) affecting available species pool, available resources (light and nutrients) and different species performance (arrival, growth and survival) (Pickett et al., 1987) along wide time scales. After a disturbance episode, either related to climate or induced by humans, plant communities recover promptly maintaining a steady level of species richness with the species turnover prolonged for an extensive time interval (Tokeshi, 1999).

Equilibrium theory supporters argue that high plant richness characterises late successional communities where species coexist in interactive equilibrium with other species in the

community. Non-equilibrium supporters claim that richness is a transient successional property that can only be maintained by an appropriate disturbance regime where species densities do not remain constant over time at each spatial location (Chesson and Case, 1986). On the other hand neutral theory supporters argue that species abundance through time is due to probability alone. There is no population regulation and assemblages are largely thrown together by chance, history, and random dispersal (Hubbell, 2001).

Species coexist because they have differences in resource use but also due to dissimilar responses to the environment. The discrepancy in resource utilization in the form of niche can be spatially or temporally determined. In the spatial scale, it involves microhabitat differentiation among the species while the temporal scale concerns the temporal separation among species, either when different resources become available at different times of the day, at different seasons of the year, or even in some decades along a century (Shugart, 1998).

Long-term forest dynamics also entails agreement on the level of the system under study. Two different approaches have emerged. One is *the individualistic response concept,* which has been the concept used by palaeoecologists (Grace and Tilman, 1990). This suggests that individual species respond to environmental changes by migrating in different directions, at different rates and during different times. As a consequence our modern communities are ephemeral associations of species (Graham, 1988). *The Community response concept*, in the contrary, affirms that communities respond to environmental changes as intact units. As a result, the communities we observe today might be quite old geologically (Chesson and Case, 1986).

The importance of palaeo-reconstructions in addressing long-term forest dynamics has been most recently acknowledge (Willis et al., 2007; Willis and Birks, 2006) as an essential instrument in the design of conservation and management strategies. The main benefit of palaeo-studies resides in the large temporal and spatial scale it covers as well as in the biological levels (from population to ecosystems) of study it can address. Such an approach provides the essential tools to discern ecological mechanisms occurring in the past as well as the processes involved in those mechanisms.

2.4. Factors causing changes on temporal forest dynamics in Mexico

Mexico is a vast territory with high biodiversity both in terms of richness and also variety of ecosystems. It occupies the fourth place in plant biodiversity in the world with a figure of 23,000 vascular plants of which ~50% are endemic (CONABIO, 1998).

Of the eleven vegetation types distributed in thirty-eight different communities reported for Mexico (Dinerstein et al., 1995), temperate forests occupy 19% of the total Mexican territory (Rzedowskii, 1994) included in the main mountains of Mexico. They comprise mainly pine forest, oak forest and fir forest. Cloud forest is a subtropical type including a mixture of the first three types.

The main arboreal components of these ecosystems are *Pinus* and *Quercus* genera with 48 and 150 species respectively (CONABIO, 1998) representing the higher number of species of any region of similar size in the world with respect to these two genera (Perry et al., 2000).

Time, climate and geological events have been regarded as the main sources of change in plant dynamics in Mexico. The strategic situation of Mexico over the continental bridge between the Americas has been the scenario of intense migrations in the past making it a convergence zone of temperate and tropical elements (Rzedowskii, 1994). Temperate elements *(Abies, Acer, Carya, Cedrus, Cornus, Engeldhartia, Fagus, Fraxinus, Liquidambar, Liriodendron, Nyssa, Picea, Pinus, Platanus, Populus, Quercus, Tilia, Ulmus, etc.)* were present since the Miocene (Graham, 1976) while tropical elements *(e.g.. Clusia, Fuchsia, Hedyosmum, Oreopanax, etc)* appeared in the Eocene from Eurasia, Africa and South America during the spreading out of mega-thermal climates and during the Miocene and Pliocene from South America (Wendt, 1993).

All through the Cretaceous and Early Tertiary some temperate elements (*Abies, Alnus, Cupressus, Pinus, Quercus and Crataegus*) used to perform a broad, uninterrupted distribution in the northern hemisphere. During the Oligocene and Early Miocene climatic conditions were cooler and drier, pushing those elements to migrate through pine and oak forests. Such migration was due to colder climates in the southeastern United States that forced elements from boreal coniferous forests extending to the south (Gulf Coast) (Graham, 1999). This induced components of the deciduous forest to be displaced further south in Mexico. Later with the arrival of warmer conditions in the Holocene, some relics were trapped in the actual mid-altitudes of the temperate zones of Mexico.

The Holocene palynological record of Mexico is still very patchy and has been centered in the Yucatan Peninsula and Central Mexico where the most recognized pre-Hispanic civilizations were settled (Table 2.1, Figure 1.5). Central Mexico is the region where most of the lakes are found, giving as a consequence more information on high-altitude-temperate vegetation.

Studies undertaken in Central Mexico are those resembling the forest types involved in this research. They are high-altitude temperate vegetation ranging from 1500 to 3100 m asl in altitude and covering the last 5000 years (Fig. 1.2, Table 2.1 and 2.2). The pollen record has primarily reported changes in the two temperate taxa that dominate most of the present-day montane forests, *Pinus* and *Quercus*. The spectrum also includes *Alnus*, other coniferous trees such as *Abies, Cupressus, Juniperus* and *Picea* and some other broad-leaved taxa (or mesophytic species) such as *Acer, Fraxinus, Carpinus* and *Liquidambar*. During the last 1000 yrs there is a steady increase in *Pinus* for Central and East Mexico although the exact date varies among the sites. Mesophytic species appear as dominant in the last 3000 yrs in Central Mexico (Almeida-Lenero et al., 2005)(Table 2.2).

Studies in the Yucatan Peninsula involve mainly lowland vegetation but the record of cultural taxa reported in this region is of outstanding importance for comparison with our results. Key changes in vegetation involve cultural taxa such as *Zea mays*, Chenopodiaceae, Amaranthaceae and Poaceae (Table 2.2). Maize first appearance is reported for 4000 to 5000 yrs BP in the South, for Central Mexico is around 3000 to 3500 yrs BP while in the East is about 1500 to 2000 yrs BP. Most of these palynological studies agree that modern and past assemblages have remained very similar although fluctuations in the pollen percentages have occurred in different episodes but mainly related to climate change and human interventions (Metcalfe et al., 2000).

Table 2.1. Late Holocene (The last 5000 yrs) forest dynamics in Mexico inferred from pollen records in high-altitude forests. ▲ increase, ▼ decrease, ● first appearance. Mesophytic species include *Acer, Liquidambar, Carpinus, Hedyosmum, Juglans* and *Artemisa*. Amaran=Amaranthaceae; Cheno=Chenopodiaceae.

	CENTRAL MEXICO							***SOUTH***		***EAST***
C^{14} yrs BP	a. Lake Paztcuaro (1975 m. asl)	b. Lake Zacapu (2000 m. asl)	c. Lake Texcoco (2270 and 2750 m. asl)	d. Lake Chalco (2200 m. asl)	e. Lake Zempoala (2800 m. asl)	f. Lake Quila (3100 m. asl)	g. Lake Chignahuapan (Almoloya), Upper Lerma (2575 m. asl)	h.Coastal plain, Northwest Veracruz (altitude?)	i.Laguna Pompal, Los Tuxtlas, South Veracruz (700 m. asl)	j.Laguna Azteca, Hidalgo (1500 m. asl)
250-0			*Pinus* ▲		Maize/ Plantago▲	*Pinus* *Abies* ▲				*Pinus*, *Quercus*, *Abies*, Maize, Poaceae/Aster ▲
500-251			*Pinus* ▲		*Abies* ▲	*Pinus* *Abies* ▲				*Pinus*, *Quercus*, *Abies*, Maize ▲ Poaceae/Aster▼
1000-501			*Pinus* ▲		*Pinus* ▲	*Pinus* *Abies* ▲	*Pinus*, Maize ▲ *Quercus* ▼			*Pinus*, *Quercus*, Maize▲ *Abies*, Poaceae/ Aster▼
1500-1001			*Pinus*▼ Cheno/ Amaran▲		*Pinus* ▲	Mesophytic species ▲	*Pinus*, Maize▲ *Quercus* ▼			*Pinus*, *Quercus*, *Abies* ▼, Aster▲
2000-1501			*Pinus*▼ Cheno/ Amaran▲	Herbaceous species ▲	*Pinus* ▲	Mesophytic species ▲	*Pinus*, Maize▲ *Quercus* ▼			*Pinus*, *Quercus* ▼ *Abies*, Aster▲ Maize●
2500-2001			*Pinus*▼ Cheno/ Amaran▲	Mesophytic species ▲	*Pinus* ▲	Mesophytic species ▲	*Pinus*, Maize▲ *Quercus* ▼			
3000-2501			Cheno/ Amaran▲	Mesophytic species ▲	Mesophytic species ▲	Mesophytic species ▲	*Pinus*, Maize ▲ *Quercus* ▼			
3500-3001	Maize/ Cheno▲	Maize● Cheno/Amaran▼ Poaceae, Cyperaceae▲	Cheno/ Amaran▲	Mesophytic species ▲	Mesophytic species ▲	Mesophytic species ▲	*Pinus*▼,*Quercus* Cheno/Amaran/ Poaceae ▲			
4000-3501		Cheno/ Amaran▼ Poaceae▲	Cheno/ Amaran▲	Mesophytic species ▲	Mesophytic species ▲	Mesophytic species ▲	*Pinus*▼,*Quercus* Cheno/ Amaran/ Poaceae ▲			
4500-4001			Cheno/ Amaran▲	Xerophytic species ▲	Mesophytic species ▲	Mesophytic species ▲	*Pinus*▼,*Quercus* Cheno/Amaran/ Poaceae ▲			
5000-4501	Cheno/ Amaran▲	*Alnus* ▼	Cheno/ Amaran ▲	Xerophytic species ▲	Mesophytic species ▲	Mesophytic species ▲	*Pinus*▼ *Quercus* ▲	Maize●	Maize●	
REF	(Watts & Bradbury, 1982)	(Arnauld et al., 1997)	(Brown, 1985)	(Gonzalez-Quintero, 1986)	(Almeida-Lenero et al., 2005)	(Almeida-Lenero et al., 2005)	a. (Ludlow-Wiechers et al., 2005)	(Sluyter & Dominguez, 2006)	(Goman & Byrne, 1998)	(Conserva & Byrne, 2002)

Table 2.2 Late Holocene climate change in Mexico (the last 4500 yrs) inferred from palaeoecological studies. Pattern in vertical lines indicates dry periods and diagonal lines wet periods.

REGION	***North***	***Central Mexico***								*South Mexico*	
SITE	1. Alta Babicora Basin-Chihuahuan Desert	2. Chalco Lake	3. Zempoala and Quila Lakes	4. Lake Patzcuaro, Michoacan	5. Lake Zacapu, Michoacan	6. La Piscina de Yuriria, Michoacan	7. Basin of Mexico	8. Upper Lerma	9. Teyotl volcano-Iztaccihuatl	10. Lake Punta Laguna, Quintana Roo	11. Lake Chichaincabab and Aguada X'caamal sinkhole, Yucatan Peninsula
PRESENT-DAY FOREST TYPE	*Quercus-Picea-Pinus-Juniperus*	*Pinus-Alnus-Quercus-Cuppresus-Juniperus*	*Pinus-Alnus-Quercus-Abies*	*Pinus-Quercus*	*Quercus-Pinus*			Mixed Pine-Oak Forest, Pine Forest, Oak Forest, Fir Forest			
GEOGRAPHICAL REFERENCE	29° N, 108° W	19° 30' N, 99° 00' W	19° 04' N, 99° 19' W		19° 51' N, 101° 40' W			19° 10'N, 99° 30'W	19° 11'-19° 16 N, 98° 34 - 98° 42 'W	20° 38' N, 87° 37' W	
PALAEO-METHOD	Pollen-Diatom	Pollen	Pollen	Geochemical sedimentology	Diatoms pollen	Diatoms	Historical records	Pollen, charcoal, sedimentology	Geomorphology and stratigraphy	Isotopes	Isotopes
DATES C^{14} yr BP											
250-0											
500-251											
1000-501											
1500-1001											
2000-1501											
2500-2001											
3000-2501											
3500-3001											
4000-3501											
4500-4001											
REFERENCE	(Metcalfe, 2002)	(Lozano-Garcia, 1993;Gonzalez-Quintero, 1986)	(Almeida-Lenero, 2005)	(Metcalfe, 2007)	(Metcalfe, 1995; Arnauld, 1997)	(Metcalfe, 1994)	(Metcalfe, 1995; O'Hara, 1997)	(Ludlow-Wiechers, 2005)	(Vazquez-Selem, 1997)	(Curtis, 1996)	(Hodell, 2001; Hodell, 2005a; Hodell, 2005b)

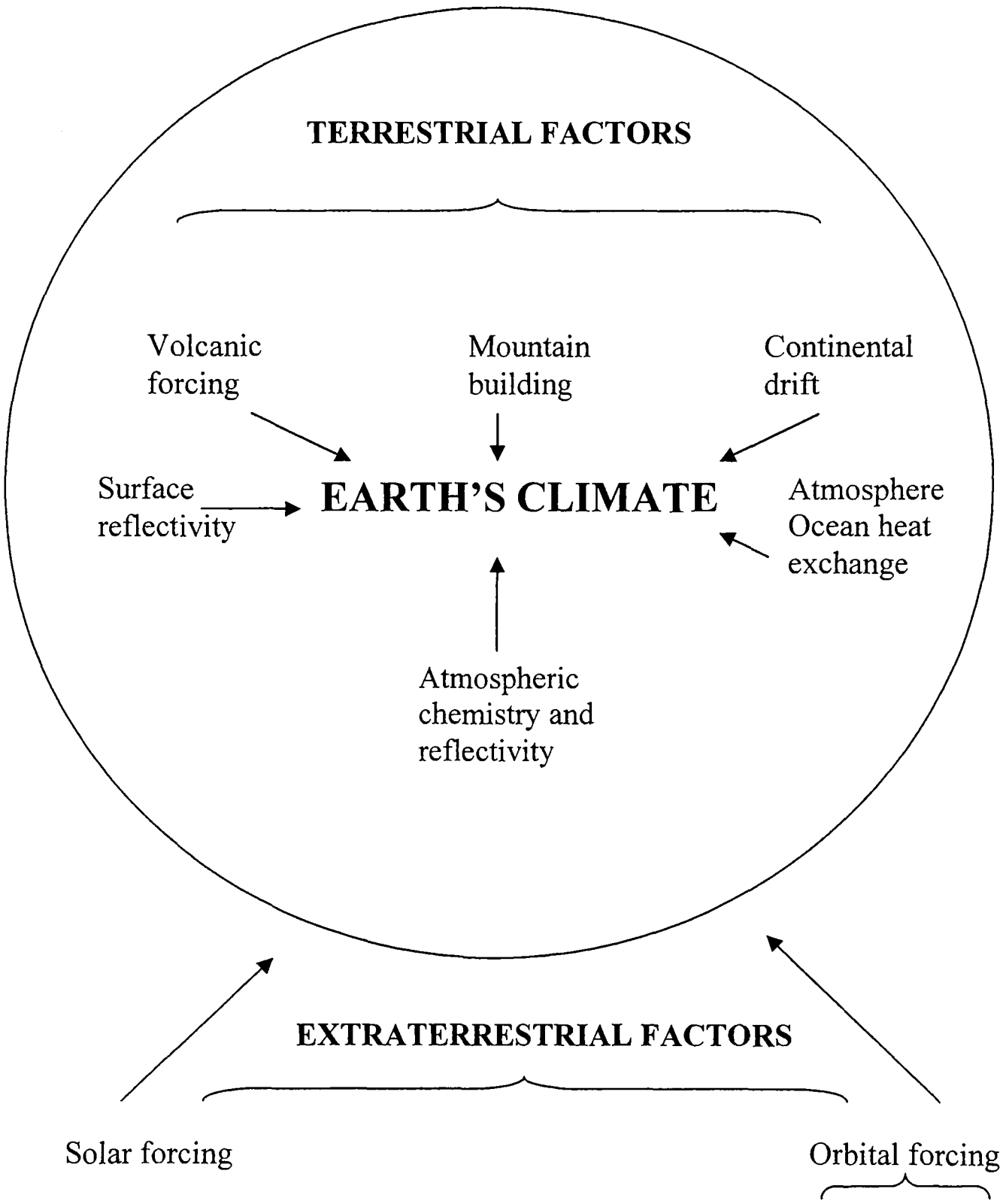
2.5. Climate change in Mexico

The endeavour of reconstructing climate change in Mexico is complicated due to the combined influence of natural and human effects on the environment; human impact in Mexico has prevailed for at least 5000 years (Denevan, 1992). Different factors have influenced climate change in Mexico during the Holocene. These include extraterrestrial (orbital and solar forces) as well as terrestrial factors (atmosphere, land and ocean forces) (Figure 2.1) acting at various scales; e.g. orbital forcing at millennial, solar forcing at centurial and volcanic forcing at decadal scales (Bradley, 2005). Some of the most important factors for climate change in Mexico are discussed as follow:

2.5.1. Atmospheric and ocean circulation

One of the most significant characteristics controlling climate in Mexico is that related with atmospheric and ocean circulation including phenomena such as the Trade winds, the subtropical high-pressure belt and the Westerlies (Metcalfe et al., 2000)(Figure 2.2).
The Intertropical Convergence Zone (ITCZ) is the section surrounding the Earth, near the equator, where the trade winds of the Northern and Southern Hemispheres converge. Both the sun and hot water of the equator warm the air in the ITCZ, resulting in rising up of humid air. The air gets cool as it elevates, liberating the moisture in the form of uninterrupted

Fig. 2.1. Causes of climate change. Modified from Michael Pidwing, 1999-2006, University of British Columbia, www.physicalgeography.net/fundamentals/7y.html.



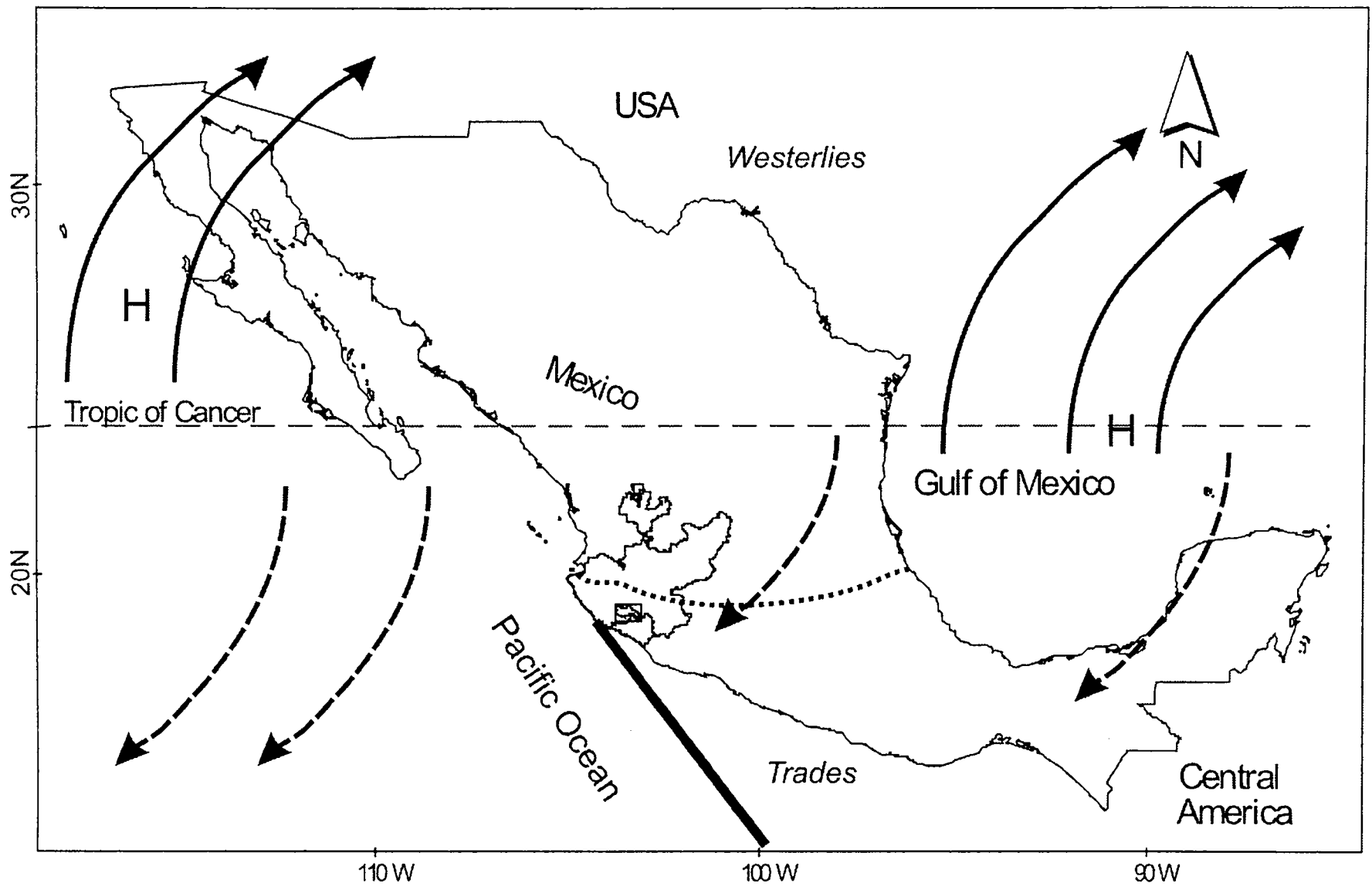


Fig. 2.2. Atmospheric circulation in Mexico. Westerlies ——→ trades - - - - - - - - - →
Trans-Mexican-Volcanic-Belt ..... H= Subtropical High Pressure Belt
Intertropical Convergence Zone during summer ▬▬▬

.

thunderstorms. Variability in the position of the ITCZ radically influences rainfall in many equatorial countries, resulting in the wet and dry seasons of the tropics. It moves to the southern hemisphere during winter and to the northern hemisphere during summer (Fig. 2.2). Longer-term changes in the ITCZ results in severe droughts or flooding, particularly the southward shift is associated to climate changes in Central and South America (Haug et al., 2000; Haug et al., 2001).

For Mexico reduction in precipitation during dry intervals have been linked to the southward displacement of the ITCZ (Berrio et al., 2006; Hodell et al., 2005a; Hodell et al., 2005b; Metcalfe et al., 2000). The ultimate cause of the ITCZ move has been explained by solar forcing during the Holocene (Hodell et al., 2001).

The subtropical high-pressure belt (subtropical ridge) is one of the two bands of high atmospheric pressure near 30°N and 30°S latitudes (Figure 2.2). Latitudinal movements of that belt explain much of within season monsoon variability as well as to year-to-year and decadal scale variability (Carleton et al., 1990). If the ridge shifts to the north it brings wetter summers (wet years) but if it moves to the south it corresponds with a reduction in summer rainfall (dry years). There is an evident dissimilarity between eastern and western areas in Mexico; therefore wet conditions in the west are connected with drier circumstances in the east (Higgings et al., 1998). This particularity brings into the scenario a link with another phenomenon, the El *Niño*-Southern Oscillation (ENSO).

ENSO is an occasional development of warm surface waters in the Pacific Ocean along the coast of equatorial South America. In a normal year, winds over the Pacific move from east to west. The warm and moist air on the eastern side of the Pacific leads to drastically increased rates of rainfall and flooding. In contrast, the high pressure and cooler waters around reduce the formation of storm clouds, leading to droughts and sometimes, to extensive fires as the vegetation dries up (Roman-Cuesta et al., 2003). ENSO is recognized as a noteworthy feature in Neotropical climate systems from about 5000 yr BP (Sandweiss et al., 1996) to present times. ENSO periodicity usually goes from 3 to 7 years but there are also mega ENSO-events

occurring from centennial to millennial scales although a regular long-term oscillation has not been established yet (Bush, 2005)

2.5.2. Solar forcing

Different evidences regarding to irradiance changes are adding important information linked to climate change. (Crowley, 2000) for instance concluded that increase in solar irradiance over the past 1000 years explains a significant amount of the pragmatic 20th century warming. Others (Lean, 2000; Lean et al., 1992; Vaquero et al., 2002) have observed that Total Solar Irradiance (TSI) had a minimum around A.D. 1645-1715 (The "Maunder Minimum"), epoch that coincides with the coldest time of the Little Ice Age (LIA).

(Lean et al., 1995) estimated that changes in TSI of ~0.24% are connected with alterations in mean annual surface temperature ~0.2-0.4°C in the northern hemisphere, while (Beer et al., 1996) using the cosmogenic isotopes ^{10}Be and ^{14}C, found that solar activity was high from A.D. 1100 to 1250 decreasing to a minimum value in the 15th century.

In Mexico, particularly in the Mayan region, the driest period reported between 800-1000 A.D. (Hodell et al., 2001) have demonstrated correlations with solar forces revealing a 208-year periodic pattern of drought analogous to the 206-year phase found in records of cosmogenic nuclide production (^{10}Be and ^{14}C).

2.5.3. Volcanic forcing

Volcanic eruptions have been reported as causes for short term cooling as a result of volcanic aerosol. This is influencing the decrease in energy reception at the earth surface as well as changes in the atmospheric circulation (Bradley, 2005). Recent evidences have also detected that cooling during the late stage of the "Maunder Minimum" corresponds with dynamic volcanism in Western Europe (Shindell et al., 2002).

For Mexico the most usual reference of volcanic force affecting climate change is that related with the eruption of *El Chichón* volcano in 1982. Evidences reported that stratospheric temperatures dropped staying cooler than average for 7 years after the eruption (Angell and Korshover, 1983). The present study is located in the west of the Trans-Mexican Volcanic Belt, where most of the volcanoes in Mexico exist. Presently one of the active volcanoes near to the study area is the *Colima Volcano*. This was originated 2500 years ago with the most important eruptions during the last 500 years included 1585, 1606, 1622, 1690, 1818, 1869, 1890, 1903 and 1913 A.D. However no evidences of those eruptions have been linked to climate change.

In general the last 4500 yrs have characterized important changes in the climatic conditions of Mexico (Table 2.3). In the Northern region, modern desert conditions started from about 4000 yr BP (Metcalfe et al., 2000). For Central Mexico humid conditions prevailed from 4000 to around 2500 yr BP (Almeida-Lenero et al., 2005; Gonzalez-Quintero, 1986; Lozano-Garcia et al., 1993; Metcalfe et al., 2000) while dry conditions occurred from 2500 to 1900 yr BP

(O'Hara, 1993; O'Hara et al., 1993). The most relevant dry period took place around 1000 yr BP (Arnauld et al., 1997; Metcalfe and Hales, 1994; Metcalfe, 1995; O'Hara, 1993).

In the Yucatan Peninsula wet conditions prevailed until 3000 yr BP and the driest period between 1500 and 900 yr BP. The dry period coincides with the collapse of the Mayans (Beach et al., 2006; Curtis et al., 1996; Hodell et al., 2005a; Hodell et al., 2001; Hodell et al., 2005b; Hodell et al., 1995)(Table 2.3).

2.6. Human disturbance in Mexico

The presence of humans within the montane-forested zones in Mexico is recorded from at least 11,000 years ago, but very little is known about the anthropogenic influence on vegetation. The record becomes complex due to incidence of dry and wet intervals on vegetation during the Holocene. This situation becomes more difficult when it is necessary to separate the contributions of climate and human disturbance (Perry et al., 2000).

Mexican history can be divided in two epochs, the pre-Hispanic era before the Spanish conquest of Mexico (before 1519 A.D.) and the post-Hispanic era (after 1521 A.D.), after the Spanish conquest. Different pre-Hispanic civilizations developed before 1519 A.D. concentrated mainly in Central and South Mexico (Table 2.3, Fig. 1.5).

Table 2.3. Chronology for the most important prehispanic civilizations in Mexico.

Date		Period	Prehispanic civilizations							
			Mayans	Olmecs	Zapotecs	Aztecs	Mixtecs	Purepechs	Toltecs	Chichimec
AD	1519-1521	Colonial								
	1200-1521	Late Postclassic								
	1200-1400	Middle Postclassic								
	900-1200	Early Postclassic								
	600-900	Late Classic								
	250-600	Early Classic								
BC	400-250	Late Preclassic								
	1200-400	Middle Preclassic								
	1800-1200	Early Preclassic								

Intricate and stratified societies expanded since 3000 cal yr BP supported on maize cultivation (Roberts, 2002) giving rise to the appearance of agriculture in Mexico. The Holocene has been an era of increasing environmental changes in Mexico. Those changes have been portrayed as a consequence of agriculture expansion (Sluyter, 1997). By 1492 A.D. when Columbus discovered the Americas, the landscape was far from pristine. According to (Denevan, 1992), Mexico was a well-populated territory with 17.2 million people.

2.6.1. Clearing the land

By 1492 A.D. pre-Hispanic indigenous civilizations mainly in Central Mexico and the Yucatan Peninsula had already altered the forest composition and structure by burning, clearing and foraging generating a mosaic of successional stages (Williams, 2003).

Giving the previously mentioned high density in prehistoric population, forest disturbance by that time was already high and the Europeans found an intensely managed landscape. With the human decline in the first half of the 18th century A.D. such forested landscape appeared more pristine than that of 1492 A.D. (Denevan, 1992). Judging those evidences (Williams, 2003) remarks that expressions such as *pre and post settlement* in the landscape of Mexico are ineffective and concepts of *natural* and *equilibrium* do not exist since the Ice Age.

The palaeoecological evidence through fossil pollen of cultural taxa, provide good indicators of human disturbance in the Holocene of Mexico. Families such as Amaranthaceae, Asteraceae, Chenopodiaceae, Poaceae and *Zea mays* are among the more reported grains in studies related to forest clearance and humans over the last 5000 years (Arnauld et al., 1997; Conserva and Byrne, 2002; Lozano-Garcia et al., 2005; Ludlow-Wiechers et al., 2005; O'Hara, 1993; Watts and Bradbury, 1982)(Table 2.1).

2.6.2. Agricultural lands

Maize is one of the most important crops in the world for which domestication origins date back to 5,000 to 10,000 years in Mexico (Farnsworth et al., 1985; Sluyter and Dominguez, 2006) (Table 2.1). Archaeologists undertaking research in the southern basin of Mexico proposed that sedentary pre-agricultural (hunter-gatherers) civilizations developed between 6000 to 3500 years B.C. (Fritz, 1995).

Civilizations engaged in plant domestication and a consequent escalation took place between 3500 to 2000 years B.C. (Fritz, 1995). Farming villagers reliant in cultigens dictated the scenario of agriculture dominance by 1500 B.C. (McClung de Tapia, 1992). Most of the pre-Hispanic indigenous civilizations (Fig. 1.5) in Mexico relying on agriculture for daily subsistence were immersed in the transformation of land into fallow or open grasslands through clearing and burning (slash-and-burn)(Denevan, 1992; Lentz, 2000; Roberts, 2002; Williams, 2003). Such endeavour brought reciprocity between land-use and environmental change that have been revealed through geochemical fluxes tied to soil erosion and climate change. Palaeoecological studies have used multi-proxy methods to discern human disturbances related to agricultural activities e.g. (O'Hara, 1993; O'Hara et al., 1993) used geochemical analysis or (Ludlow-Wiechers et al., 2005) used sedimentology (Table 2.2). Other studies have provided chronologies for maize (Almeida-Lenero et al., 2005; Goman and Byrne, 1998; Pope et al., 2001; Sluyter and Dominguez, 2006; Wahl et al., 2006; Watts and Bradbury, 1982) and other important cultigens (Pope et al., 2001) as well as centres of domestication (Lentz, 2000).

Dependence on agricultural activities was necessarily attached to the supply of water, either as a temporal resource via rainfall (terraces, floodplain and sloped piedmont cultivation) or by humidity control (chinampas, drained fields, permanent and floodwater irrigation) driving to the initiation of different agricultural systems (McClung de Tapia, 2000). Water resources were unavoidably linked to climate changes causing hazards such as the droughts reported for the 11th century (Florescano, 1980) or the recurrent drought patterns (between 1300 and 1100 yr BP) every 206 years in the Yucatan Peninsula which have been reported as the main cause of the Mayan state collapse (Hodell et al., 2005a; Hodell et al., 2001; Hodell et al., 2005b; Hodell et al., 1995).

2.6.3. Burning the land

Mexico has a long and interesting history of forest fires. The conditions exist for natural fires, though human settlement has, for millennia, dominated the geography and dynamics of burning. Historically forest fires have been an important tool for agriculture and to assist hunting and cattle ranching on grasslands. Such practices have contributed to fire occurrences even to the present day. With human colonization, fire risk, fire danger, and fire frequency all gradually increased through the Holocene, altering both fire regimes and vegetation (Rodriguez Trejo, 1998).

The frequent superficial fires in several regions of Mexico have helped to maintain forests. The most widespread forest types in Mexico, Pine and Pine-Oak forest are greatly related to fire. Fire is vital to the regeneration of some *Pinus* species and this taxon has developed many adaptations to cope with fires including thick bark, serotiny, rapid growth and sprouting (Agee, 2000).

Pines are considered as aggressive post-disturbance colonizers (Richardson and Rundel, 1998) growing faster than the hardwood species with which they are associated. They are able to grow on soils left by agriculture, cattle ranching or logging interventions where burning is employed. As pines become dominant in the stand their canopies become closed preventing light reaching the forest floor. Pine seedlings are shade-intolerant so their regeneration is difficult under their own parent trees. Consequently in the absence of fires other species such as cloud forest species, which behave as shade-tolerant elements, grow under pine forests eventually replacing pines. Burning histories during the Holocene have been inferred through charcoal analysis in southern (Goman and Byrne, 1998), eastern (Conserva and Byrne, 2002) and central Mexico (Lozano-Garcia et al., 2005) mainly in temperate vegetation such as cloud forest, pine forest, pine-oak forest, oak forest and fir forest. All indicate an increase of forest fires over the last 1000 years.

In summary, the present literature review has provided the necessary information on the variety of the physical environs in Mexico including the vast physiographical heterogeneity that derived in a mosaic of different climate and vegetation types over millennia. What is also clear from this review is that forests in Mexico are very diverse in the spatial as well as in the temporal scale creating different patterns of response. Concerning the scale of this study (the last 4200 years), the main drivers of the temporal forest dynamics in Mexico are climate and human disturbances. These two factors have impacted vegetation causing important changes in its composition and structure. The knowledge acquired during the literate review represents the basis for subsequent discussions on the results obtained in this study.

3. PAPER 1

Can modern pollen reflect the diversity and structural complexity of high-altitude vegetation in West-Central Mexico?

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Abstract

The forests of the Sierra de Manantlan Biosphere Reserve in West central, Mexico are internationally recognized as an important biodiverse and economic resource.

This study analyses the modern pollen signature of three different high-altitude (1820-2570 m asl) forest types in this reserve; pine forest, cloud forest and a transitional stage between these two. The aims of this study were to investigate the reliability of pollen records from this region in reconstructing past vegetation dynamics. A detailed analysis of vertical and horizontal structure of the forest was undertaken including density, frequency, basal area, stand age and size classes. Pollen abundances were estimated for arboreal and non-arboreal

taxa by forest type. Ordination (DCA) for pollen was undertaken to display variation in taxa composition among the three forest types while a cross-tabulation contingency table, together with a Pearson chi-squared test of independence was used to reveal the modern pollen-forest assemblage relationship.

Results indicated that each forest type has a distinctive pollen signature from a less diverse and simple structural pine forest to a highly diverse and complex cloud forest. The best indicator taxa for cloud forest are epiphytes (Adiantaceae and Aspleniaceae) whereas for Pine and the transitional forest the canopy trees *Pinus, Quercus, Carpinus, Alnus* and *Magnolia* were the best indicators. Results also suggest that structural variables influence pollen abundance and that in forests dominated by animal dispersion there is a strong directional signal in the pollen distribution, probably indicating the behavioural characteristics of the pollen dispersers.

Keywords: pollen; cloud forest; forest structure; ordination; pine forest; transitional forest.

3.1. Introduction

The mountainous regions of the Sierra de Manantlan, West-central Mexico contain a number of important ecosystems in terms of biodiversity and climate regulation. These ecosystems include forest types such as pine forest, pine-oak forest and oak forest with mainly temperate taxa, and also cloud forest, which contains mostly tropical taxa. All those forests are dominated by two genera, *Pinus* and *Quercus*, of which Mexico has the largest number of species in the world (Lanner, 1998; Nixon, 1993) while cloud forest has the highest diversity

per unit area in Mexico when considering terrestrial ecosystems. Cloud forest is also extremely fragmented (Luna Vega et al., 1999) covering less than 1% of the country.

Ecological studies have indicated that forests in Manantlan encompass high species richness with 2,700 species of vascular plants and 540 of vertebrates, high number of endemic species, and significant economic forestry potential (INE-SEMARNAT, 1995).

Very little is known, however, about their long-term dynamics and temporal variability in response to climate change and past anthropogenic activity. Before such records can be constructed, however, it is imperative that an understanding of the relationship between the pollen signature and the surrounding vegetation (Bunting et al., 2004) is developed. This paper presents the results of a study to examine the relationship between pollen and its representation of the three forest types in the Sierra de Manantlan.

Traditionally in pollen-vegetation studies there is the tendency to rely upon a simplified floristic list or presence/absence data in studies of vegetation; however, recent work (Gosling et al., 2005; Jackson and Kearsley, 1998; Vincens et al., 2000) has indicated that pollen abundance is strongly influenced by structural variables in the forest.

Tree maturity can be measured through different structural variables (density, basal area, diametric class distribution, height and number of strata) (Davies et al., 1998; Fule et al., 2005; King et al., 2006; Poorter et al., 2005). These are therefore good attributes to be considered in vegetation surveys to assess the relationship between modern pollen and the forest assemblage. The structure is also influenced by stand type and, in this respect, species composition and the forest assemblage are determinant in the pollen productivity. Dispersal mechanisms for seeds are also influenced by structural characteristics of the forest and therefore when dealing with a variety of forest types interrelated at close distances in highly

diverse regions there may be different pollen dispersal mechanisms. pine forest, for instance, is dominated by anemophilous taxa while cloud forest contains species relying on animals for their dispersion creating compositional dissimilarities in the canopy.

This research therefore aimed to address the following questions: Is it possible to distinguish between different forest types (pine forest, cloud forest and transitional forest) in the Sierra de Manantlan by modern pollen signature? Are there particular taxa that are good indicators for the three forest types? Is pollen abundance related to forest structure?

3.2. Study Area

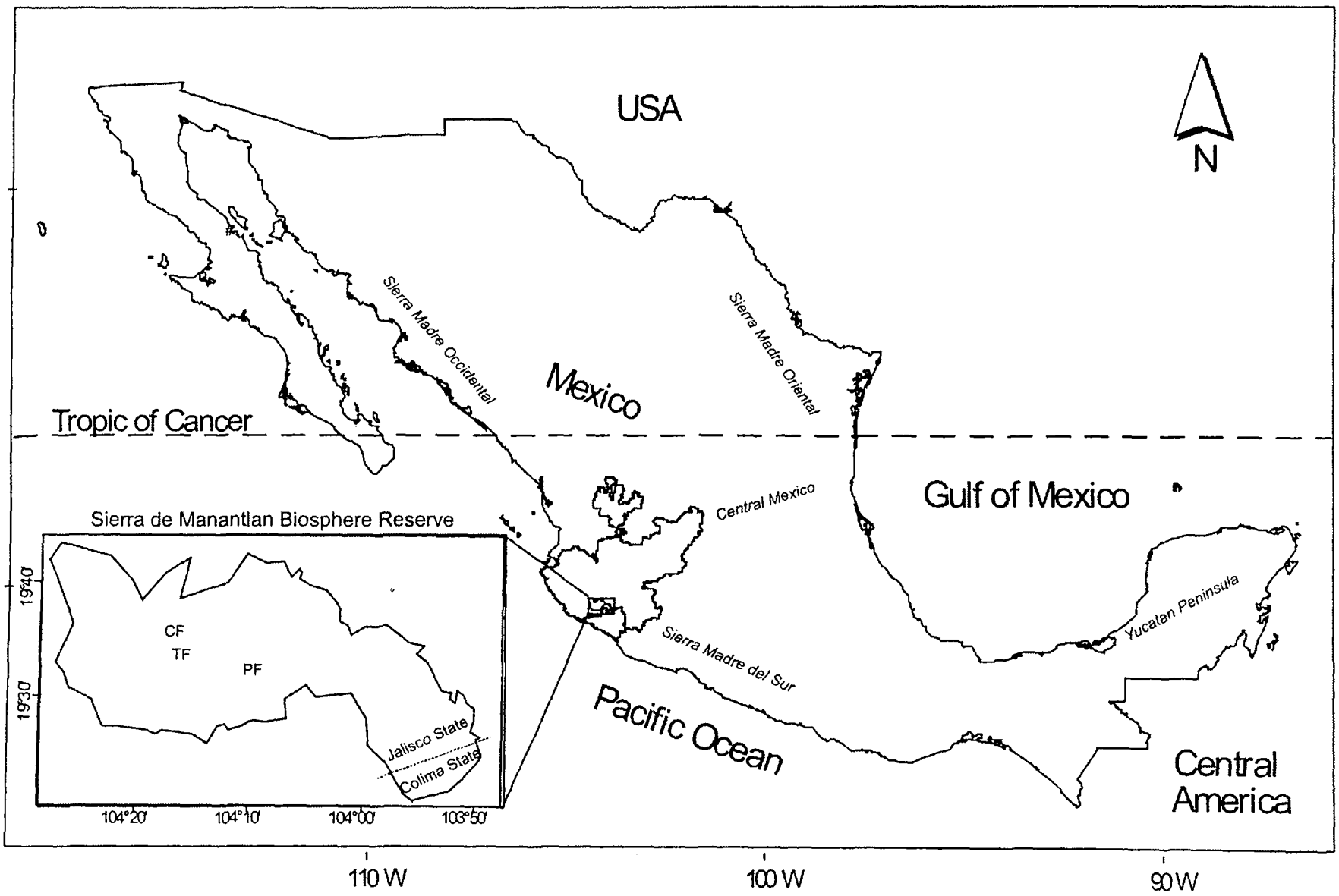
The three forests under study were located in the Sierra de Manantlan, Biosphere Reserve (SMBR) in the south-east of Jalisco and in the north-east of Colima in West-Central Mexico (Fig. 3.1) between 19°26'-19°42'N and 103°51'-104°27'W. Physiography of this region is heterogeneous and irregular. Soils comprise Alfisols with an extension of 892 ha (73.4%), Ultisols with 204.3 ha (16.8%), and Inceptisols with 119.7 ha (9.8%) (Martinez Rivera et al., 1993). Climate, according to Köppen and modified by (García, 1987) is temperate subhumid with an average temperature of 18°C and precipitation between 1500 and 1800 mm/yr. The Manantlan region emerged in the late Cretaceous as part of the Sierra Madre del Sur as a result of subduction volcanism in Central Mexico (Rossotti et al., 2002).

The main forest types of the reserve include oak forest, pine forest, pine-oak forest, pine-fir forest, fir forest, cloud forest, tropical dry forest, tropical semi deciduous forest and riparian forest. For this study the vegetation-pollen dynamics were examined for the following forest types:

3.2.1. Pine forest

This forest is a well-defined physiognomic unit dominated by *Pinus* species (Rzedowskii, 1981). The sampling site for this forest was located at 2510-2570 m asl. The plant association in this unit comprises trees such as *Pinus pseudostrobus, Quercus laurina* and *Alnus jorullensis* while in the herbaceous layer there are elements from families such as Asteraceae, Poaceae, Fabaceae, Lamiaceae, Solanaceae and Schropulariaceae (SEMARNAP, 2000).

Figure 3.1. Map showing the three study sites, CF= cloud forest, PF= pine forest and TF= transitional forest.



3.2.2 Transitional forest

This forest is an association of *Pinus-Carpinus-Quercus* representing a transitional stage between a pine and cloud forest. It was located at 1880-2100 m asl comprising *Pinus douglasiana* as the clear canopy dominant followed by *Carpinus tropicalis* and by three oak species, *Q. candicans, Q. praineana* and *Q. scytophylla*. Other trees include *Alnus jorullensis, Clethra vicentina, Cornus disciflora Prunus cortapico, Tilia americana var. mexicana* and *Buddleja sp*. The herbaceous component contains *Senecio salignus, Stevia sp., Euphorbia schlechtandalii, Festuca breviglumis, Melinis minutiflora, Muhlenbergia dumosa, Zea sp., Castilleja arvensis* and *Solanum sp.*

3.2.3 Cloud forest

This is a highly heterogeneous formation in terms of physiognomy, species association and biodiversity, with both temperate and tropical elements. The cloud forest site was located between 1820-1890 m asl and includes *Pinus douglasiana, Quercus candicans, Q. salicifolia, Q. vicentensis, Q. xalapensis, Ilex brandegeana, Tilia americana* var. *mexicana, Clethra sp., Juglans major* var. *glabrata, Cinnamomum pachypodum, Persea hintonii, Inga eriocarpa, Magnolia iltisiana, Meliosma dentata, Cornus disciflora, Zinowiewia concinna, Dendropanax arboreus, Carpinus tropicalis, Ostrya virginiana, Hedyosmum mexicanum, Fraxinus uhdei, Prunus cortapico,* etc. Non-arboreal families consist of Asteraceae, Solanaceae, Celastraceae, Araceae, Poaceae, Adiantaceae, Aspleniaceae and Polypodiaceae among others.

3.3. Methods

3.3.1 Forest Inventory and Structural Analysis

Trees and shrubs were inventoried in circular plots 100m² (5.7 m radius) in the three forest types recording species name, diameter at breast height (DBH), height, crown width and crown position (Olvera Vargas et al., 1996). The sampling procedure was undertaken in 300 m transects along the four cardinal points with a 100m distance from each other. A tree core was extruded from pine individuals in each 100m² plot using a Presler increment borer to determine stand age. Two increment cores were taken from the height of 1.3 m above the ground level (Pazdrowski and Szaban, 2005) in two directions. Herb species were identified and counted in plots of 1m² (located at the centre of each 100m² plot). Site variables such as altitude and aspect were also registered.

The following stand variables were considered as follows:

- Abundance was estimated according to density (Number of trees, shrubs or herbs/ha) and frequency (Kent and Coker, 1998). Age, height and diameter by species were also calculated by their main statistical parameters.
- Basal Area, the cross-sectional area of a tree at breast height (Philip, 2002), was estimated by each species in $m^2\ ha^{-1}$ to determine dominance.
- Crown width was registered as the projection of the crown width on the forest floor (expressed in meters) on the direction of the slope.

- Stand age was estimated counting the number of tree rings observed in the cores extracted from the trees.
- Crown position was recorded according to a modified (Olvera Vargas et al., 1996) Kraft classification (Kraft, 1884) in the following categories.

Dominant: They are outstanding trees in the canopy with vigorous and well-shaped crowns; diameters and heights are the biggest in the stand.

Codominant: Trees whose crowns are smaller and narrower than the dominant ones, generally below the upper stratum.

Intermediate: Trees with atrophied crowns, sometimes with no competition above them. They are shorter than dominants and codominants and commonly located in the middle stratum.

Suppressed: Trees with crowns entirely below the general level of dominants and codominants. Their diameters are below the stand mean diameter, with smaller and weaken crowns.

To determine the contribution of each taxa to the dominance of the stand we derived importance value indexes (IVI)(Moore and Chapman, 1986) for the arboreal component. This index is obtained by the sum of relative density (number of trees-shrubs per taxa/total number of trees-shrubs all taxa), relative frequency (number of samples in which taxa appear/total number of samples) and relative basal area (total basal area per taxa/total basal area all taxa). For non-arboreal taxa only relative values for density and frequency were estimated.

3.3.2 Pollen Sampling and Analysis

Modern pollen samples were taken at each plot surveyed for vegetation, in average 12 pollen samples per forest type. The focus was in the collection of moss samples from the top 1-2 cm of the forest floor but if moss was absent, a handful of litter was sampled instead (Hjelle, 1999).

Pollen was isolated from the moss or the litter sample using a standard acetolysis method (Bennett and Willis, 2001; Faegri and Iversen, 1989; Moore et al., 1991). *Lycopodium* spore tablets were added to the pollen samples acting as markers to estimate concentrations (pollen grains cm^{-3}).

Pollen identification was supported by exhaustive pollen and spore reference collection of 300 specimens (trees, shrubs and herbs) elaborated with regional material gathered during the vegetation survey in the study area. The reference collection held in the Long-term Ecology Laboratory, Oxford University Centre for the Environment was also consulted. At least 400 pollen grains were counted for each sample at 400x magnification to ensure statistical significance (Maher, 1972). Fungi spores, concealed, broken, degraded, crumpled and unknown pollen and spores were counted but excluded from the pollen sum. Pollen counts were expressed as percentage of the total pollen and spore sum (Lowe and Walker, 1997), herein considered as pollen abundance.

Pollen abundance was determined in each aspect (North, West, South and East) by forest type (pine, transitional and cloud forest) to evaluate two important issues; 1) if wind direction evaluated through aspect is related to pollen abundance, 2) if pollen abundance varies among vegetation types.

3.3.3 Statistical Analyses

Detrended Correspondence Analysis (DCA) was undertaken for pollen using presence-absence data in CANOCO v. 4.02 (Ter Braak and SMilauer, 1988). DCA is an ordination technique which recognize and visualize the major directions of variance characterizing tendencies in a smaller number of dimensions (Bennett and Hicks, 2005).

To ascertain whether there is a dependable pattern of pollen abundance with respect to vegetation presence a cross-tabulation contingency table was elaborated by forest type, together with a Pearson chi-squared test of independence to find a relationship between two variables (Sokal and Rohlf, 1981). To assess if vegetation abundance is dependent on aspect, the same Pearson chi-squared was computed considering the four aspect categories in columns and the presence-absence of the different species with respect to vegetation abundances in rows; the same procedure was repeated for pollen abundances. In both cases the statistics was undertaken by forest type. These analyses tested the null hypothesis that vegetation and pollen follow a random course and are independent of aspect.

In order to examine whether there is a correlation between the structural variables (age, density and basal area) of the forest and pollen abundance, Pearson correlation coefficients were estimated for *Pinus* by forest types. *Pinus* was chosen to test this relationship because this is a species known to produce annual rings thereby allowing an accurate age determination. Statistical estimations were developed in (SPSS, 2005).

3.4. Results

In total thirty-six sites were surveyed in the forest inventory and samples were analysed for their surface pollen signature from the same sites. The total area covered by forest type during the forest inventory comprised 28 hectares.

3.4.1 Pollen

The highest average pollen concentration is in the cloud forest surface sample. In the cloud forest there is also a strong signal according to aspect (Table 3.1) with the highest pollen concentration in south expositions. In contrast the lowest concentration of pollen is measured for the transitional forest (Fig. 3.2) and there is no significant association with aspect. Pine forest has intermediate values in pollen concentration but again no significant association with aspect.

Table 3.1 Pearson chi-square goodness of fit for pollen frequencies by aspect and forest type.

Forest type	Pollen	Aspect				*p*
		North	*South*	*West*	*East*	
Pine forest	*Absence*	32	28	29	31	0.77
	Presence	11	15	14	12	
Transitional	Absence	25	23	25	29	0.60
forest	Presence	18	20	18	14	
Cloud forest	Absence	14	24	27	19	0.02
	Presence	29	19	16	24	

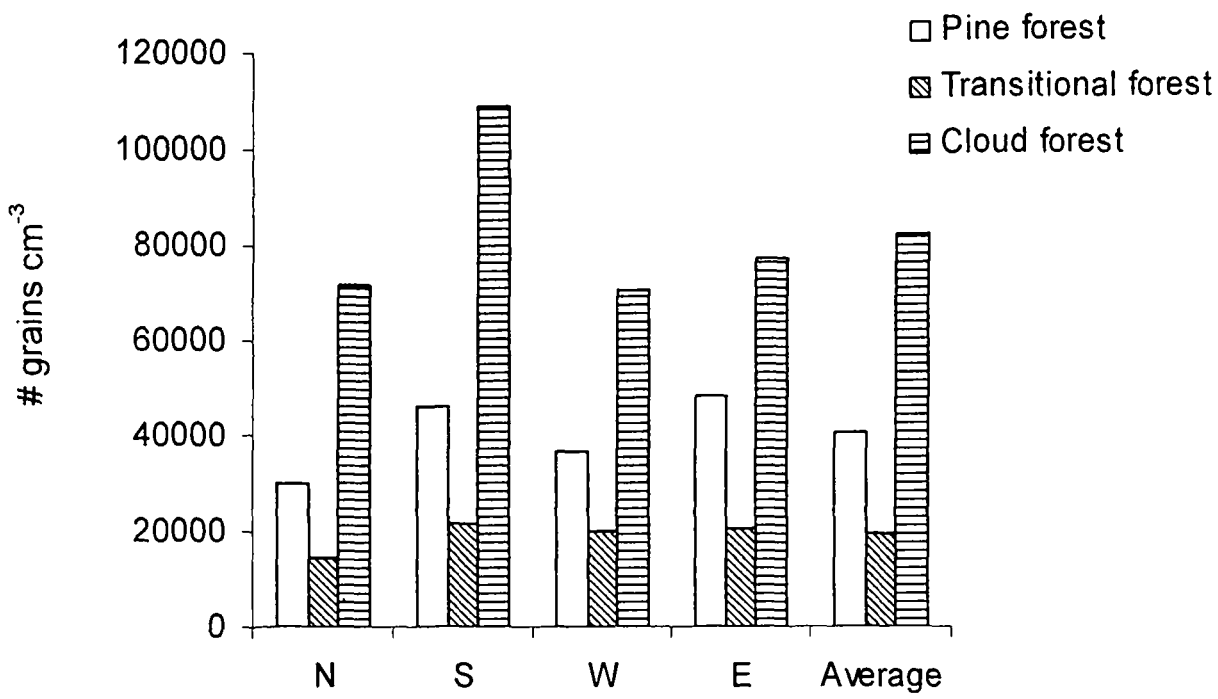


Figure 3.2. Pollen concentration according to aspect and average values by forest type.

In the pine and the transitional forest *Pinus* is the most abundant arboreal taxa followed by *Quercus*. Cloud forest performs an opposite pattern with *Quercus* dominating the pollen sum. As secondary components, *Alnus* and *Fuchsia* are abundant in pine forest, *Carpinus* and *Clethra* in the transitional forest and Melastomataceae, *Abies* and *Rubus* in cloud forest (Fig. 3.3a).

Taxa specific to pine forest include *Xylosma* and Umbelliferae. Those specific to transitional forest are *Acacia, Rondeletia, Trophis* and the Lauraceae family. For cloud forest they are *Parathesis, Fraxinus, Sebastiana, Arbutus, Zinowiewia, Pteridium* and Liliaceae family.

For Non-arboreal pollen, Asteraceae and Poaceae represent the families with the highest pollen concentration in the three forest types. Poaceae is more abundant in pine forest whereas taxa including *Zea, Salvia* and *Crotalaria* are more copious in cloud forest (Fig. 3.3b). The cloud forest pollen signature contains more abundant epiphytes with the exception of Hymenophyllaceae, which dominates in the transitional forest signature (Fig. 3.3c). The rest

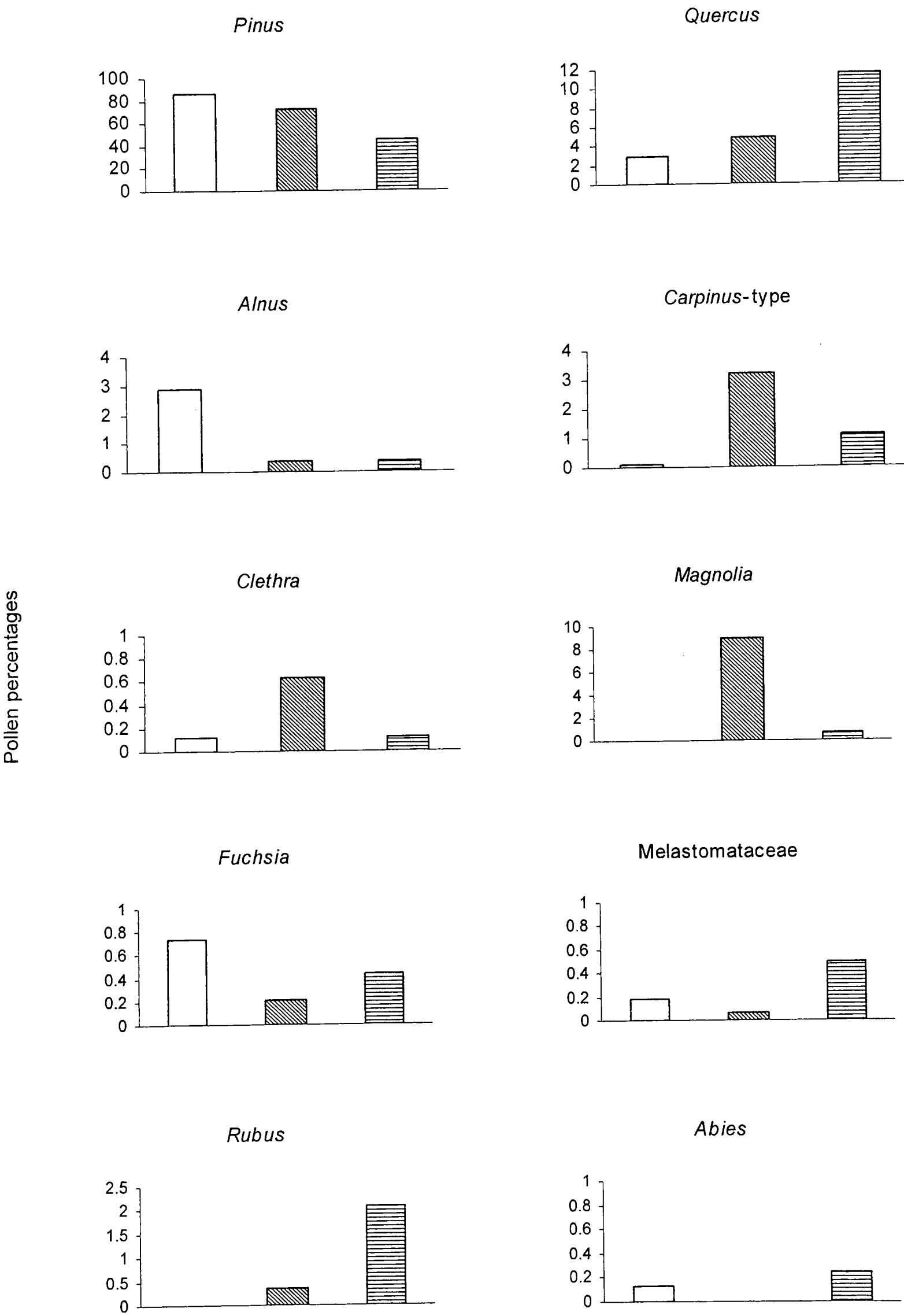
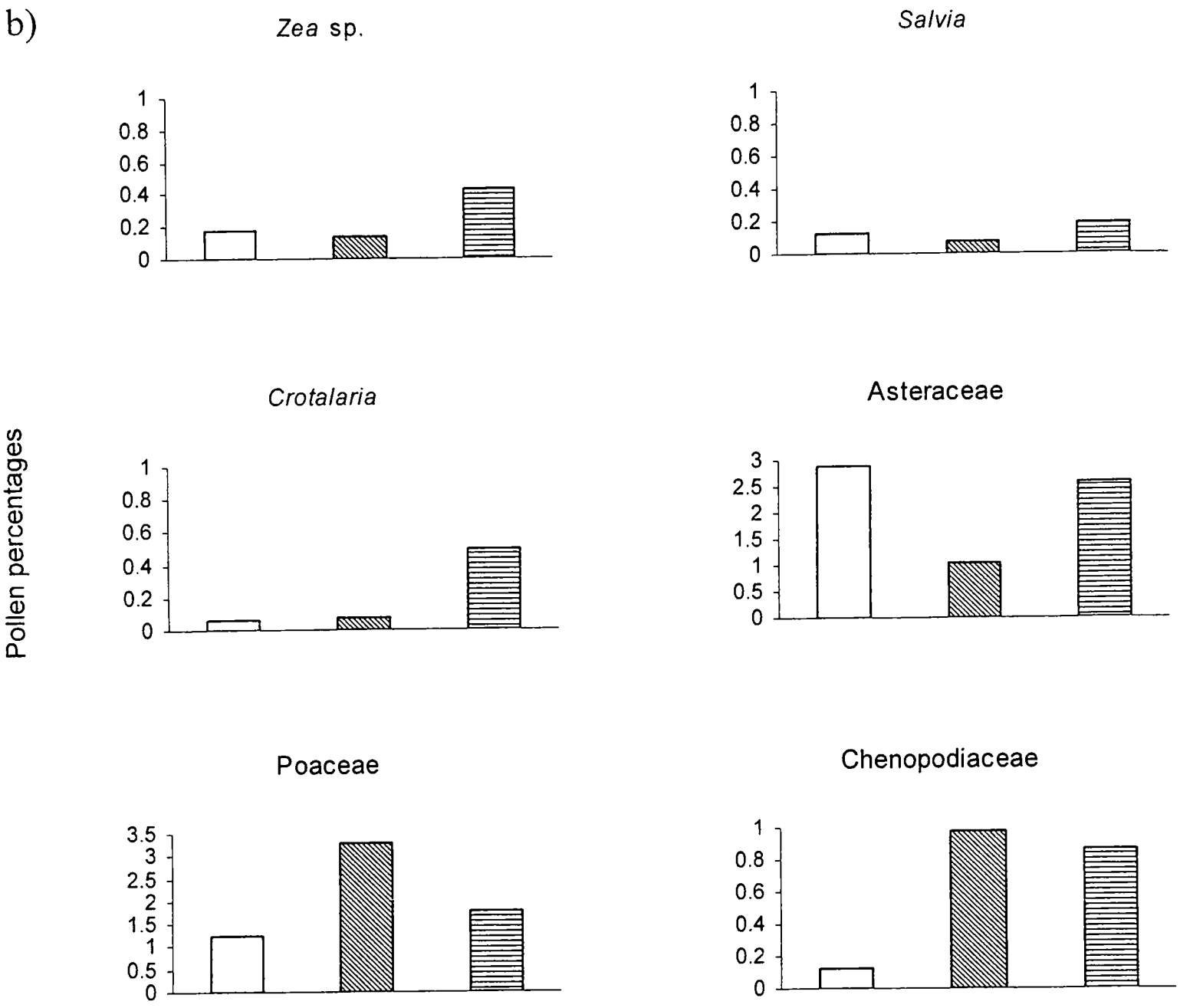


Figure 3.3. Pollen taxa common to three high altitude vegetation types in West-Central Mexico a) trees/shrubs, b) herbs, c) epiphytes: pine forest is in white rectangles, transitional forest in diagonal lines and cloud forest in horizontal lines.

b)



c)

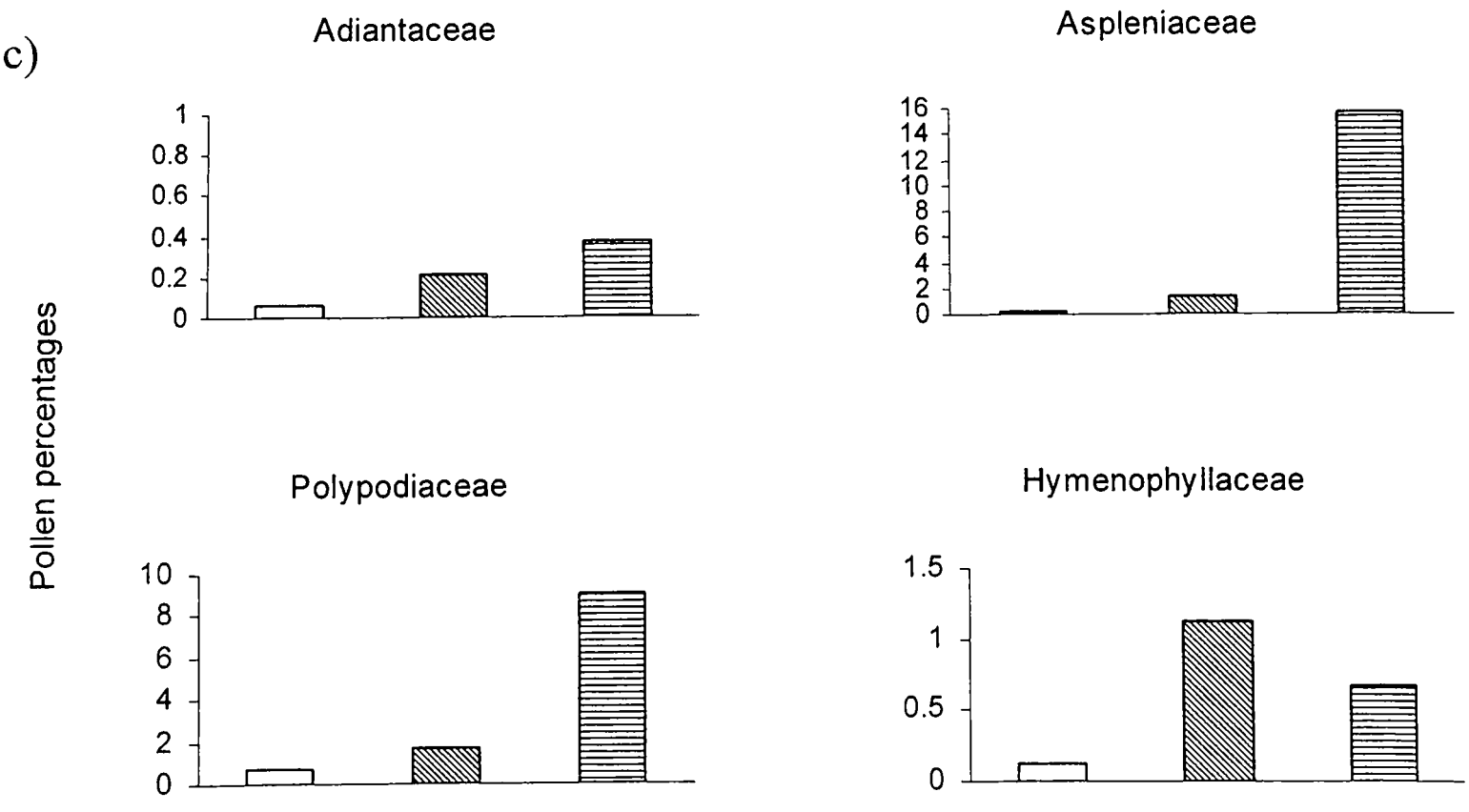


Figure 3.3 *(continued)*

of the non-arboreal taxa which are known to occur in these three forest types are very scarce in the pollen signature (< 1%) and they are just either present in one or two samples. These types are not display graphically.

3.4.2 Forest structure

3.4.2.1 Pine forest

Results indicate that this forest type is less diverse in terms of arboreal components than the other two forest types (cloud forest and transitional forest). *Pinus pseudostrobus* is monodominant and is the most important in terms of importance value indexes (Table 3.2). The stands range from 30 to 49 years old with an average height of 17±3 m (Fig. 3.4a). *Pinus pseudostrobus* individuals perform an irregular diametric distribution representing a multi-aged population with most individuals in diameter classes smaller than 40 cm with a small cohort with diameters > 70 cm (Fig. 3.5).

The pine forest contains the highest number of non-arboreal taxa with *Salvia* sp. as the most abundant and frequent followed by *Alchemilla* sp. The rest are very scarce and with site-specific behaviour as indicated by their low frequencies < 10% (Table 3.2).

3.4.2.2 Transitional forest

The transitional forest in this region represents an intermediate stage between cloud and pine forest. *Pinus douglasiana* individuals are dominant with ages between 23 and 39 years old and

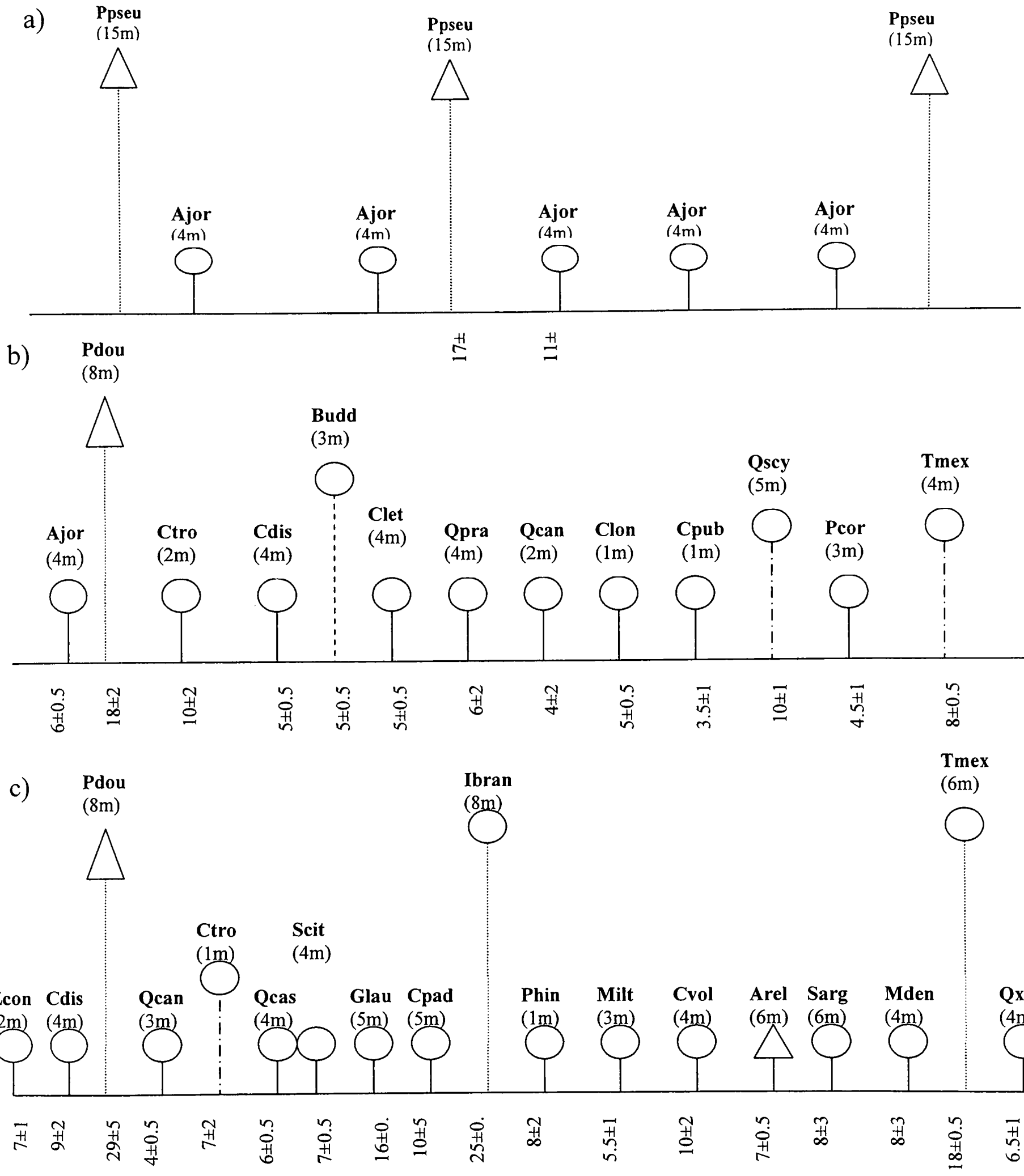


Figure 3.4. Crown width, crown position and height for trees in a) pine forest, b) transitional forest and c) cloud forest. Abbreviations for tree species are in Table 3.2, 3.3 and 3.4; the number in parenthesis is the mode for crown length; average height and its confidence limits is in the bottom of each species; for crown position:
Dominant ·····; Codominant - - - - - -;Intermediate -·-·-·; Suppressed ——

Table 3.2. Importance value index (IVI) for arboreal taxa and relative values for density (RD) and frequency (RF) for non-arboreal taxa in pine forest; RBA=Relative Basal Area.

FAMILIES	SPECIES	RD (%)	RF (%)	RBA (%)	IVI (%)
	Arboreal Taxa				
BETULACEAE	*Alnus jorullensis* (Ajor)	30.99	36.36	15.28	82.63
PINACEAE	*Pinus pseudostrobus* (Ppseu)	**69.01**	**72.73**	**84.72**	**226.46**
	Non-Arboreal Taxa				
ASTERACEAE	*Eupatorium lasioneuron*	0.97	9.09		
	Gnaphalium sp.	3.92	18.18		
	Senecio sp.	0.97	9.09		
	Sonchus oleraceus	1.95	9.09		
	Vernonia sp.	0.97	9.09		
CYPERACEAE	*Cyperus sp*	1.95	9.09		
FABACEAE	*Lupinus sp.*	0.00	9.09		
POACEAE	*Festuca breviglumis*	9.31	18.18		
	Piptochaetium virescens	3.92	9.09		
LAMIACEAE	*Salvia sp.*	**28.94**	**72.73**		
ROSACEAE	*Alchemilla sp.*	**19.63**	**36.36**		
RUBIACEAE	*Galium sp.*	9.81	18.18		
SCROPHULARIACEAE	*Penstemon apateticus*	2.95	9.09		
SOLANACEAE	*Solanum sp.*	7.84	9.09		
SMILACACEAE	*Smilax sp.*	2.95	9.09		
VERBENACEAE	*Verbena carolina*	3.92	18.18		

an average height of 18±2 m; very similar to that in Pine forest although their crowns are half the length (Fig. 3.4b). Most of the *Pinus douglasiana* individuals are in the smaller diametric classes (< 30 cm) and few in bigger categories (> 70 cm) with a bimodal distribution (Fig. 3. 5); this species has the highest relative density, basal area and frequency, followed by *Carpinus tropicalis* and *Quercus praineana*. In the vertical space, *Quercus scytophylla* individuals are intermediate together with *Tilia americana* var. *mexicana* whilst the other two oak species, *Q. candicans* and *Q. praineana*, are suppressed as well the rest of the associated species (Table 3.3, Fig. 3.4b). *Quercus* in this forest represents young populations with small height and crowns and low values in basal area (Table 3.3, Fig.3.4b). The only co-dominant tree is *Buddleja* sp. but this is a negligible element in the horizontal space with the minimum values in density, frequency and basal area (Table 3.3).

Nine herbaceous taxa occur in the transitional forest. *Melinis minutiflora*, a member of Poaceae family, is the most abundant taxon either in density than in frequency. Site-specificity is similar to pine forest with most non-arboreal taxa frequencies < 10% (Table 3.3).

Table 3.3 Importance value index for arboreal taxa and relative values for density and frequency for non-arboreal taxa in the transitional forest. RBA=Relative Basal Area.

FAMILIES	SPECIES	RD (%)	RF (%)	RBA (%)	IVI (%)
	Arboreal Taxa				
BETULACEAE	*Alnus jorullensis* (Ajor)	1.84	9.09	0.11	11.04
	Carpinus tropicalis (Ctro)	**17.60**	18.18	**5.01**	**40.80**
BUDDLEJACEAE	*Buddleja sp.* (Budd)	0.92	9.09	0.32	10.33
CORNACEAE	*Cornus disciflora* (Cdis)	1.39	9.09	0.10	10.58
CLETHRACEAE	*Clethra sp.* (Clet)	0.92	9.09	0.08	10.09
FAGACEAE	*Quercus candicans* (Qcan)	0.92	9.09	0.05	10.06
	Quercus praineana (Qpra)	**7.42**	**27.27**	1.13	**35.83**
	Quercus scytophylla (Qscy)	3.70	18.18	0.97	22.85
MIMOSACEAE	*Calliandra longepedicellata* (Clon)	1.39	9.09	0.11	10.59
PINACEAE	*Pinus douglasiana* (Pdou)	**61.15**	**63.64**	**91.48**	**216.27**
ROSACEAE	*Prunus cortapico* (Pcor)	1.84	18.18	0.21	20.23
TILIACEAE	*Tilia americana var mexicana* (Tmex)	0.92	9.09	0.42	10.43
	Non-Arboreal Taxa				
ASTERACEAE	*Senecio salignus*	3.03	9.09		
	Stevia sp.	3.03	9.09		
EUPHORBIACEAE	*Euphorbia schlechtandalii*	1.51	9.09		
POACEAE	*Festuca breviglumis*	7.62	9.09		
	Melinis minutiflora	**64.20**	**18.18**		
	Muhlenbergia dumosa	4.59	9.09		
	Zea sp.	12.21	9.09		
SCROPHULARIACEAE	*Castilleja arvensis*	1.51	9.09		
SOLANACEAE	*Solanum sp.*	2.29	9.09		

3.4.2.3 Cloud forest

The cloud forest in this region contains the highest diversity and structural complexity. Three species are dominant in the vertical structure, *P. douglasiana, Ilex brandegeana* and *Tilia americana* and reach heights of 18, 25 and 29 m respectively, and crowns lengths of 6 and 8 m. In the intermediate stratum *Carpinus tropicalis* is present and the rest of the arboreal taxa are located in the lower stratum (Fig. 3.4c, Table 3.4). Structural complexity in the forest is apparent by the hierarchy in dominance, some taxa are more frequent than others while some

Table 3.4. Importance value index for arboreal taxa and relative values for density and frequency for non-arboreal taxa in cloud forest. RBA=Relative Basal Area

FAMILIES	SPECIES	RD (%)	RF (%)	RBA (%)	IVI (%)
	Arboreal Taxa				
AQUIFOLIACEAE	*Ilex brandegeana* (Ibran)	0.96	10	0.97	11.93
BETULACEAE	*Carpinus tropicalis* (Ctro)	5.81	50	1.64	**57.45**
CELASTRACEAE	*Zinowiewia concinna* (Zcon)	2.92	20	10.65	**33.57**
CORNACEAE	*Cornus disciflora* (Cdis)	27.22	60	10.30	**97.53**
FAGACEAE	*Quercus candicans* (Qcan)	1.46	10	0.07	11.53
	Quercus castanea (Qcas)	0.96	10	0.05	11.01
	Quercus xalapensis (Qxal)	2.42	20	0.19	**22.61**
GARRYACEAE	*Garrya laurifolia* (Glau)	0.96	10	1.40	12.37
LAURACEAE	*Cinnamomum pachypodum* (Cpad)	4.38	10	7.84	**22.22**
	Persea hintonii (Phin)	3.88	20	2.22	**26.10**
MAGNOLIACEAE	*Magnolia iltisiana* (Milt)	1.93	10	0.08	12.01
MELASTOMATACEAE	*Conostegia volcanalis* (Cvol)	3.88	10	2.11	15.99
PINACEAE	*Abies religiosa* (Arel)	0.96	10	0.07	11.03
	Pinus douglasiana (Pdou)	31.11	50	55.60	**136.71**
SABIACEAE	*Meliosma dentata* (Mden)	6.30	30	5.15	**41.45**
STYRACACEAE	*Styrax argenteus* (Sarg)	2.92	10	0.32	13.23
SYMPLOCACEAE	*Symplocos citrea* (Scit)	0.96	10	0.05	11.01
TILIACEAE	*Tilia americana var mexicana* (Tmex)	0.96	10	1.29	12.25
	Non-Arboreal Taxa				
ARACEAE	*Arisaema macrospathum*	1.25	10		
ASCLEPIADACEAE	*Metastelma sp.*	3.13	**20**		
ASTERACEAE	*Eupatorium lasioneuron*	1.89	10		
CARYOPHYLLACEAE	*Alsine sp.*	1.89	10		
	Cerastium sinaloense	16.99	10		
DENNSTAEDTIACEAE	*Pteridium aquilinum*	6.27	10		
POACEAE	*Melinis minutiflora*	3.78	10		
	Oplismenus burmannii	**36.48**	10		
	Piptochaetium virescens	11.33	10		
	Zeugites sp.	3.78	10		
SOLANACEAE	*Solanum appendiculatum*	13.22	10		

dominate in density or basal area. Stand age ranges from 31 to 47 years old. In terms of importance value indexes (sum of density, frequency and basal area) *Pinus douglasiana* is the dominant taxa followed by *Cornus disciflora* and *Carpinus tropicalis*.

The highest number of *Pinus* individuals are included in the 30 cm diameter class, followed by a cohort around 60 cm and few with diameters >80 cm (Fig. 3.5). For non-arboreal taxa, Poaceae family with *Oplismenus burmannii* is the most abundant but *Metastelma* sp. is the most frequent (Table 3.4).

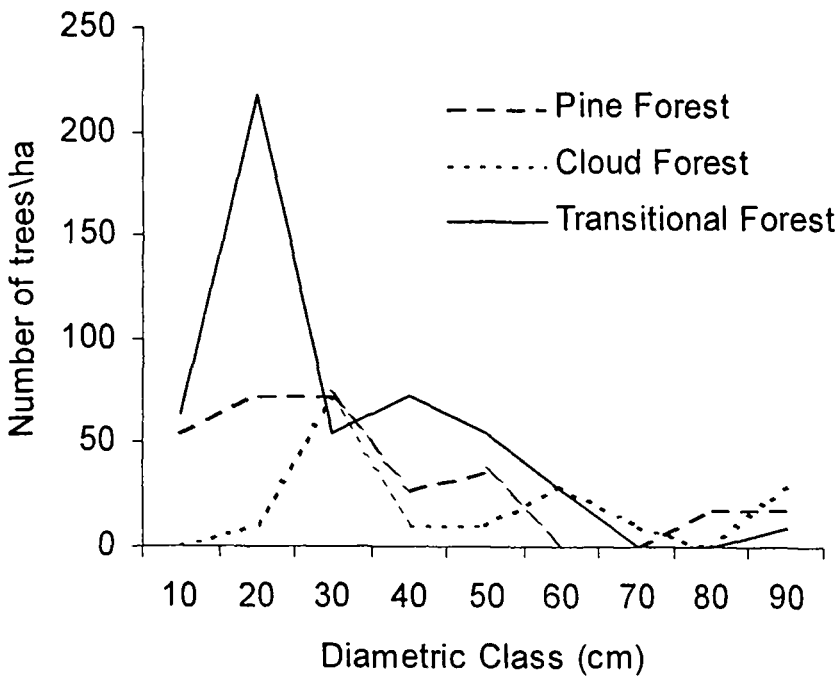


Figure 3.5. Diametric class frequencies for *Pinus* species in the three forest types.

3.4.3 Association between pollen and forest assemblages

Forty-one different vegetation types are recorded in the vegetation plots whereas forty-three pollen taxa are recorded in the surface samples. According to results from the chi-square test, in each forest type the pollen is closely associated with vegetation ($p < 0.05$) suggesting a high pollen-vegetation concordance (Table 3.5). *Pinus* pollen abundance is positively correlated with *Pinus* basal area only in pine forest. In the transitional and the cloud forest, age is positively correlated to *Pinus* pollen abundance while density is negatively correlated (Table 3.6).

Table 3.5. Pearson chi-square goodness of fit for Vegetation-Pollen concordance by forest type. Pearson chi-square goodness of fit for pollen frequencies.

Forest type	***Pollen***	***Vegetation***		*p*
		Absence	Presence	
Pine forest	Absence	118	2	0.003
	Presence	36	16	
Transitional forest	Absence	100	2	0.003
	Presence	56	14	
Cloud forest	Absence	80	4	0.006
	Presence	72	16	

Table 3.6. Pearson correlation coefficients between *Pinus* pollen abundance and structural variables of *Pinus* individuals in the three forest types.* corresponds to $p<0.05$ and ** to $p<0.01$.

	Forest types		
	Pine forest	*Transitional forest*	*Cloud forest*
Pollen-Tree Age	-0.157	0.581*	0.874**
Pollen-Tree Basal Area	0.590*	-0.368	-0.552
Pollen-Tree Density	0.047	-0.937**	-0.581*

Results of the DCA ordination indicated that those taxa common to all three forest types are grouped at the centre of the diagram. These mainly include cultural taxa such as Poaceae, Asteraceae, Chenopodiaceae, *Zea, Pinus* and *Rubus* (Fig.3.6). Site-specific taxa are located at the edges of the diagram from left to right showing the transition from pine forest to cloud forest passing through transitional forest. *Sebastiana* sp. (SebaP) was an exception in this case because it was located at the center of the plot even it represents cloud forest taxa. Pine forest taxa, located on the left of axis 1, represents a less diverse habitat. Cloud and transitional forest taxa, expressing highly diverse associations, are dispersed along axis 2, but one group is restricted to the top and the other to the bottom (Fig. 3.6).

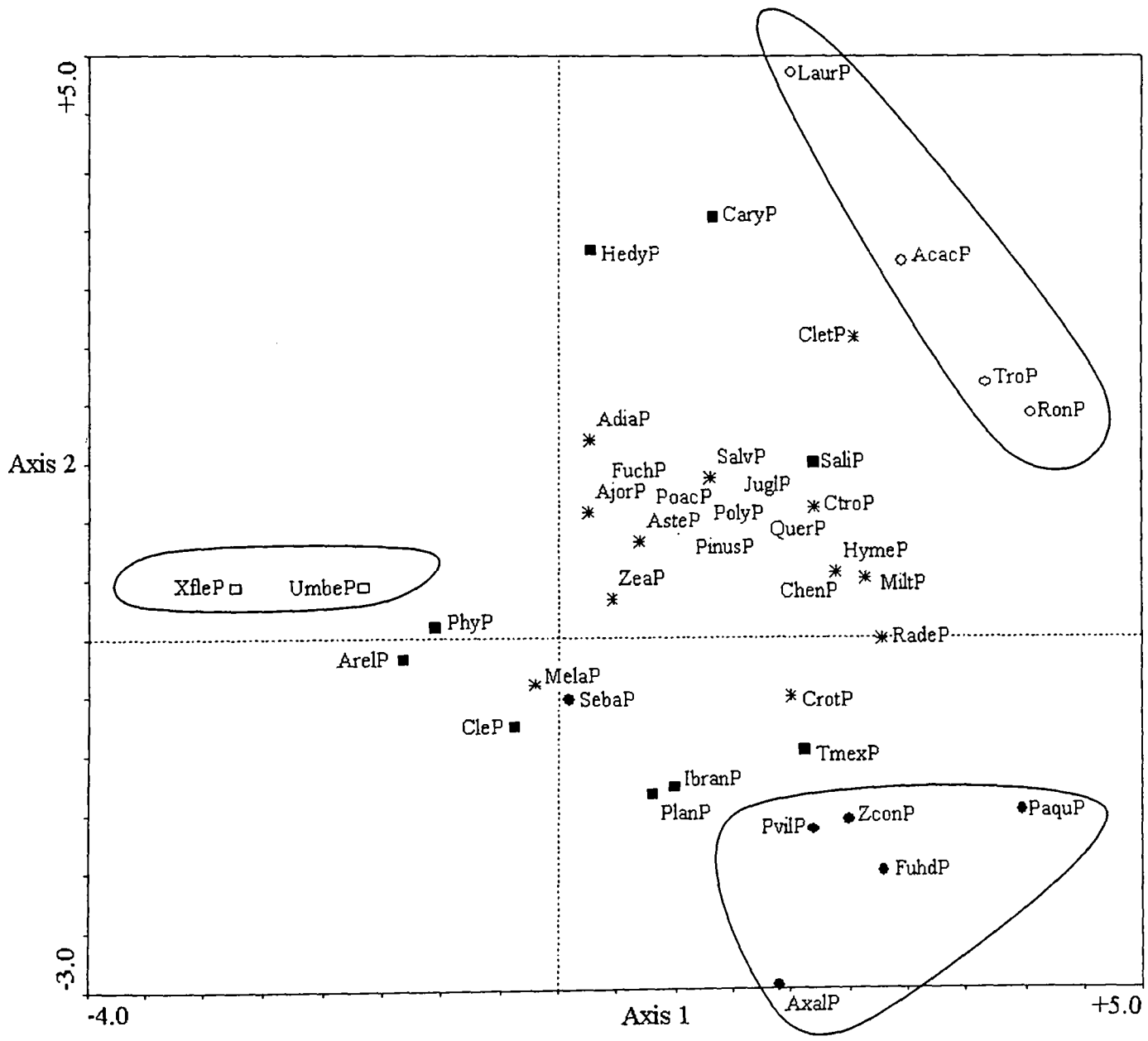


Figure 3.6. Ordination (DCA) for pollen data with species display. Significant species common to the three forest types * ; common to two ■; specific to cloud forest ●; specific to transitional forest ○; specific to pine forest □. Taxa names in Appendix 2.

3.5. Discussion

3.5.1 Is there a difference on pollen representation by forest type?

Results from this study clearly demonstrate that in the Sierra de Manantlan modern pollen (as revealed in litter and moss samples) is reflecting local vegetation at stand level. Distinctiveness in diversity and differences in the abundances of arboreal and non-arboreal taxa characterizes the three forests and these results are statistically significant ($p < 0.05$). This provides certainty on the relationship pollen-vegetation to aid in actual and future vegetation reconstructions through fossil pollen in similar assemblages.

In the arboreal taxa temperate trees such as *Pinus* and *Quercus* dominate the pollen sum in the three forest types. The representation of pine pollen is very strong which is understandable in view of the fact that *Pinus* individuals dominate the canopy of high-altitude vegetation in Manantlan with high importance value indexes (226.46% in pine forest, 216.27% in the transitional and 136.71% in cloud forest). Moreover *Pinus* is anemophilous characterized by high production and well-dispersed pollen (Franco Mujica et al., 2001). Pine pollen has been a common aspect in the reconstruction of mountainous zones during the Holocene in Mexico where the records have reported an increase in *Pinus* over the last 1000 years, event mainly associated with human impacts (Metcalfe et al., 2000).

Other anemophilous taxa apparent are *Alnus* in pine forest and *Quercus* in cloud forest. This finding is in accordance with the actual vegetation pattern of dominance as these taxa are situated with the highest importance values in their respective forests. *Alnus* is renowned as a shade intolerant, early seral component that fills open areas together with *Pinus* (Bjorkman et al., 2003) and associated with disturbance, predominantly fire (Brown and Hebda, 2003),

while *Quercus* species have the ability to behave as mid-shade tolerant or shade-intolerant (Crow, 1988; Kolb et al., 1990; Quintana-Ascencio et al., 1992).

Fuchsia pollen could not be identified to species level but is known to occur in the three forests in different life form. For example, this genus contains species such as *F. encliandra* and *F. fulgens* in the shrub form in pine forest, but it also conveys as a tree, *F. arborescens,* in cloud forest (Cuevas-Guzmán et al., 2004).

The pollen of taxa regarded as mesophytic and properly distinctive of cloud forest, *Magnolia, Clethra* and *Carpinus* are copious only in the transitional forest while very scarce in the actual cloud forest. *Carpinus tropicalis* and *Clethra* sp. are very distinctive elements in the cloud forest reported both in modern and past community assemblages in the mountainous zones of Mexico (Alcantara et al., 2002; Almeida-Lenero et al., 2005; Arriaga, 2000; Conserva and Byrne, 2002; Guerrero and Equihua, 2005; Williams-Linera, 2000). An explanation for such absence is that *Clethra* sp. individuals are completely missing in cloud forest analysed in this study and those of *C. tropicalis* were small in terms of crown, height, basal area and density and this may have affected their pollen productivity.

The absence of distinct cloud forest taxa (*Cornus, Zinowiewia, Persea, Cinnamomum, Meliosma, Tilia*) in the pollen representation of surface samples from the cloud forest may be due to pollen productivity and dispersal mode. The tropical constituent in cloud forest contains canopy species with a number of different dispersal syndromes including anemochory, barochory and zoochory with endozoochory prevailing (Vazquez-Garcia and Givnish, 1998). These types produce less pollen and therefore the pollen signature may well become obscured by the anemophilous pollen types. In addition, the prevalence of endozoochorus species in the

cloud forest may explain why the cloud forest pollen taxa appear to be significantly dependent on south aspects since the pollen dispersal may be tied to the dispersal characteristics of the different species (Jackson and Kearsley, 1998; Parshall and Calcote, 2001) co-occurring in Manantlan. Previous research has indicated for example, that animal paths can be more oriented to certain directions that influence differential dispersal behaviour among species (Kelly and Sork, 2002).

Likewise in Manantlan physiography, predominantly in cloud forest, is heterogeneous with various combinations of soils, topographies and aspects coming together in small areas (Olvera Vargas and Figueroa-Rangel, 2000); as a consequence dissimilarity in aspect is taking place as long as topography varies.

Finally; rare taxa are an important attribute in each of the three forest types; their presence is an indication of site-specificity, so when discerning forest demarcation in vegetation reconstructions, they must be included as routine, even though their abundances are low. This finding is in disparity to the common scheme in pollen analysis where rare taxa are excluded if their abundance is <5% of abundance (Bennett and Willis, 2001).

This is especially the case when dealing with cloud forest, considering important to recognise the three elements incorporated in cloud forest according to (Luna Vega et al., 1999); the temperate mainly in trees of Neartic derivation such as *Pinus, Quercus* and *Alnus*, the Neotropical with *Fuchsia* and *Hedyosmum*, and finally the endemic which contains rare taxa with low abundances such as *Clethra* and the Lauraceae family.

Different non-arboreal pollen dominates each forest; Chenopodiaceae and Poaceae in transitional forest, Asteraceae in pine forest while *Crotalaria, Zea* and *Salvia* in cloud forest. But this distinction was not apparent in the vegetation of these three forest types when the

surveys were undertaken. The only exception to this was Poaceae, which dominates the importance value indexes in transitional forest and is also a dominant in the pollen signature. It is likely that this is due to the flowering season of these annuals. The surface samples were collected during the dry season when the plants were past flowering and therefore were probably missed in field identification.

Another interesting result from the study is that there is not an apparent relationship between canopy closure and herbaceous pollen abundance. Even with the obvious disparity among canopy cover estimates during the vegetation survey (*personal observation*), pine forest with 70%, followed by cloud forest (50%) and transitional forest (15%), no trend is observed between canopy closure and herbaceous pollen decrement.

In the results from the epiphyte spore abundance there is a clear transition from low to high epiphyte spore abundance (from pine forest, transitional forest to cloud forest) confirming that epiphytes can be used as good indicators to detect differences among forest types. As they are also related to number of vertical strata, tree sizes (DBH and height) and ages (Flores-Palacios and Garcia-Franco, 2006; Lyons et al., 2000; Ruchty et al., 2001), they may also detect structural dissimilarities. Cloud forest, for example, which reports the older trees with a higher number of vertical strata and bigger diameters, also has the highest epiphyte spore abundances. Epiphytes characterized high-altitude forests in Mexico, in particular cloud forests (Luna Vega et al., 1999). They are considered to be life form as rich as trees. A positive correlation has been demonstrated between tree and epiphyte density (Williams-Linera et al., 2005). On the other hand, Polypodiaceae is the most diverse family with 47 species identified (Rzedowski, 1996) but other taxa, *Asplenium, Hymenophyllum* and *Blechnum*, are rich as well (Wolf and Flamenco-S., 2006).

3.5.2 Is pollen abundance related to forest structure?

From this study results indicate that *Pinus* pollen abundance is linked to the structure of the different forest types. *Pinus*, which is dominant taxa in terms of vertical structure in the three forest types, contributes in different ways to the total *Pinus* pollen production in the three forests. In pine forest, the positive significant correlation of pollen with basal area suggests that the greater the biomass (basal area) of the trees, the more pollen is produced. For the transitional forest and the cloud forest results indicate that age is more important than size (diameters and basal area) and abundance (density). This is demonstrated in the significant positive correlation of *Pinus* pollen with age and the negative significant correlation with density. In these two forest types *Pinus* is not dominating all strata and other taxa are contributing to the total pollen sum. However the *Pinus* trees that are apparent in these forest types are older (age) and therefore producing pollen that contribute to the total pollen sum.

Despite the lack of age data an interesting pattern arise with oak pollen representation; while basal area and density are higher in the transitional forest than in the cloud forest, oak pollen abundances are higher in cloud forest. In this case it would appear that structural variables are not playing an important role as much as taxa composition. Here the different oak species in the site may be performing a masting year, producing a higher number of pollen grains per tree than those in transitional forest. It has been recognized that oak pollen production is not constant year by year and there are particular years (masting years) when pollen production increases (Figueroa-Rangel and Olvera Vargas, 2000; Gonzalez-Espinosa et al., 2006). In this way the masting year for each oak species determines the amount of pollen more than density and basal area.

Much has been speculated about how the fossil pollen record reflects past forest structures. In a study on Irish woodlands a high oak pollen record was related to open canopies (Mitchell, 2005). This interpretation was based on the understanding that oak require gaps to regenerate. For the Sierra de Manantlan region however it has previously been demonstrated that oaks perform a multi-strategy for regeneration due to the high heterogeneity in the understory, this results in large variations in micro-sites and producing numerous niches for the establishment of the different oak species. With this behaviour different species produce different amount of pollen depending on the diversity of oak species and enhanced by their synchronous masting years (Figueroa-Rangel and Olvera Vargas, 2000) . For Manantlan, a high oak pollen production cannot therefore always be related to open canopies

3 5.3 Can forest types be discerned through pollen assemblages?

The significant relationship between vegetation and pollen in this study confirms that in this region at stand level there is a close correspondence between vegetation type and pollen signature. This result has significant implications for reconstruction of some of the most biodiverse and threatened forest types in West-Central Mexico. Nevertheless some taxa in the vegetation are not represented in the pollen record and vice versa. Firstly, those types with dispersal syndromes that are reliant upon animals (e.g. *Styrax* and *Conostegia*) are underrepresented in the pollen record; this is particularly true for the cloud forest taxa. Secondly, there is evidence of some non-local pollen (Liliaceae, Umbelliferae and *Pteridium*) adding to the total pollen signature, possibly reducing the representation of the underrepresented pollen types.

Other aspects of note from comparison of the pollen-vegetation results include that epiphytes are a much better representative of cloud forest than arboreal taxa.

Many of the herbaceous families (e.g. Asteraceae, Poaceae and fern families) could not be identified beyond the family level. Also the multiple life-form of some families or even genera presents, p. eg. Onagraceae, whose plasticity allows individuals to perform as a tree, shrub and epiphytes could not be distinguished. Any measures of richness for these types in the pollen record will therefore be seriously under-representative.

Even considering the above-mentioned drawbacks, results from the DCA clearly separate the three forest types showing a gradient from less diverse to more diverse sites. Pine forest can be seen as the least diverse followed by cloud forest and then the transitional forest. It is highly probable that humidity is the central environmental gradients in axis 1 going from drier pine forests on the left to wetter forests (cloud forest and transitional forest) on the right, a pattern that has been described for these ecosystems elsewhere in Mexico (Gonzalez-Espinosa et al., 2006; Loock, 1947; Perry et al., 1998; Rzedowskii, 1981; Vazquez-Garcia and Givnish, 1998). Axis 2 probably represents an elevation gradient with lower elevations on the bottom (cloud forest plots are at 1820-1890 m asl) and higher on the top (transitional forest plots are at 1880-2100 m asl).

What it is also evident from these results is the valuable information that site-specific taxa (*Acacia, Rondeletia, Trophis* and Lauraceae) enable discrimination among forest types; they appear on the edges of the ordination diagram while the common ones are at the centre.

3.6. Conclusions

This study indicates that the use of modern pollen assemblages to reconstruct vegetation dynamics through time in the Sierra de Manantlan is a valuable and useful technique. Differential species performances of these highly diverse communities such as pollen dispersion, structural characteristics and compositional divergences add a level of complexity to the interpretation. Nonetheless the results of this research demonstrate that the spatial distribution of modern pollen is expressing spatial forest demarcations as well as structural and compositional responses.

The three forests in this study represent different stages in forest succession going from pine forest (first stage in succession), transitional forest to cloud forest. Each of these forest types has well-defined pollen assemblages. Pine forest is the less diverse and expresses a simple horizontal and vertical structure with *Pinus, Alnus* and *Fuchsia* dominating the arboreal component in the pollen. The transitional forest has *Carpinus, Clethra* and *Magnolia* as the dominant arboreal taxa and finally cloud forest with a complex structure and a higher diversity which pollen sum is dominated by *Quercus* and epiphytes. Structural characteristics of the forest also appear to influence pollen production with the greatest production occurring in pine forest where biomass is greatest whereas in the transitional and cloud forest, the older the trees the more pollen is produced. In the cloud forest, pollen dispersed by animals is an important component and interestingly, there is a strong directional signal to this pollen, the majority of the pollen produced in this forest is mostly found in south aspects. We hypothesize that this is indicative of the behavioural characteristics of the pollen dispersers.

Finally results from this study indicate that characterization of these forest types is much more robust when all pollen types are included in the analysis. This is in contrast to the usual method in pollen analysis where rare taxa are excluded in ordination analysis (e.g. taxa with <5% of abundance are usually left out of the analysis.

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4. PAPER 2

4200-years of pine-dominated forest dynamics in the uplands of West-Central Mexico: A human or natural legacy?

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Abstract

The pine-dominated forests of West-Central Mexico are internationally recognized for their high biodiversity and some areas are already protected through various conservation measures including prohibition of human activity. In this region, however, there is evidence for human settlement dating back to at least ~1200 A.D. It is therefore unclear whether the present forest composition and structure are part of a successional stage following utilization by indigenous human populations in the past, or due to natural processes (e.g. climate). This paper presents the results of a study reconstructing the vegetation dynamics of the pine-dominated forest over the past 4200 years using palaeoecological techniques. Results from fossil pollen and charcoal indicate that in this region, the pine-dominated forests are the native vegetation type and not anthropogenically-derived secondary succession. The predominant driving mechanism for the

expansion of the pine-dominated forest appears to be intervals of aridity and naturally induced burning. A close association is noted between pine abundance and longer-term climatic trends including intervals of aridity between ~4200-2500, 1200-850, and 500-200 cal. yr BP and shorter term trends. There is evident periodicity in pine and Poaceae abundance every 200 and 80 years. These short-term quasi-periodic oscillations have been recorded in a number of lake and ocean sediments in Mexico (Haug et al. 2000, Hodell et al. 2001) and are thought to be linked to solar forcing resulting in drought-cycles at approximately these time intervals.

Key words: pine dynamics; fire; forest management; palaeoecology; human disturbance.

4.1. Introduction

Half of the world's Pinus species are prevalent in ecosystems of México (Saenz-Romero et al. 2003) but there are few studies of the genus, particularly those examining the relative contribution of human activity and/or climate change to their spread and persistence (Richardson and Rundel 1998). Pines are considered as pioneer species (Johnston and Crossley Jr. 2002), post-disturbance colonizers that dominate early-successional stages (Ramirez-Marcial et al. 2001, Galindo-Jaimes et al. 2002, Cayuela et al. 2006) and grow faster than hardwood species in bright light of isolated soils such as those left by agriculture or logging. As pines become dominant in the stand their canopies close preventing light from reaching the forest floor; therefore in the absence of human disturbances other taxa such as *Quercus* or cloud forest species, become the next step in forest succession eventually replacing pines. This process of replacement can take decades to become perceptible and the process of

these events can also be affected by factors others than human disturbances, particularly climate change. In Mexico, pines can exist in a wide variety of climatic conditions, from a dry-temperate climate in the Sonoran desert to a humid-tropical in the Yucatan Peninsula; adapting from the lowlands in the warmer base of a mountain to the cold weather uplands (Perry et al. 1998).

Palaeoecological studies in Mexico have been predominantly focused in the Central region (19°04'N, 101°40'W) and the Yucatan Peninsula where there is a greater concentration of evidence for settlement of pre-Hispanic civilizations (Watts and Bradbury 1982, O'Hara 1993, Xelhuantzi-Lopez 1994a, 1994b, Arnauld et al. 1997, Conserva and Byrne 2002, Almeida-Lenero et al. 2005, Lozano-Garcia and Vazquez-Selem 2005, Ludlow-Wiechers et al. 2005). Studies from the central region (mainly on high-altitude temperate vegetation ranging from 1500 to 3100 m asl) have suggested that much of the late Holocene pine forests are as a consequence of anthropogenic activity mainly land clearance through logging and agricultural activities. In particular during the last 1000 yrs there has been a steady increase in *Pinus* that has been attributed to these two processes (Almeida-Lenero et al. 2005, Ludlow-Wiechers et al. 2005). On the other hand, such studies have also indicated that the last 5000 yrs have been characterized by important changes in the climatic conditions of Mexico (Metcalfe et al. 2000). In the Northern region the modern desert conditions, with increasing aridity, began around 4000 yr BP. In the Central region humid conditions prevailed from 4000 to around 2500 yr BP (Gonzalez-Quintero 1986, Lozano-Garcia et al. 1993, Metcalfe et al. 2000, Almeida-Lenero et al. 2005) and dry conditions from 2500 to 1900 yr BP (O'Hara 1993) with the most rigorous around 1000 yr BP (O'Hara 1993, Metcalfe and Hales 1994, Metcalfe 1995, Arnauld et al. 1997). For the Yucatan Peninsula, paleoclimatic records of precipitation in the

past 2600 years have demonstrated correlations with solar forcing influences at periods of ~810, 208, 100, 50 and 39 years revealing periodic patterns of droughts, particularly in the Mayan region. The driest period is reported between 800-1000 A.D. (Hodell et al. 2001).

The Sierra de Manantlan Biosphere Reserve (SMBR) is a distinctive area with high-diversity forests and environmental heterogeneity located in West-Central Mexico (19°26'-19°42'N and 103°51'-104°27'W) in the transition of the Neartic and Neotropical realms where tropical and temperate elements congregate (Olvera Vargas 2007). This is a protected area including zones with 20 years of strict prohibition of human interventions such as logging and agriculture. Pine is highly valuable for its timber, therefore timber extraction has been focused on pine stands under the condition that the forest is managed according to sustained silvicultural strategies which will maintain the stand at short rotations (SEMARNAP 2000). Archaeological studies have indicated that this region has been occupied ~1200 A.D. with a technologically sophisticated population practising agricultural activities and using forest resources since that time (Kelly 1945). Fire is an important disturbance factor which has contributed vastly to the occurrence of pines. Currently human-induced fires, mainly associated with agricultural activities, are common in the SMBR affecting ~6852 ha of the total 139577 ha per year (Jardel-Pelaez et al. 2004).

Much of the work on pine distribution in West-Central Mexico, however, has been based on species lists and short-term ecological records spanning less than 20 years (Olvera Vargas and Moreno Gómez 1993, Sanchez-Velasquez and Garcia-Moya 1993, Vazquez-Garcia et al. 1995, Cuevas-Guzmán et al. 2004) with no palaeoecological or paleoclimatic research included. It remains unclear therefore whether the current distribution of pines in this region

are as a consequence of past human activity (which is the current assumption) or as a result of naturally occurring processes including climate change (e.g. as a result of increasing aridity over the past 1000 years). In this study, therefore, we used palaeoecological methods to reconstruct 4200 years of pine forest dynamics in the SMBR in order to examine the relative influence of human activity and climate change on the temporal ecological variability of pine mountainous regions in West-central Mexico thereby addressing the following questions: Has climate or human activity favoured the expansion of pine over other tree species? What has been the role of fire in this process? If the forest is an anthropogenically-derived vegetation type, then what specific management techniques were essential to its long-term preservation? Are the protected pine forests of the SMBR a human or a natural legacy?

4.2. Study Area

The site is located in the Sierra de Manantlan Biosphere Reserve (SMBR), southeast of Jalisco and in the northeast of Colima of West-Central Mexico (19°26'-19°42'N and 103°51'-104°27'W) (Fig. 4.1) between the Nearctic and the Neotropic encompassing part of the Sierra Madre del Sur physiographic province which geological origin dates from late Cretaceous (Martinez-Rivera and Ramirez 1998). Its evolution is also related to the Cenozoic subduction volcanism in Central Mexico that built two major volcanic arcs: the Sierra Madre Occidental silicic volcanic province and the roughly east-west trending Trans-Mexican Volcanic Belt (Rossotti et al. 2002). The altitudinal range of the reserve is between 400 to 2,860 m asl. and the climate is temperate subhumid with an average temperature of 18°C and precipitation between 1500 and 1800mm/yr (García 1987).

Fig. 4.1. Map with the location of the pine-dominated forest inside the Sierra de Manantlan Biosphere Reserve; * archaeological sites.

The site is a protected area established by government decree in 1987 due to the high plant floristic richness of this region with over 2774 species identified (Vazquez-Garcia et al. 1995). Six key plant communities are recognised in the reserve namely pine-dominated forest, pine-oak forest, pine-fir forest, cloud forest, gallery forest and secondary vegetation. Some of the most distinctive species found in each zone are listed in Table 4.1. Eleven pine species can be found in Manantlan in different degrees of association with other conifers (mainly *Abies* sp.) and broadleaved elements (*Quercus* and cloud forest tree species) and in different altitudinal gradients.

There is a strong legacy of prehistoric and historic human activity in the reserve with more than 79 settlements surrounding or included inside the SMBR (SEMARNAP 2000). The earliest archaeological evidence for occupation dates back to 3400±200 yr BP (Kelly 1980). In more recent times there is evidence that the pine-dominated forests in the SMBR have been logged for timber since the early 1900's leaving scattered standing trees and big gaps in the canopy as a consequence of extraction. The main threat for natural regeneration is thought to be grazing (Sanchez-Velasquez et al. 2002) and periodic fires which are linked to anthropogenic factors rather than to natural origins (Jardel-Pelaez et al. 2004).

Table 4.1. Distinctive taxa for high-altitude vegetation types in the Sierra de Manantlan Biosphere

TAXA NAME	PINE FOREST	PINE-OAK FOREST	PINE-FIR FOREST	CLOUD FOREST	GALLERY FOREST	SECONDARY VEGETATION
Trees/Shrubs						
Abies religiosa			*	*		
Acacia sp.						*
Alnus jorullensis	*	*				
Balmea stormae					*	
Buddleja sp.		*				
Calliandra laevis					*	
Calliandra longipedicelata						*
Carpinus tropicalis		*		*		
Chiococca pachyphylla					*	
Cinnamomum pachypodum				*		
Citharexylum mocini				*		
Cirsium sp.						*
Clethra mexicana		*		*		
Cleyera integrifolia					*	
Cleyera theaeoides				*		
Clusia salvinii				*		
Conostegia volcanalis				*		
Cornus disciflora		*		*		
Cornus excelsa					*	
Cupressus lusitanica	*		*			
Dendropanax arboreus				*		
Fraxinus uhdei				*		
Fuchsia arborescens				*		
Garrya laurifolia				*		
Hedyosmum mexicanum				*		
Ilex brandegeana				*		
Inga eriocarpa				*		
Juglans major				*		
Lippia alba				*		
Magnolia iltisiana				*		
Matudea trinervia				*		
Meliosma dentata				*		
Oreopanax echinops				*		
Ostrya virginiana				*		
Parathesis villosa				*		
Perrottetia longistylis				*		
Persea hintonii				*		
Photinia parviflora					*	
Pinus douglasiana	*	*		*		
Pinus herrerae	*	*				
Pinus oocarpa	*	*				
Pinus pseudostrobus	*		*			
Prunus cortapico		*		*		
Quercus candicans		*		*		
Quercus castanea	*	*				
Quercus laurina	*		*			
Quercus magnoliifolia	*					
Quercus praineana		*				
Quercus salicifolia				*		
Quercus scytophylla		*				
Rhamnus hintonii				*		
Rondeletia manantlanensis				*		
Rubus adenotrichos						*
Salix microphylla					*	
Sebastiana jalicensis				*		
Styrax argenteus				*		
Symplococarpon purpusii				*		
Symplocos citrea				*		
Tilia americana var mexicana		*		*		

Triumfetta			*			
Trophis racemosa				*		
Vaccinium sp.	*	*	*			
Xylosma flexuosum			*			
Zinowiewia concinna			*			
Herbs Families (including epiphytes)						
Acanthaceae				*		
Adiantaceae						
Amaranthaceae						*
Araceae			*			
Asclepiadaceae			*			
Aspleniaceae			*	*		
Asteraceae	*	*	*	*		*
Begoniaceae			*	*		
Bromeliaceae			*			
Chenopodiaceae						*
Convolvulaceae		*	*			
Cyperaceae			*	*		*
Dennstaedtiaceae	*		*			
Equisetaceae				*		
Euphorbiaceae		*	*			
Gesneriaceae				*		
Hymenophyllaceae			*			
Juncaceae				*		
Lamiaceae	*					
Leguminosae			*			*
Liliaceae				*		
Malvaceae						*
Melastomataceae			*			
Nyctaginaceae				*		
Ophioglossaceae			*			
Orchidaceae			*			
Piperaceae			*			
Plantaginaceae						*
Poaceae	*	*	*			*
Polygonaceae				*		
Polypodiaceae			*			
Rosaceae		*				
Rubiaceae			*			
Schropulariaceae	*	*		*		
Solanaceae	*	*	*			*
Thelypteridaceae			*	*		
Umbelliferae			*			
Urticacaceae			*			
Valerianaceae			*			

The sedimentary core for reconstructing the long-term vegetation dynamics of this study was collected from a small forest hollow (natural basin approximately 70m x 25m in diameter with no inflowing or outflowing streams) in a region of pine-dominated forest (2510-2570 m asl; 19°, 33 '954'' N; 104°, 10' 531" W)(Fig. 4.1). Presently the vegetation surrounding the hollow is dominated by *Pinus pseudostrobus*, but also contains *Quercus laurina, Alnus jorullensis* and in some areas *Abies religiosa.* In the understory herbaceous taxa include *Eupatorium, Sonchus*, *Festuca*, *Piptochaetium, Penstemon, Verbena, Solanum, Smilax, Gnaphalium, Senecio, Vernonia, Cyperus*, *Lupinus*, *Salvia, Alchemilla*, and *Galium.* The nearest archaeological sites to the study area (Fig. 4.1) were occupied before the Spanish Conquest (1521 A.D.) and include finds of pre-Hispanic tools corresponding to the *Autlan, Mylpa* and *Cofradia* ceramic complexes that seem to correlate with the Aztec I, II- III and IV periods from the Valley of Mexico (Kelly 1945) which date to between 1200 to 1500 A.D. (Hodge 1998).

4.3. Methods

4.3.1. Sediment collection

An organic sedimentary core 188 cm long was recovered from the forest hollow using a modified Livingstone corer (Moore et al. 1991). The core was extruded in the field, wrapped and transported back to the Oxford Long-term Ecology Laboratory where the following analyses were undertaken:

4.3.2. Dating

Six organic samples from the sedimentary sequence were analysed for AMS radiocarbon dating. Results were calibrated using the INTCAL04.14 calibration dataset and CALIB v5.02 program (Stuiver and Reimer 1993) (Table 4.2). Measurements of ^{210}Pb were also performed (*Ortec* Coaxial Well Photon Detector in the Oxford Long-Term Ecology Laboratory) to provide a chronology for the past 150 years using samples from the top of the core and applying the constant rate of supply (CRS) model (Appleby and Oldfield 1978). Age-depth models including calibrated radiocarbon and ^{210}Pb dates were examined using linear interpolation and polynomials with two, three and four terms (Bennett 1994). At the end, linear interpolation was used in the analysis.

4.3.3. Magnetic susceptibility and loss on ignition

The sedimentary sequence was measured incrementally every 1cm through a magnetic susceptibility loop using a Bartington MS2 device in order to determine the presence of iron-bearing minerals within the sediments (Thompson and Oldfield 1986); The core was then sectioned continuously at 1 cm increments using a custom-made sampler device and sub-samples of 1 cm^3 were subject to loss-on-ignition analysis (LOI) to determine the percentage of inorganic material in the core relative to its organic carbon and carbonate contents (Dean 1974).

4.3.4. Fossil pollen analysis

Pollen extraction was carried out using a standard acetolysis method (Bennett and Willis 2001). A known quantity of the exotic spore *Lycopodium* was added to each sample in order to estimate pollen concentrations (pollen grains cm^{-3}) (Stockmarr 1971). Pollen identification was carried out using detailed pollen and spore reference collection of 300 specimens (trees, shrubs and herbs) prepared from modern material collected during the field season in the study area and the reference collection held in the Long-term Ecology Laboratory, Oxford University Centre for the Environment. A minimum of 400 pollen grains was counted for each level at 400x magnification to ensure reasonable statistical reliability (Maher 1972).

4.3.5. Microfossil charcoal analysis

Microfossil charcoal abundance was quantified in each level using the point count method (Clark 1982). The number of *Lycopodium* grains was also counted, thereby permitting estimation of charcoal concentrations. Charcoal analysis provides basic data on the abundance of charcoal in the sediment, which is considered to be reflection of fire occurrence within the catchment of the basin (Clark 1988, Figueiral and Mosbrugger 2000, Moore 2000).

4.3.6. Statistical analyses

Pollen counts were converted to percentages and plotted in a pollen percentage diagram using PSIMPOLL 4.25 and PSCOMB 1.03 software (Bennett 2005). The pollen percentage diagram was divided into zones. Different zonation methods were examined including binary and

optimal splitting as well as constrained cluster analysis available in PSIMPOLL 4.25 and PSCOMB 1.03 software (Bennett 2005). At the end, constrained cluster analysis technique (CONISS) was used for the zonation. Spectral analysis of the pollen data and cross-correlations between selected pollen types were computed according to the methods described by (Box and Jenkins 1970) using POLSTA v.7.0 software (Green 1989). A Bartlett window was used for the estimates. Cross correlations were also carried out between the three main tree taxa (*Pinus, Quercus* and *Alnus)* and microfossil charcoal data (see below).

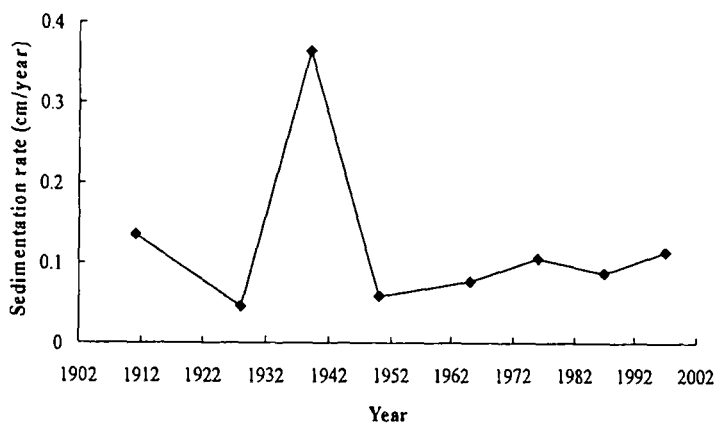
4.4. Results

4.4.1. Dating

Six ^{14}C AMS ages were obtained for the sedimentary sequence (Table 4.2) from two laboratories (*Poznan,* Poland and *East Kilbride*, UK) and these are stratigraphically consistent. Sediment deposition in the basin occurred from approximately 4200 cal. yr before present (BP) and continues to the present with no evidence of a hiatus in sedimentary deposition. Age-depth modelling of the ^{14}C and ^{210}Pb dates indicates that the most realistic description for the data points is a linear interpolation (Fig. 4.2). Deposition time calculated according to this linear age-depth model indicates that 1cm of sediment accumulated every ~22 years.

Table 4.2. Radiocarbon dates and calibrated dates from CALIB v5.02 using the INTCAL04.14 calibration data through the probability method (Stuiver and Reimer 1993).

Depth (cm)	Laboratory code	^{14}C age (yr BP)	Calibrated age (cal yr BP)(2-sigma (σ))
20	Poz-10804	660±30	650±22
40	Poz-10805	775±30	700±32
60	SUERC-5867	895±24	875±30
76	SUERC-5868	1395±25	1315±29
100	Poz-10746	3260±35	3485±84
188	Poz-4749	3910±30	4260±15



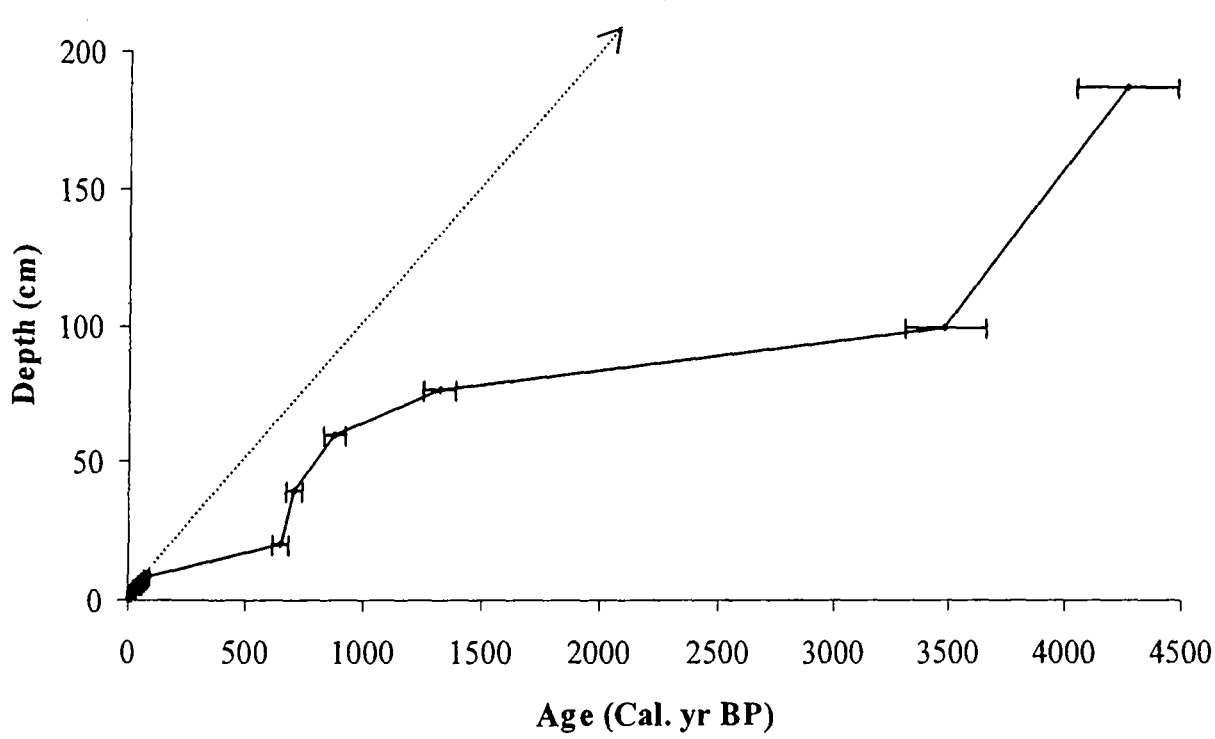


Fig 4.2. Age-depth model based on radiocarbon (open squares) and Pb^{210} dates (black diamonds) using linear interpolation. On the top line, sedimentation rates (using Pb^{210} dates) for the past hundred years interval are displayed estimated from the constant rate of supply (CRS) model (Appleby and Oldfield 1978). Error bars display the 95% confidence intervals for age determinations.

4.4.2. Pollen

Pinus is present throughout the entire core representing nearly 4200 years of forest dynamics in the Sierra de Manantlan (Fig. 4.3). Cloud forest trees (e.g. *Hedyosmum, Magnolia* and *Carpinus*) are poorly represented in the sequence and show the lowest abundance throughout. However, epiphytes usually associated with cloud forest (e.g. Aspleniaceae, Adiantaceae, Hymenophyllaceae, Polypodiaceae) show much higher percentages and from studies of present-day pollen rain in the region, are known to be representative indicator taxa for this vegetation type (Figueroa-Rangel *et al.* in prep). Zonation of the pollen diagrams indicates that four numerically derived zones can be recognised as following ages/depths (Fig. 4.3):

Zone Z1 (188-90 cm, c. 4260 – 2580 cal. yr BP) pre-Hispanic phase I

Pinus is abundant in the lowermost zone of the sequence (from ~ 4260 cal .yr BP) together with *Quercus*, *Rubus*, Asteraceae, Poaceae, Hymenophyllaceae and *Pteridium.* However, from approximately 3500 cal. yr BP a decrease in *Pinus* is apparent with a corresponding increase in *Alnus*, and the epiphyte taxa Aspleniaceae and Adiantaceae. Other forest taxa to disappear at this time include *Carpinus* and *Rubus.*

Zone Z2 (90-74 cm, c. 2580 – 1260 cal. yr BP) pre-Hispanic phase II

From the beginning of this zone at approximately 2580 cal. yr BP there is a further decrease in *Pinus* and a large increase in epiphytes (e.g. Aspleniaceae, *Pteridium* and Adiantaceae). Other

taxa to decline at this time include *Abies* and the open-ground herbaceous types Asteraceae and grasses. *Salix* has a significant presence in the arboreal vegetation from approximately 1800 cal. yr BP along with an increase in *Pteridium* and a decline in *Alnus*.

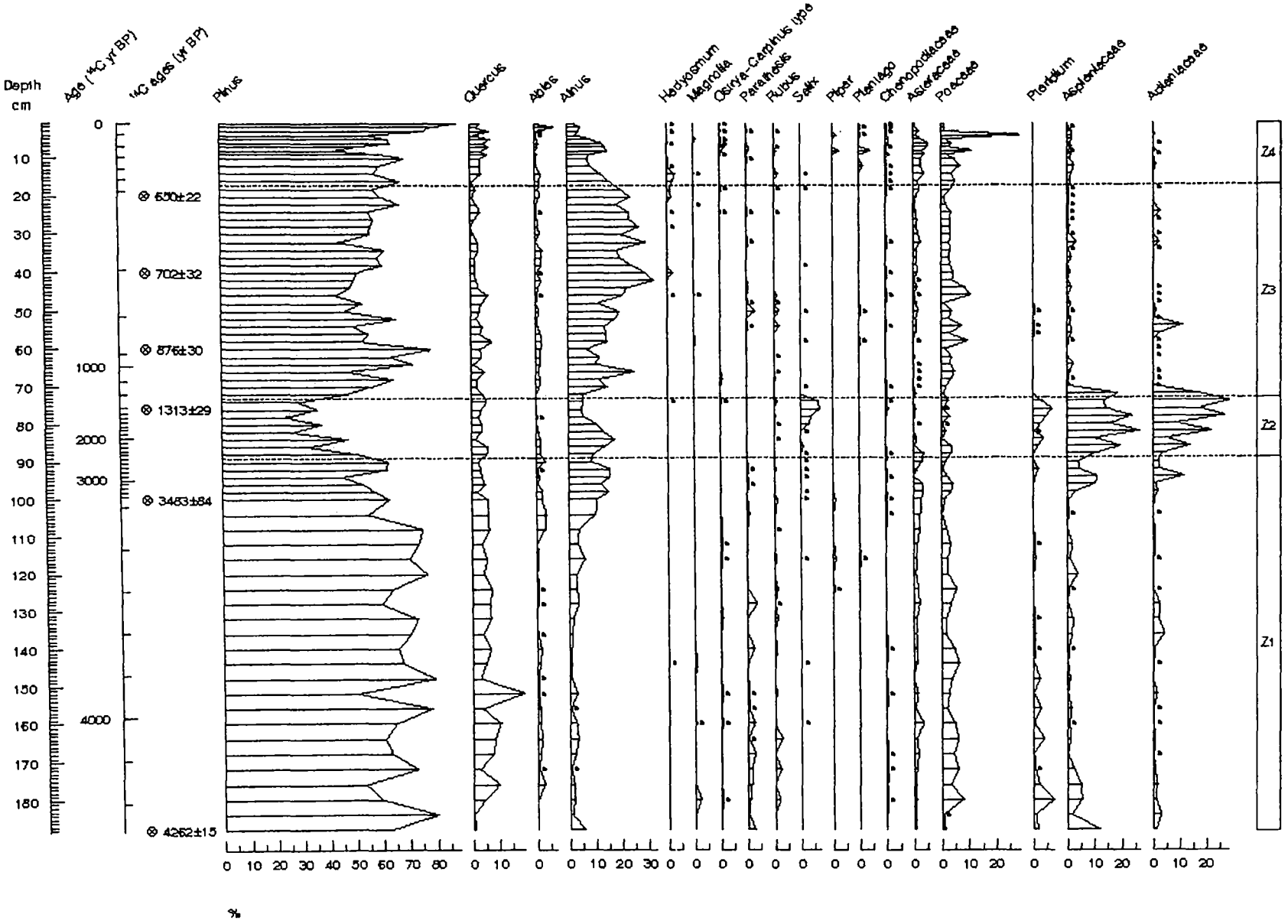
Zone Z3 (74-16 cm, 1260 - 510 cal. yr BP) pre-Hispanic phase III

At the beginning of this zone a total change in the vegetation occurs with *Pinus* showing a dramatic increase and a decline in *Salix,* Aspleniaceae and Adiantaceae. *Alnus* also increases from the beginning of this zone and reaches its highest abundance at around 850 cal. yr BP.

Zone Z4 (16-0 cm, 510 cal. yr BP to present) post-Hispanic phase

Pine dominates throughout this zone with a continued presence of *Alnus*. There is also a noticeable presence of taxa linked to anthropogenic influence such as Asteraceae, Chenopodiaceae, Poaceae, *Plantago* and *Rubus*.

Pine–Dominated Forest, West–Central Mexico



FIig. 4.3. Percentage pollen diagram displaying vegetation dynamics of the pine-dominated forest in West-Central Mexico over the past 4200 years. Taxa are arranged by life form with trees and shrubs on the left followed by herbs and ferns. Ages are calibrated years BP. Divisions are delineated by zones according to CONISS available in PSIMPOLL 4.25

Pine–Dominated Forest, West–Central Mexico

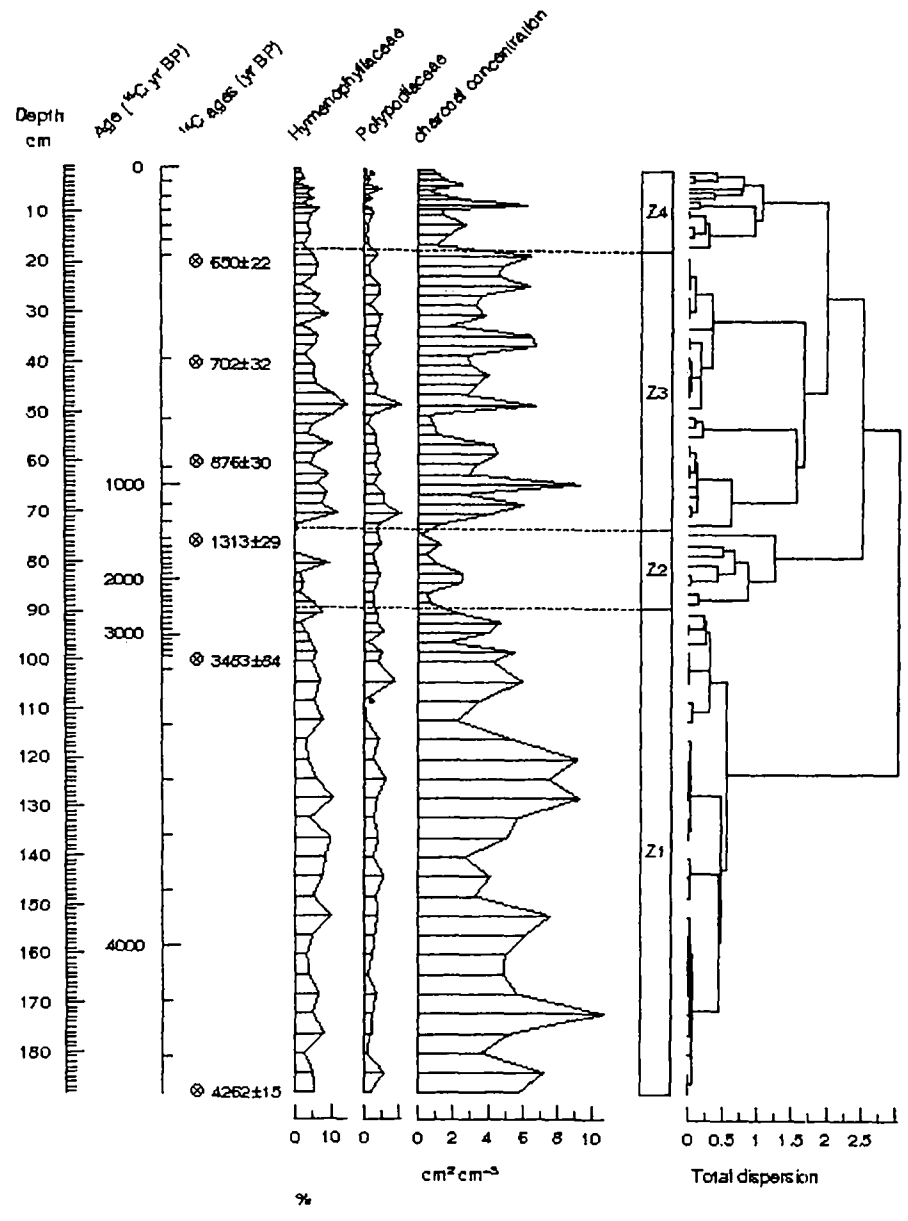


Fig. 4.3. (*Continued.*)

Results from the spectral analysis of the pollen data (Fig. 4.4) suggest that there is a clear cyclical peak at 80 years in the pollen spectrum of *Pinus, Alnus, Plantago, Rubus,* Poaceae and Adiantaceae. The latter two also show a cycle at 2000 years. (This latter result, however, is unsurprising given that the total sequence spans 4200 years and these two taxa become dominant in the sequence once during this time). Spectral analysis of the *Quercus* pollen data suggests three high cycles but different periodicities (~2000, 250 and 135 years).

Results from the cross-correlation analysis that considers the relationship between different taxa (Fig. 4.5) reveal that *Alnus, Salix,* Adiantaceae, Aspleniaceae and *Pteridium* are negatively correlated ($p<0.05$) with *Pinus* abundance at time lag 0; this implies that their abundances are shifting inversely but coinciding at approximately the same time intervals. Thus an increase in *Pinus* coincides with a decrease in *Alnus, Salix,* Adiantaceae, Aspleniaceae and *Pteridium.* In contrast, *Rubus* and *Parathesis* are correlated positively with *Pinus* abundance but at a lag –7; thus increases in *Pinus* are followed by increases in these two species but with a long time lag of around ~ 280 years.

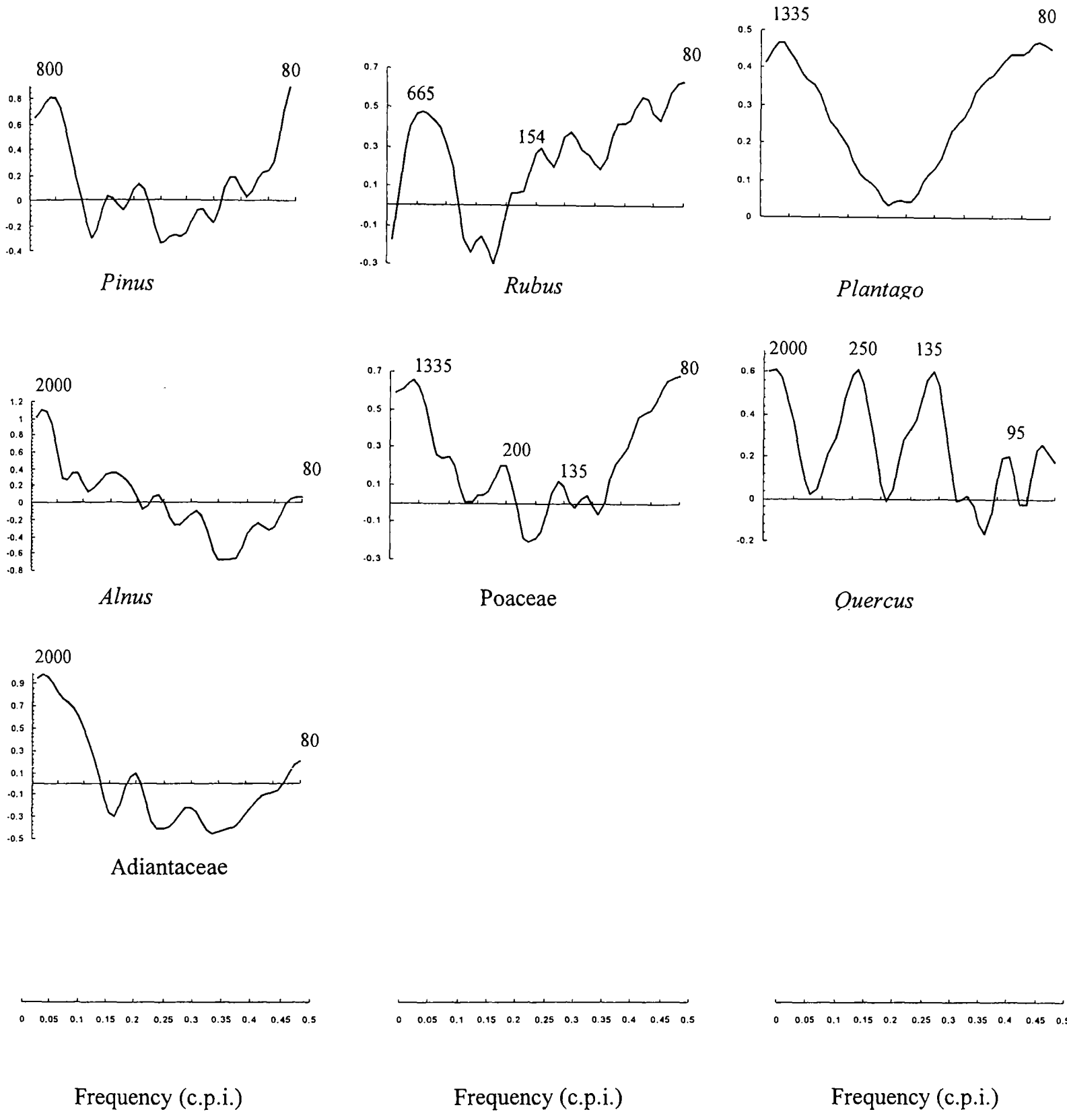


Fig. 4.4. Power spectra of pollen abundance in pine-dominated forest of West-Central Mexico for the last 4000 years. Vertical axes give spectral power in arbitrary units; horizontal axes give frequency in cycles per interval (c.p.i.). They represent the following periods in years; 0.1 = ~ 400, 0.2= ~200, 0.3= ~135, 0.4= ~ 100, 0.5= ~80; some specific periods are expressed at the highest peak.

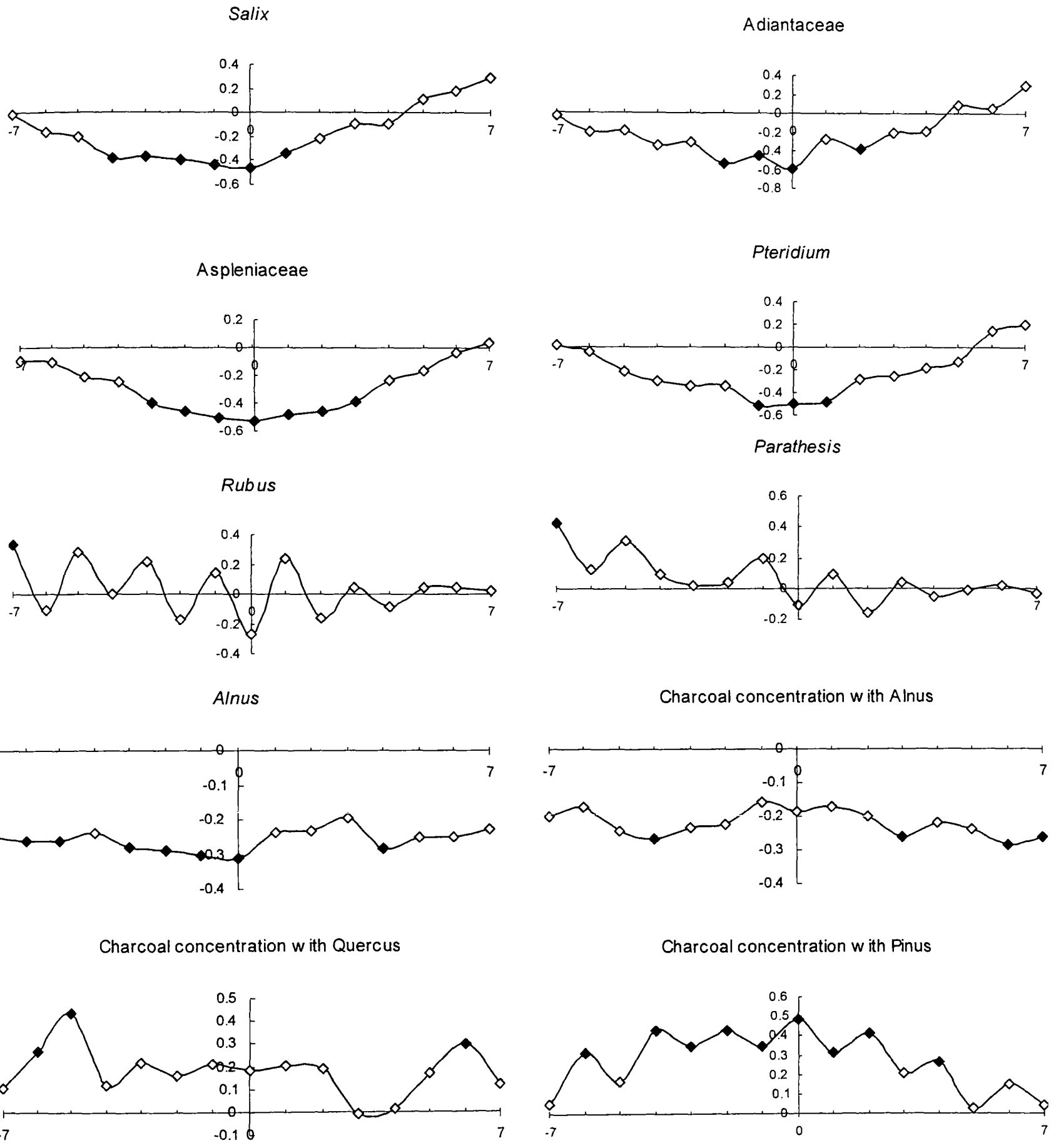


Fig. 4.5. Cross-correlations of *Pinus* pollen abundance with selected taxa. Vertical axes show correlations with non-significant ($p<0.05$) ones in open diamonds and significant ones in black filled diamonds. Horizontal axes give time in lags. Every lag has a sampling interval ~ 40 yrs. Positive lags correspond to delays and shift a series back in time; negative lags correspond to leads and shift a series forward in time.

4.4.3. Charcoal, magnetic susceptibility and loss-on-ignition

Results from microfossil charcoal analyses, magnetic susceptibility and percentage of organic matter in the sedimentary sequence are presented in Figure 6. *Pinus* pollen percentage values are also provided for comparison with these other three proxies.

Evidence from the charcoal record indicates that burning has occurred in this region throughout the last 4200 years. However, a higher input of microfossil charcoal, possibly suggests that a greater intensity of burning may have occurred between approximately 4200-2500 cal. yr BP and 1200- 500 cal yr BP (Fig. 4.6). These intervals of increased burning closely correspond to Pollen zones 1 and 3 and appear to coincide with a high abundance of *Pinus*. Similarly in the intervening period i.e. pollen zone 2 (2580 – 1260 cal. yr BP) there is a decline in *Pinus* abundance and a decline in charcoal concentration (Fig. 4.6). Results from the measurement of magnetic susceptibility indicate low values at the base of the sedimentary sequence with little variation from 4200-800 cal. yr BP. A dramatic increase occurs from approximately 800 cal. yr BP onwards and indicates a high input of fine-grained magnetic material into the basin. A gradual decline in magnetic susceptibility values is then apparent from approximately 300 cal. yr BP to the present.

Trends similar to the magnetic susceptibility results are apparent in the % organic matter estimated through loss-on-ignition. The percentage of organic material remains high throughout the sequence until approximately 800 cal. yr BP when the sediments contain increasing amounts of inorganic material (Fig. 4.6).

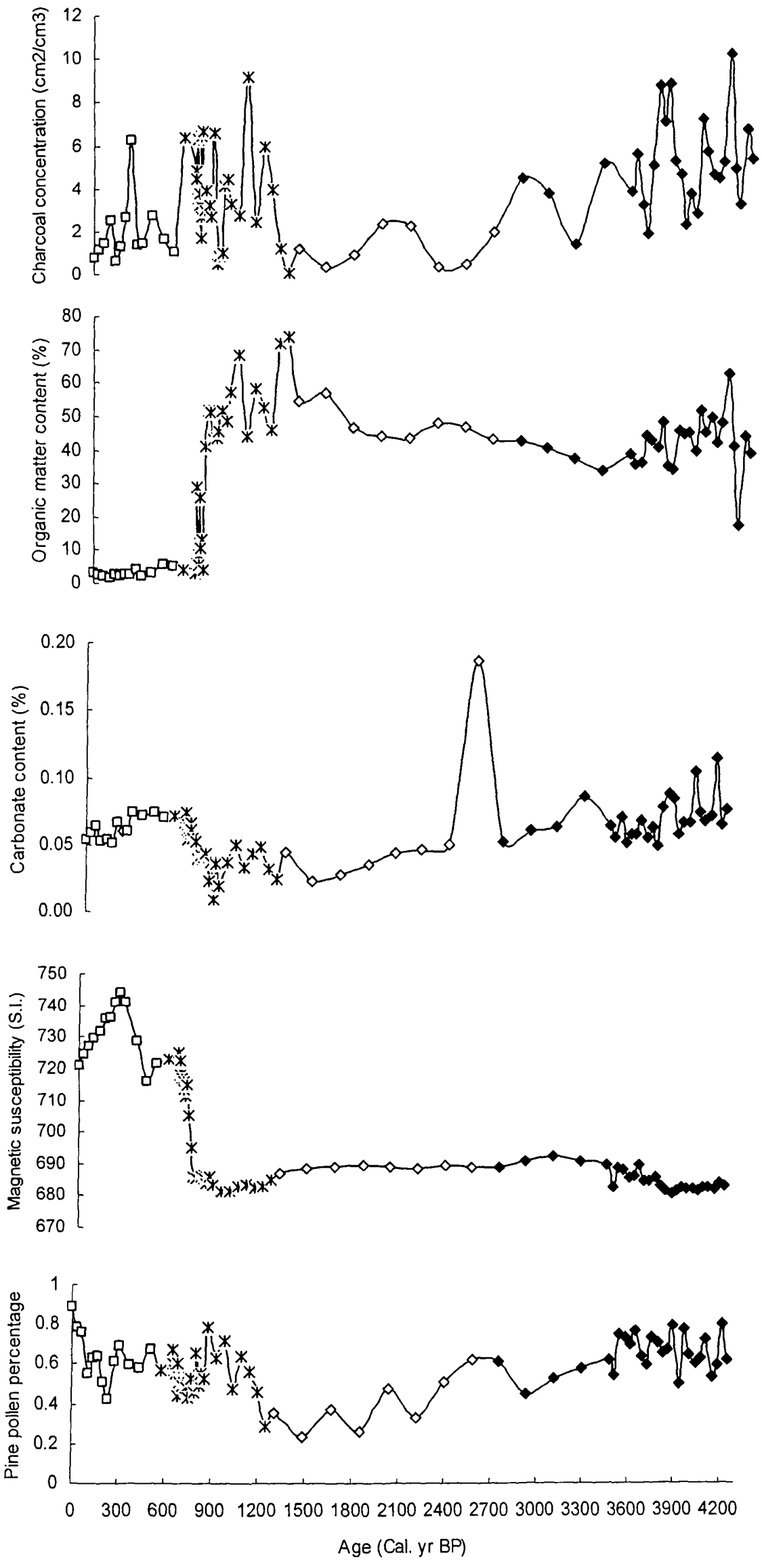


Fig. 4.6. Charcoal, magnetic susceptibility and percentage of organic matter in the sedimentary sequence from pine-dominated forests of West-Central Mexico over past 4200 years. Also displayed are the pine pollen abundance and the 4 pollen zones (displayed in Figure 3).

Results from cross-correlation analysis between the microfossil charcoal data and *Pinus* and *Alnus* pollen data (Fig. 4.5) indicate that charcoal is correlated negatively to *Alnus* but positively to *Pinus* and *Quercus*, but only *Pinus* shifts together with charcoal (lag 0). In contrast, increases in *Quercus* abundance occur 200 years after a charcoal peak.

4.5. Discussion

4.5.1. Dynamics of the pine-dominated forests over the past ~ 4200 years

Results from this study indicate that *Pinus* abundance has been fluctuating continuously for the past 4200 years in the uplands of West-Central Mexico (Fig. 4.3) with an evident periodicity every 80 yrs (Fig. 4.4). Throughout much of the time *Pinus* has been the forest dominant but *Alnus* became an important co-dominant from 3500 cal. yr BP and a large-scale contraction of the *Pinus forest* occurred ~ 2580-1260 cal. yr BP (630 B.C.-690 A.D.). With the decline in *Pinus* during this interval there was a corresponding increase in epiphytes associated with cloud forest and *Salix* but a decrease or even the absence of some open ground herbaceous vegetation including *Rubus* and Poaceae. The pine-dominated forest recovered from approximately 1200 cal. yr BP but became slightly less dominant once again from approximately 800 cal. yr BP with a corresponding increase in the open-ground herbaceous taxa along with taxa usually associated with anthropogenic activity and secondary vegetation e.g. *Plantago* and *Parathesis*. Cloud forest epiphytes (e.g. Adiantaceae, Aspleniaceae) and *Pteridum* also increased at this time.

Charcoal concentrations, indicative of burning in the region, appear to closely match variability in the pine vegetation over the past 4200 years (Figs 5 & 6); during times of high pine abundance, burning was widespread, whereas during intervals of reduced pine, there was reduced burning (Fig. 4.6). Burning, however, has been a constant feature of this landscape over the past 4200 years and there is no evidence to suggest an increase in frequency or amount of burning in recent decades related to anthropogenic activity.

4.5.2. Processes driving the observed changes

It is apparent that over the past 4200 years there has been significant variation in the composition of the forests in this region. Processes responsible for these changes include climate and anthropogenic activity. Each is considered in turn:

4.5.3. Climate

Previous work on the climate of Mexico reconstructed from various fossil proxies has revealed that over the past 4500 years BP broad-scale climate changes have occurred in both temperature and precipitation (Whitmore et al. 1996, O'Hara and Metcalfe 1997, Metcalfe et al. 2000, Almeida-Lenero et al. 2005). These changes were widespread and detected in records from Bolson de Mapimi in Durango and Coahuila, lake Zacapu in Michoacan, lakes Zempoala, Quila and Texcoco in Central Mexico, the northern Yucatan peninsula and the Pacific Guatemalan coastline. A general pattern that has emerged from these regions is one of widespread aridity between 4200-2500, 1200-850, and ~500-200cal. yr BP (Haug et al. 2000, Neff et al. 2006) probably driven by changes in the position of the Inter-tropical convergence

zone (ITCZ). Between these intervals of aridity were relatively moist periods. The longest of these was the interval of 2500-1200 cal. yr BP where a number of records indicate significant higher levels of humidity.

The links between this climate record and the changes in the pine/cloud forest taxa recorded in the pine-dominated forest pollen diagram are striking. During known intervals of aridity (i.e. 4200-2500, 1200-850, ~500-200 cal. yr BP) *Pinus* is the dominant taxon and there is significant burning in the region, whereas during intervals of increased humidity, cloud forest indicators (i.e. epiphytes) and a rise in the dominance of *Salix* is apparent. It is also noticeable that the boundaries for the pollen zones are extremely close to the transitions in climate recorded in these other records. The beginning of intervals of aridity at 1200 and 550 cal. yr BP, for example, coincide almost exactly with the lower boundaries of pollen zones 3 (dated to 1260 cal. yr BP) and pollen zone 4 (dated to 520 cal yr BP). Likewise the pollen zone boundary Z1 is dated at 2500 cal. yr BP, the time when proxies from other records indicate a transition into relatively moist conditions and in the pollen diagram (Fig. 4.3) there is evidence for a large increase in cloud forest taxa.

Evidence from the pollen diagram, however, also appears to suggest that the climate started to become more humid from approximately 3500 cal. yr BP (Fig. 4.3) when the first rise in *Alnus* and cloud forest taxa becomes apparent. *Alnus* is an arboreal element associated with humid Montane Forest in Mexico (Lozano-Garcia and Vazquez-Selem 2005) and is also associated with disturbed soils in the central Mexican highlands (Almeida-Lenero et al. 2005). There is no evidence from the magnetic susceptibility record (Fig. 4.6) to indicate that disturbance

resulting in topsoil erosion was occurring at this time interval and its expansion plus that of *Salix* is therefore almost certainly related an increase in humidity.

Superimposed on these longer climatic trends, it is also necessary to consider shorter climatic trends that have been recorded in other sedimentary sequences from Mexico. These include quasi-periodic oscillations at 200 and ~50-80 years recorded in lake and ocean sediments (Haug et al. 2000, Hodell et al. 2001) and thought to be linked to solar forcing resulting in drought-cycles at approximately these time intervals. Again there is evidence from the pine-dominated forest pollen record to indicate that the vegetation was probably responding to similar variations. In particular there are clear spectral peaks at ~80 years in *Pinus, Rubus, Plantago,* Poaceae and Adiantaceae. Less strong cyclicity is apparent at a 200-year interval in the dynamics of Poaceae. On both longer and shorter temporal timescales, therefore, there is clear evidence to suggest that the vegetation dynamics in the pine-dominated forests around the site have been strongly influenced by climatic changes and in particular by alterations in the precipitation regime.

4.5.4. Anthropogenic activity

So what impact did humans have on this landscape and the vegetation dynamics of the pine-dominated forest over the past 4200 years? Given the close links apparent above between known intervals of aridity, changes in the dominance of pine in the forest, and evidence for an increase in burning during these intervals, it is tempting to ignore the role of humans in this landscape. However, archaeological evidence from this region indicates that humans were present in the region from at least 3400±200 yr BP (Kelly 1980). Ceramics from the nearest

archaeological excavation to the site (e.g. Autlan – approximately 30 km), however, are considerably younger than this with dates to suggest occupation between 800-500 cal. yr BP (Kelly 1945).

Evidence from the pollen record does not indicate an early human impact on this landscape. There are no occurrences of early cultivars e.g. *Zea, Phaseolus, Cucurbita* that have been associated with agricultural practices as early as 6000 cal yr BP in other parts of Mexico (Perry et al. 1998) or any clear indications of clearance of forest vegetation along with a rise in weeds associated with agriculture (e.g. Chenopodiaceae, Asteraceae and Amaranthaceae) and charcoal (Pope et al. 2001). There is also no evidence from the magnetic susceptibility or percentage organic matter data for any soil erosion into the basin (Fig. 4.6). In fact both of these indicators suggest that despite the significant changes occurring in the vegetation and burning regime, the slopes around the basin remained remarkably stable from 4200 – 800 cal yr BP. However, from approximately 800 cal. yr BP a dramatic increase occurs in magnetic susceptibility and there is a corresponding large increase in inorganic material. Although this is also known to be one of the climatically wetter intervals, it is likely that the increase in these two proxies at this time (and not seen during previous wetter intervals) is related to soil erosion around the basin probably resulting from clearance for agricultural activities. A decline in *Pinus* also occurs at this time and a rise in a number of other taxa including types found presently in secondary vegetation (e.g. *Rubus, Parathesis*) and open-ground herbaceous vegetation (e.g. Poaceae, Asteraceae, Chenopodiaceae and *Plantago)*. Poaceae thrives well in sites with recurrent burning (Yallop et al. 2006). Evidence from the magnetic susceptibility and organic matter content also suggests that topsoil erosion has been occurring into the basin since 800 cal. yr BP to present even though archaeological evidence only indicates occupation

until 500 cal. yr BP; thus the slopes around the basin have never regained their former stability.

In contrast to evidence for anthropogenically induced topsoil erosion (probably through agricultural practices), there is little evidence to support a significant increase in burning associated with human activity. Between 800-500 cal yr BP there was a relatively high influx of charcoal into the basin but this was no higher than experienced in previous intervals in the record (Fig. 4.6) and since 500 years ago to present, charcoal influx has been less (with the exception of a single peak at 250 years ago) than in the previous 1000 years.

4.5.5. Are the pine-dominated forests an anthropogenically-derived forest-type?

Results from this study provide for the first time a detailed record documenting the long-term natural variability of the pine-dominated forests in West-central Mexico. From this study there are a number of assumptions about the origins of this forest type that need to be reassessed. The first question of whether the pine-dominated forests are an anthropogenically-derived forest-type? Results from this study would indicate that they are not but rather they are a product of intervals of aridity; when the climate becomes drier, the pine-dominated forests expand into this region. There is also no evidence to suggest that oaks and other broadleaved species are the natural trees in this region and the pine-dominated forests are consequence of secondary succession following disturbance as being suggested in other studies (Franco Mugica et al. 2005, Cayuela et al. 2006). In fact evidence from the pollen record indicates that although *Quercus* has maintained a remarkably stable presence in the forest over the past 4200 years (Fig. 4.3) it has never been the dominant vegetation type. Instead it has been an

intermediate element in the canopy and this has remained unchanged even during wetter intervals (e.g. 2500-1200 cal. yr BP) when *Pinus* became reduced and was replaced by cloud forest taxa, *Alnus* and *Salix*. The present dominance of *Quercus* in other parts of the reserve, often thought to be due to differences in levels of previous anthropogenic activity, must therefore be due to other factors. These include geology and soils, dispersal limitation and density-dependent recruitment (Olvera Vargas et al. 2006) rather than regional forest management that this taxon experienced in the past.

4.5.6. What is the role of fire in the maintenance of the pine-dominated forests?

Results from this study indicate that fire has been an important part of this ecosystem throughout the past 4200 years. In particular, burning appears to have been a key component of the pine-dominated forests and much of this burning was probably naturally induced and related to increased intervals of aridity; a result in agreement with studies of other temperate forests in North America (Faison et al. 2006, Nelson et al. 2006). As known from previous studies, fire is central to the regeneration of some pine species with many species having adaptations to cope with fires including thick bark, serotiny, rapid growth and sprouting (Agee 2000). What is also apparent from this study, however, is that in reduced intervals of burning, oaks do not become the dominant tree. This is in contrast to other regions, for instance, in Durango, Mexico where the suppression of natural fires is driving oaks to be favoured at the expense of pines due to their vegetative reproduction (Park 2001).

4.5.7. Human vs Natural legacy: Management implications

Results from this study indicate that in contrast to other areas in Mexico (Butzer 1992, Denevan 1992), this region has remained relatively unchanged by human activity over the past 4200 years and although it is highly probable that humans were in the region from at least 3400 years ago there is very little evidence for a significant impact on the landscape around the pine-dominated forest basin before approximately 800 cal. yr BP.

In terms of management of the study area, removal of humans in zones allocated for conservation therefore appears to be an appropriate decision because these pine-dominated forests are probably a naturally occurring vegetation type in response to drier climatic conditions. In wetter conditions this vegetation type is replaced by cloud forest taxa and an increasing dominance of *Alnus* and *Salix* in the forest. Such information should be incorporated into any climate-change conservation strategies for this region. What also emerges from this study, however, is the evidence that people have been using these forests for at least the past 800 years with little apparent detrimental effect. Thus the current conservation practice that allows some human activity (timber production, small-scale agriculture, prescribed burning) in some zones of the protected area also appears to be in keeping with the long-term viability of the pine-dominated forests. One final observation to emerge from this study is that fire is an important natural part of this pine-forest ecosystem. Therefore any management decision that involves suppression of fires will have a detrimental effect on the dominance of pines in these forests and should be avoided at all costs.

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5. PAPER 3

Cloud forest dynamics in the Neotropics during the Holocene

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Abstract

Questions: This paper aims to question how human disturbance and climate change have affected the temporal taxa turnover in a cloud forest assemblage in West-central Mexico over the last ~1400 years? Are the current conservation strategies undertaken in the cloud forest in accordance with its long-term dynamics?

Location: Sierra de Manantlan, Biosphere Reserve, West-central Mexico.

Methods: The temporal dynamics of the cloud forest is documented using palaeoecological studies. Analyses undertaken include fossil pollen, microfossil charcoal, and sediment geochemistry from an organic sedimentary sequence. A high sample resolution of one sample every ~32 years was assumed in order to provide data that is of relevance to the forest stand age.

Results: A high temporal taxa turnover has occurred in the cloud forest assemblage over the last ~1400 years with an apparent expansion of cloud forest from ~810 to 565 cal yr BP. There is also an apparent cyclicity in the dataset with turnover of certain taxa occurring between 150-65 years. Over the past 1400 years the main canopy dominants have been *Pinus*, *Quercus, Tilia, Carpinus, Fraxinus, Magnolia* and *Ilex* while epiphytes have been constant throughout. Climate change (in particular an interval of aridity between ~1200-810 cal. yr BP) and human disturbances through anthropogenic burning are the main drivers exerting changes on the dynamics of this cloud forest.

Conclusions: The cloud forest of the Sierra de Manantlan in West-central Mexico has not been a constant assemblage over the last 1400 years. The high vulnerability of this forest in response to climatic change and to anthropogenic influences is expressed in a high temporal taxa turnover with arboreal and non-arboreal components fluctuating in different cycles. The present results support the actual protection scheme for cloud forests in West-Central Mexico where areas are kept in exclusion zones to avoid timber extraction, grazing and agriculture.

Key words: *Agriculture; Conservation; Fire; Forest Ecology; Logging; Palaeoecology*

5.1. Introduction

Cloud forest is recognized as the terrestrial ecosystem with the highest diversity per unit area in Mexico and includes 10% of the Mexican flora and 12% of terrestrial vertebrates (Pineda & Halffter 2004). It is characterized by a complex biogeographical history that combines temperate and tropical elements and has specific environmental requirements including

constancy of humidity through fog presence, altitudinal distribution between 800-2700 m asl; precipitation range of 1000-3000 mm and temperatures from 12-23°C (Rzedowskii 1981). In terms of geographical distribution it is more continuous on the Atlantic slope than the Pacific and it is mainly restricted to humid ravines (Rzedowski 1996). The West-central region of Mexico, in particular, contains several cloud forests blocks discontinuously distributed within the Pacific part of the Serranias Meridionales province (Luna Vega et al. 1999). Presently cloud forest is an extremely fragmented forest (Luna Vega et al. 2000) covering less than 1% of the country, a situation exerting threats on its current structure and functioning. The causes thought to be responsible for its fragmentation are climate change and human activities comprising clearing for agriculture, livestock grazing and logging (Bubb et al. 2004). Several stands containing this forest are located inside the Sierra de Manantlan Biosphere Reserve in West-Central Mexico, a protected area by government decree since 1987. In the Sierra de Manantlan forests have been strictly protected and excluded from any human intervention (grazing, logging, agriculture) for at least the past 20 years though human activity is known to have occurred in this area since pre-Hispanic times (~1200 A.D) (Kelly 1945, Kelly 1980).

Cloud forest in Manantlan represents mature communities and contains ~23% of all vegetation types in the area and the highest taxonomic richness (Cuevas-Guzmán et al. 2004); these characteristics, in concert with its fragmented character, high beta diversity (Vazquez-Garcia & Givnish 1998), heterogeneous structure and few individuals by species highlight this forest of high conservation priority.

Considering that many of the tree types in the cloud forest (*Quercus, Tilia, Clethra, Dendropanax, Carpinus*, etc.) have generation times > 50 years, a longer-term perspective it is essential to fully appreciate the processes responsible for its current fragmentation and to determine adequate conservation and management strategies (Willis & Birks 2006). At present, the longest perspective of cloud forest dynamics in Mexico are data spanning no more than one decade (Alvarez-Aquino et al. 2004, Ramirez-Marcial 2003, Suarez Guerrero & Equihua 2005, Williams-Linera 2002); longer studies of several decades and centuries are still very patchy in Mexico and centered in the Yucatan Peninsula in lowland vegetation (Curtis et al. 1996, Hodell et al. 2005a, Hodell et al. 2001, Hodell et al. 2005b) or in Central Mexico mainly in Pine, Pine-Oak and Fir forests (Almeida-Lenero et al. 2005, Arnauld et al. 1997, Gonzalez-Quintero 1986, Lozano-Garcia et al. 1993, Metcalfe 1995, Metcalfe et al. 2007).

The aim of this study, therefore, was to reconstruct the long-term dynamics of the cloud forest in the Sierra de Manantlan in order to address the following key questions: How have past human disturbances and climate change affected the temporal taxa? What are predominant processes responsible for its present day composition and distribution? Are conservation strategies currently in place for the cloud forest in this region in accordance with its long-term dynamics?

For the reconstruction of the temporal vegetation dynamics proxies analysed include fossil pollen, microfossil charcoal, inorganic and organic sedimentary analyses. The data spans the last ~1400 years covering Pre and Post Hispanic occupation periods and a crucial time of important climatic change occurring in Mexico (Beach et al. 2006, Curtis et al. 1996, Hodell et al. 2005a, Hodell et al. 2001, Hodell et al. 2005b, Hodell et al. 1995).

5.2. Study Area

The cloud forest selected for this study is located at 19°, 35 '325'' N, 104°, 16' 559" W approximately 1820-1890 m asl (Fig. 5.1) in the Sierra de Manantlan, Biosphere Reserve in West-Central Mexico. The environmental characteristics most influential in determining the distribution of the cloud forest in the SMBR are a temperate subhumid climate with temperatures from 8-25°C, rainfall range of 1000-1700 mm and the constancy of fog and humidity throughout the year (Vazquez-Garcia et al. 1995).

The geological history of the region dates back to the Cenozoic subduction volcanism in Central Mexico that built two major volcanic arcs: the Sierra Madre Occidental silicic volcanic province and the roughly east-West trending Trans-Mexican Volcanic Belt (Rossotti et al. 2002).

The cloud forest is a highly diverse community with 483 taxa including trees, shrubs and herbs (Cuevas-Guzmán et al. 2004). In the arboreal component the predominant trees are *Carpinus tropicalis, Clethra vicentina, Cornus disciflora, Ilex brandegeana, Magnolia iltisiana, Ostrya virginiana, Persea hintonii, Pinus douglasiana,*

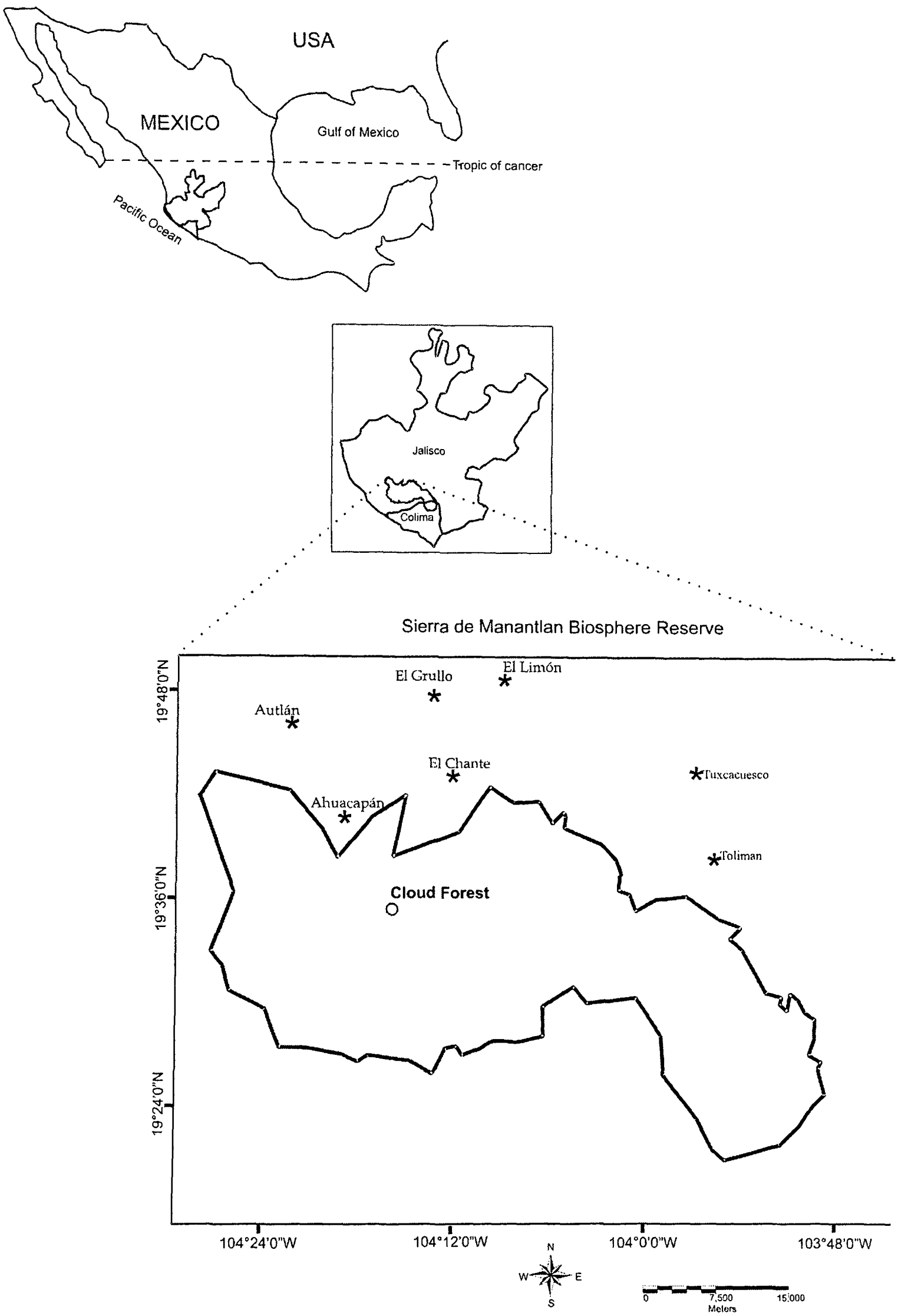


Fig. 5.1. Map with the location of the cloud forest in the Sierra de Manantlan Biosphere Reserve; * archaeological sites; ○coring site.

Quercus xalapensis, Quercus candicans, Quercus castanea, Quercus xalapensis, Tilia americana var. mexicana and *Zinowiewia concinna*; in the understory *Parathesis villosa* and *Euphorbia* sp. are the most common shrubs (Vazquez-Garcia et al. 1995). The non-arboreal component of the cloud forest includes terrestrial herbs, climbers and epiphytes (mosses, lichens, orchids and bromeliads) with the following families being the most representative: Adiantaceae, Aspleniaceae, Grammitidaceae, Hymenophyllaceae, Lycopodiaceae, Orchidaceae and Polypodiaceae.

In the early 1900's the cloud forests of the Sierra de Manantlan Biosphere Reserve were extensively logged until 1987 when they became protected in Core zones of the biosphere reserve. This protection scheme excluded most human interference such as grazing, timber harvesting and agriculture (SEMARNAP 2000) from these zones.

5.2.1. Archaeology and culture

One of the nearest archaeological sites to the cloud forest was located in Autlan (19°, 46 '05'' N, 104°, 21' 59" W)(Fig. 5.1) which, at present, is the largest population center around the Sierra de Manantlan Biosphere Reserve (53,269 inhabitants). Forty-three archaeological sites have been explored in the Autlan Zone spanning from ~1200 to 1500 A.D. (Kelly 1945). A detailed account of early occupations revealed that Autlan was a region of high civilization, Toltec in origin and Otomi as the main language. Human activities, mainly based on agriculture, have been continuous in this region even before the Spanish conquest (before 1521 A.D.); maize and chilli were the main staples whilst clothing was manufactured using

cotton and maguey (Kelly 1945). Ceramics, which are designated as *Cofradia* spanning to the *Aztec I-Chichimec* period, were also developed.

5.2.2. Climate change

Detailed records of climate change for this particular region are unavailable, as most palaeo-reconstructions of climate change in Mexico have focused on Central Mexico and the Yucatan Peninsula. From these studies it is apparent that in Central Mexico humid conditions prevailed from 4000 to around 2500 yr BP (Almeida-Lenero et al. 2005, Gonzalez-Quintero 1986, Lozano-Garcia et al. 1993, Metcalfe et al. 2000), dry conditions from 2500 to 1900 yr BP (O'Hara et al. 1993) with another period of pronounced aridity around 1000 yr BP (Arnauld et al. 1997, Metcalfe & Hales 1994, Metcalfe 1995, O'Hara et al. 1993). In the Yucatan Peninsula wet conditions prevailed until 3000 yr BP and again evidence for an arid interval between 1500 and 900 yr BP that coincides with the collapse of the Mayans (Beach et al. 2006, Curtis et al. 1996, Hodell et al. 2005a, Hodell et al. 2001, Hodell et al. 1995).

5.3. Methods

5.3.1. Coring and Sediment sampling

A 96 cm sedimentary core of black organic material was retrieved from a small forest hollow (approximately 11m x 8m diameter) in the cloud forest the Sierra de Manantlan Biosphere

Reserve at 19°, 35 '325'' N, 104°, 16' 559" W (Fig. 5.1), using a Russian corer (Glew et al. 2001). The core was extruded in the field, wrapped and returned to the Oxford Long-term Ecology laboratory for further analyses.

In the laboratory, magnetic susceptibility was assessed every 1cm through a susceptibility loop using a Bartington MS2 appliance to measure the occurrence of iron-bearing minerals as a proxy for erosion of mineral soil or fire created magnetite or maghemite (Thompson & Oldfield 1986). The core was then sectioned in 1 cm^3 sub-samples for loss-on-ignition analysis (LOI) to measure the contents of carbonate and organic carbon in the sedimentary sequence (Dean 1974).

5.3.2. Chronology

A chronology for the sedimentary sequence was established by AMS radiocarbon dating from two laboratories (*Poznan,* Poland and *East Kilbride*, UK). Six organic samples taken at regular intervals down through the core were analysed and the results were calibrated using the CALIB v5.02 and INTCAL04.14 programs (Stuiver & Reimer 1993). The age-depth relationship was modelled using linear interpolation (Bennett 1994).

5.3.3. Fossil Pollen analysis

The standard acetolysis method was used to extract pollen (Bennett & Willis 2001); *Lycopodium* spore tablets were added to the pollen samples to act as markers to estimate concentrations (pollen grains cm^{-3}). To obtain a statistically significant sample size at least 400

pollen grains were counted per sample (Maher 1972). The sequence was analysed every two centimetres totalling 48 samples.

Pollen types were identified using a pollen and spore reference collection of trees, shrubs and herbs collected during the field season in the study area together with the reference collection held in the Long-term Ecology Laboratory, Oxford University Centre for the Environment.

Microfossil charcoal analysis

Microfossil charcoal concentration was evaluated by the point count method (Clark 1982) using the same sample interval (two centimetres) as for pollen.

5.3.4. Geochemical analysis

Sample resolution for geochemical analysis was the same as for the pollen analysis. A modified technique of the acid digestion method (Bengtsson & Enell 1986) was undertaken whereby soluble concentrations of different elements were determined using ICP-MS (Inductively Coupled Plasma Mass Spectometer) with a Perkin Elmer spectometer based in the Earth Sciences Department of the University of Oxford. These analyses can provide an insight into process of land degradation originated by disturbance (logging, clearance, fire) (Haberle & Bennett 2001, Willis et al. 1997, Willis et al. 1998).

5.3.5. Statistical Analysis

Pollen data was plotted and divided into zones by optimal splitting and significant zones were determined using a broken-stick model (Bennett 1996, Bennett 2005); rarefaction analysis (Birks & Line 1992) was applied to provide an estimate of the palynological richness for each sample. The above-mentioned procedures were undertaken using PSIMPOLL 4.25 and PSCOMB 1.03 software (Bennett 2005). To detect significant differences in variables among the zones determined by optimal splitting (elemental concentrations, microfossil charcoal, magnetic susceptibility, organic matter, carbonate content, pollen concentration and palynological richness), a one-Way ANOVA was calculated using (SPSS 2005). Spectral analysis was used to detect peaks symptomatic of cyclical changes in pollen taxa, microfossil charcoal, magnetic susceptibility, organic matter and elemental concentrations according to the methods described by (Box & Jenkins 1970) using POLSTA v.7.0 software (Green 1989). All spectral estimates were carried out using a Bartlett window.

5.4. Results

5.4.1.Chronology

Results of the AMS dating indicate that sediment accumulation began about 1635 ± 35 ^{14}C yr BP and continues to present showing a consistent stratification with no interruption (Table 5.1). Deposition time indicates that 1cm of sediment accumulates every 16 years. The resulting sampling interval considers a reconstruction every 32-years starting at approximately

1400 cal yr BP (pollen preservation before this time was poor and did not allow preservation of a statistically significant sample size). The sequence covers pre (dates before A.D. 1519) and post Hispanic (after A.D. 1521 including the Spanish Colony, A.D. 1521-1821) episodes.

Table 5.1. Radiocarbon dates and calibrated dates for cloud forest using CALIB v5.02 and INTCAL04.14 programs through the probability method (Stuiver, 1993).

Depth (cm)	Laboratory code	^{14}C age (yr BP)	Calibrated age range (cal yr BP)
16	SUERC-5872	205±24	190-215
40	SUERC-5873	585±21	540-565
60	SUERC-5874	745±24	665-715
75	SUERC-5877	925±21	790-915
82	Poz-10750	1100±30	950-1060
96	Poz-4747	1635±35	1515-1570

5.4.2. Temporal vegetation dynamics

The reconstruction is based on dates from ~1400 cal yr BP to present. All pollen types are displayed in the results, even those with scarce number of grains, in order to portray the different rare taxa (Fig. 5.2). This is because previous work on the modern pollen signature indicates that for the determination of cloud forest it is essential to include rare or very infrequent taxa (Figueroa-Rangel et al. *In preparation*). Arboreal taxa indicative of cloud Forest (Table 5.2) are represented throughout the entire sequence though with low abundances. However, as has been previously demonstrated epiphyte spores such as Other Aspleniaceae, Hymenophyllaceae and Polypodiaceae are good indicators of cloud forest presence and their percentages are high at certain intervals in the diagram (Fig. 5.2). The first appearance for maize is about 1310 cal yr BP but other cultural taxa, Chenopodiaceae, Poaceae and Asteraceae, are present since 1400 cal yr BP (Fig. 5.2).

Table 5.2. Present-day taxa representative of cloud forest in the Sierra de Manantlan, Biosphere Reserve, west-central Mexi

Arboreal taxa (species)	**Non-Arborea taxa (familie**
Abies religiosa	Araceae
Alnus jorullensis	Betulaceae
Carpinus tropicalis	Asclepiadaceae
Cinnamomum pachypodum	Aspleniaceae
Citharexylum mocini	Asteraceae
Clethra mexicana	Begoniaceae
Cleyera theaeoides	Bromeliaceae
Clusia salvinii	Convolvulaceae
Conostegia volcanalis	Cyperaceae
Cornus disciflora	Dennstaedtiaceae
Dendropanax arboreus	Euphorbiaceae
Fraxinus uhdei	Hymenophyllaceae
Fuchsia arborescens	Leguminosae
Garrya laurifolia	Melastomataceae
Hedyosmum mexicanum	Ophioglossaceae
Ilex brandegeana	Orchidaceae
Inga eriocarpa	Piperaceae
Juglans major	Poaceae
Lippia alba	Polypodiaceae
Magnolia iltisiana	Rubiaceae
Matudea trinervia	Solanaceae
Meliosma dentata	Thelypteridaceae
Oreopanax echinops	Umbelliferae
Ostrya virginiana	
Parathesis villosa	
Perrottetia longistylis	
Persea hintonii	
Pinus douglasiana	
Prunus cortapico	
Quercus candicans	
Quercus salicifolia	
Rhamnus hintonii	
Rondeletia manantlanensis	
Sebastiana jalicensis	
Styrax argenteus	
Symplococarpon purpusii	
Symplocos citrea	
Tilia americana var mexicana	
Triumfetta	
Vaccinium sp.	
Xylosma flexuosum	
Zinowiewia concinna	

The four pollen zones by optimal splitting are named according to Mexican history; pre-Hispanic (before A.D. 1519), before the Spanish conquest and post-Hispanic (after A.D. 1521) including the Spanish conquest, Spanish Colony and recent times (Fig. 5.2):

Z1 (92-74 cm; 1400-830 cal. yr BP; 560 A.D.-1120 A.D.) pre-Hispanic I

In this zone only a few arboreal taxa predominate (*Pinus, Quercus, Alnus, Magnolia* and *Carpinus*) and some are only present in the first half of the zone (*Clethra*, Lauraceae and *Tilia*)(Fig. 5.2a). Although these are taxa commonly found in present-day cloud forest (Table 5.2), the sum including all cloud forest taxa indicates that the cloud forest assemblage has lower percentage values that the following zone (Figure 2b). This is due to the low values for Aspleniaceae (Fig. 5.2b). Other epiphytes (Polypodiaceae and Hymenophyllaceae) however show their highest values for this zone.

In terms of herbaceous taxa the high percentage values in Poaceae and Asteraceae indicate that the canopy was probably fairly open. The lowest pollen concentrations occurred at 1235 cal. yr BP (715 A.D.) and another at 830 cal. yr BP (1120 A.D.)(Fig.5.3, Table 5.3).

Z2 (72-42cm; 810-565 cal. yr BP; 1140 A.D.-1385 A.D.) pre-Hispanic II

This zone is a flourishing stage for cloud forest as is revealed by the highest percentages in cloud forest taxa (Fig. 5.2b) as well as the highest values in pollen concentration with a peak in richness at 580 cal. yr BP (1370 A.D.) (Fig. 5.3). *Quercus* expresses high percentages in this zone together with *Clethra, Meliosma, Carpinus, Parathesis, Adiantum* and *Anograma*

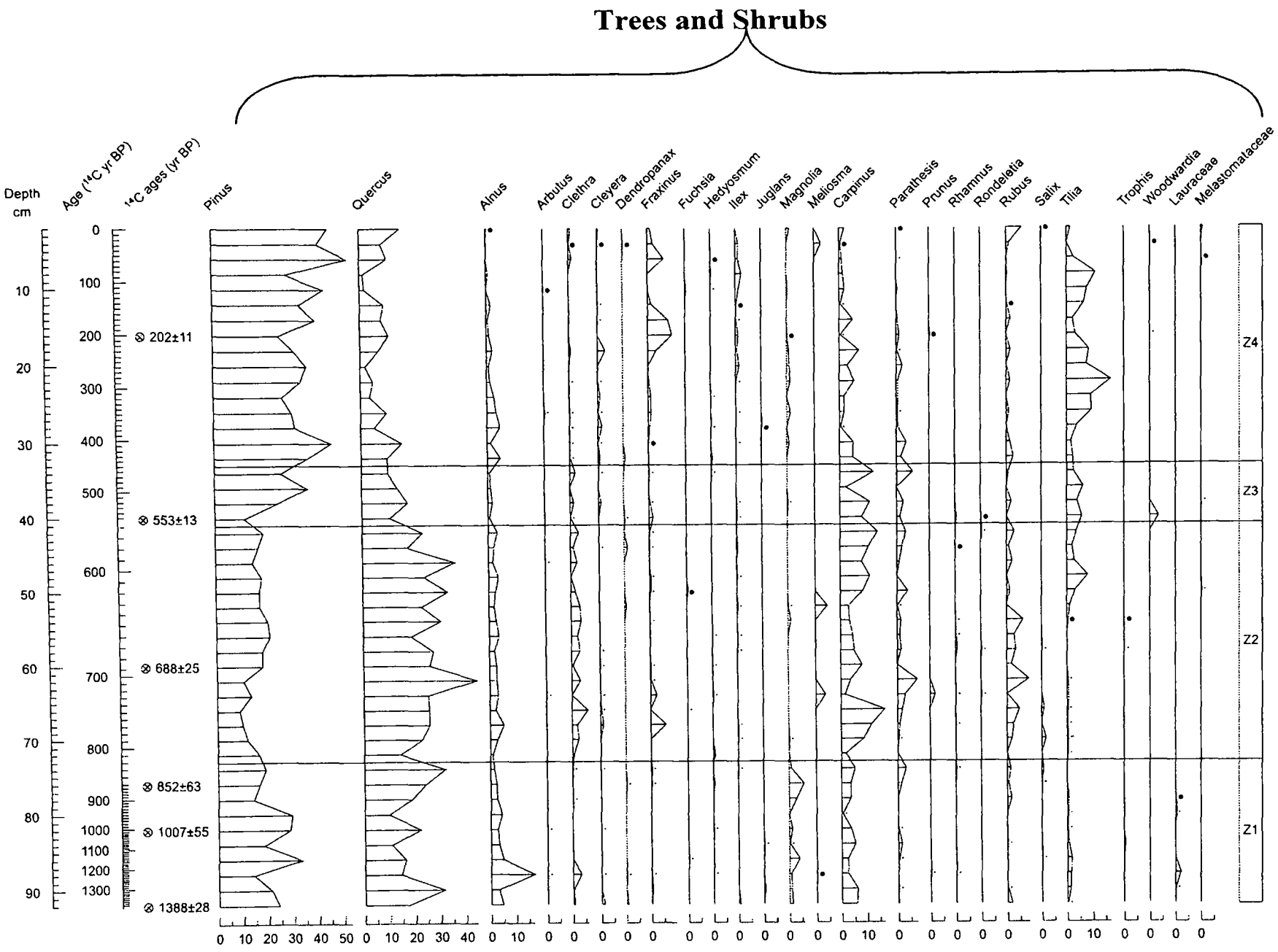


Figure 5.2a. Pollen diagram of cloud forest trees and shrubs in West-Central Mexico. Ages are calibrated years BP. Divisions are delineated by zones according to optimal splitting using PSIMPOLL 4.25 .

(Fig. 5.2a and 2b). *Pinus* shows constant percentages throughout the zone though the lowest of the whole sequence.

Z3 (40-34cm; 555-465 cal. yr BP; 1395 A.D.-1485 A.D.) pre-Hispanic III

This is also a predominant cloud forest stage, although an evident increase in *Pinus* beginning in this zone coincident with a decline in *Quercus* and low percentages in *Alnus*. Cultural taxa such as *Zea* sp. and the families Chenopodiaceae, Asteraceae and Poaceae are scarce or even absent (Fig. 5.2b). This is also the zone with an abrupt decrease in palynological richness at ~495 cal. yr BP (1455 A.D.) (Fig. 5.3, Table 5.3).

Z4 (32-0cm; 435-cal. yr BP to present; 1515 A.D.-to present) post-Hispanic

Some cloud forest taxa decrease in this zone (*Quercus, Clethra,* and *Carpinus*) while others (*Cleyera, Fraxinus, Ilex* and *Tilia*) increase (Fig. 5.2a). When considering all the taxa representative of cloud forest (epiphytes included) a clear decrease in cloud forest taxa can be observed (Fig. 5.2b).

Pinus shows its highest percentages in this zone while the maximum number of rare pollen types (e.g. *Dalea, Polygonum,* Umbelliferae, Juncaceae and Liliaceae) is observed for these ages although they are not displayed graphically.

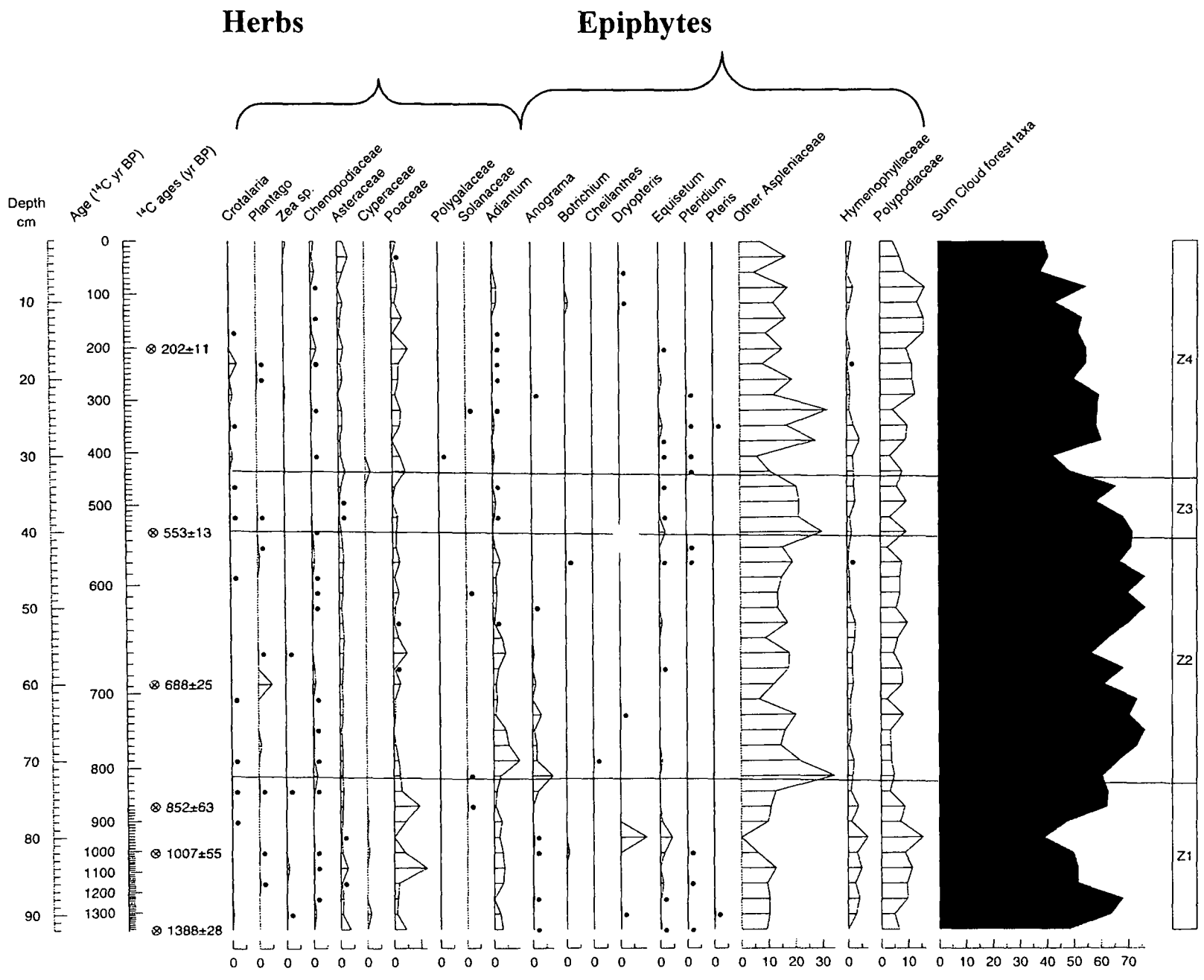


Figure 5.2b. Pollen diagram of cloud forest herbs and epiphytes in West-Central Mexico. The sum of all cloud forest taxa contributing to the total pollen sum is also displayed. Ages are calibrated years BP. Divisions are delineated by zones according to optimal splitting using PSIMPOLL 4.25 .

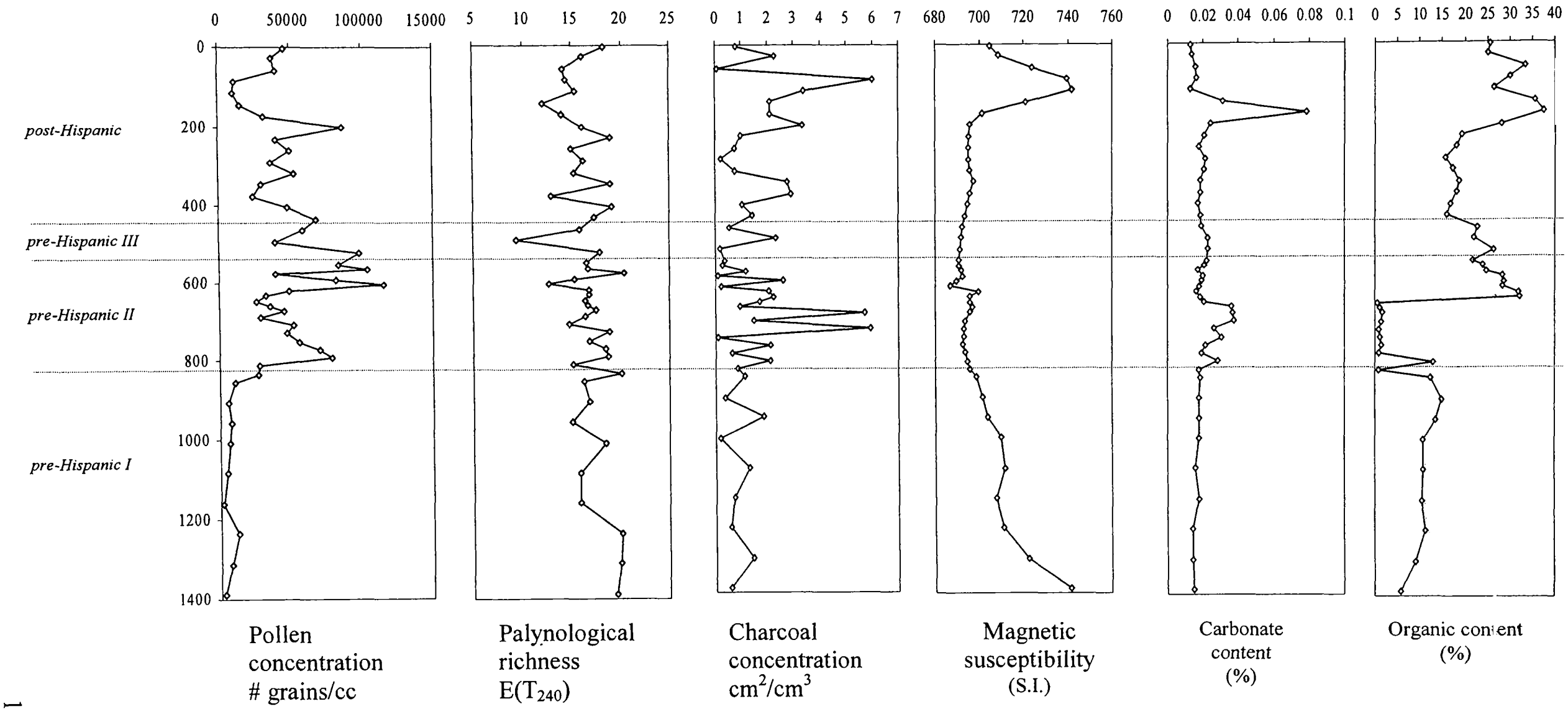
5.4.3. Environmental dynamics

The environment surrounding the cloud forest has been changing over the last 1400 yrs in tandem to the pollen fluctuations (Figs. 5.2a, 5.2b and 5.3). Burning has occurred irregularly over those years with the greatest peak in the pre-Hispanic II and post-Hispanic zones. The organic content of the sedimentary sequence experiences a noticeable increase around ~650 cal. yr BP (1300 A.D.) (Fig. 5.3, Table 5.3). Carbonate content has remained stable throughout the past 1400 years except for an abrupt raise at ~175 cal. yr BP (1775 A.D.) coinciding with a peak in organic matter. Magnetic susceptibility exhibits its highest values in the basal section of the core gradually declining until an abrupt increase around 115 cal. yr BP (1835 A.D.) (Fig. 5.3). Maximum values for most of the inorganic geochemical elements occur in zone Z1 while minimum values occur in zone Z3 (Fig. 5.4, Table 5.3).

Table 5.3. Descriptive statistics and ANOVA significant values (in bold) among the four zones delineated according to optimal splitting for the inorganic, organic and palynological components in the sedimentary sequence recovered in cloud forest of West-Central Mexico.

	Zones				
	Z1	Z2	Z3	Z4	
Variables					Sig.
Pollen concentration (# grains cm^{-3})	6217±2432	52324±14564	69992±41705	39301±10763	**0.000**
Palynological richness $E(T_{240})$	17.76±1.4	16.73±0.9	14.90±6.0	15.90±1.1	0.093
Charcoal concentration (cm^2/cm^3)	1.01±0.4	1.84±0.9	0.84±1.6	1.93±0.8	0.272
Magnetic susceptibility (S.I.)	717.03±14.4	693.54±1.7	691.50±0.9	706.16±8.7	**0.000**
Carbonate content (%)	0.02±0.0	0.02±0.0	0.02±0.0	0.02±0.0	0.289
Organic matter content (%)	10.61±2.0	13.75±7.3	23.38±3.5	23.87±3.9	**0.003**
Geochemical Elements					
Mg ($g\ kg^{-1}$)	4.02±1.1	0.78±0.1	1.04±0.9	1.73±0.6	**0.000**
Al ($g\ kg^{-1}$)	21.52±6.2	18.37±4.1	16.78±14.1	20.77±4.0	0.626
Fe ($g\ kg^{-1}$)	13.56±3.2	4.04±1.1	3.82±3.4	8.54±2.0	**0.000**
Ca ($g\ kg^{-1}$)	1.21±0.4	1.14±0.2	0.71±0.7	1.19±0.2	0.270
P ($g\ kg^{-1}$)	0.77±0.4	0.77±0.1	0.58±0.5	0.89±0.2	0.527
Na ($mg\ kg^{-1}$)	51.84±23.8	41.84±37.2	25.26±30.0	43.44±13.7	0.820
K ($mg\ kg^{-1}$)	340.18±83.4	75.50±28.1	10.3.09±45.7	41.20±43.3	**0.000**
V ($mg\ kg^{-1}$)	95.08±22.7	76.93±15.9	45.54±41.7	45.14±10.7	**0.000**
Cr ($mg\ kg^{-1}$)	12.53±3.0	6.34±1.2	3.80±3.5	5.07±1.1	**0.000**
Mn ($mg\ kg^{-1}$)	140.65±37.9	32.89±6.3	33.80±22.4	85.71±25.8	**0.000**
Co ($mg\ kg^{-1}$)	8.61±2.2	1.82±0.4	2.37±1.8	4.39±1.1	**0.000**
Cu ($mg\ kg^{-1}$)	32.98±8.3	22.97±4.3	22.22±17.3	25.20±5.3	0.081
Sr ($mg\ kg^{-1}$)	7.44±1.8	10.26±2.0	7.28±6.3	11.14±2.1	**0.047**
Cd ($mg\ kg^{-1}$)	0.06±0.1	0.10±0.0	0.06±0.1	0.09±0.0	**0.032**
Ba ($mg\ kg^{-1}$)	97.19±23.9	52.18±8.7	45.72±37.3	85.71±19.0	**0.000**
La ($mg\ kg^{-1}$)	9.97±2.5	8.41±1.3	7.65±6.0	10.53±2.0	0.203
Ce ($mg\ kg^{-1}$)	23.22±6.3	18.66±3.2	18.28±14.9	22.95±4.5	0.307
Nd ($mg\ kg^{-1}$)	15.40±4.0	12.84±2.2	13.18±11.3	16.62±3.1	0.223
Pb ($mg\ kg^{-1}$)	3.97±1.1	2.30±0.4	2.41±2.1	4.54±1.0	**0.000**
Th ($mg\ kg^{-1}$)	1.73±0.5	1.14±0.2	1.07±0.9	2.01±0.8	0.075
U ($mg\ kg^{-1}$)	0.36±0.1	0.24±0.1	0.24±0.2	0.31±0.1	**0.042**
Zn ($mg\ kg^{-1}$)	117.88±29.1	62.01±11.8	52.95±41.5	70.88±12.6	**0.000**

Fig. 5.3. Environmental and vegetation dynamics of a cloud forest in West-Central, Mexico. Zones are delineated according to optimal splitting and labeled following cultural events in Mexican history.



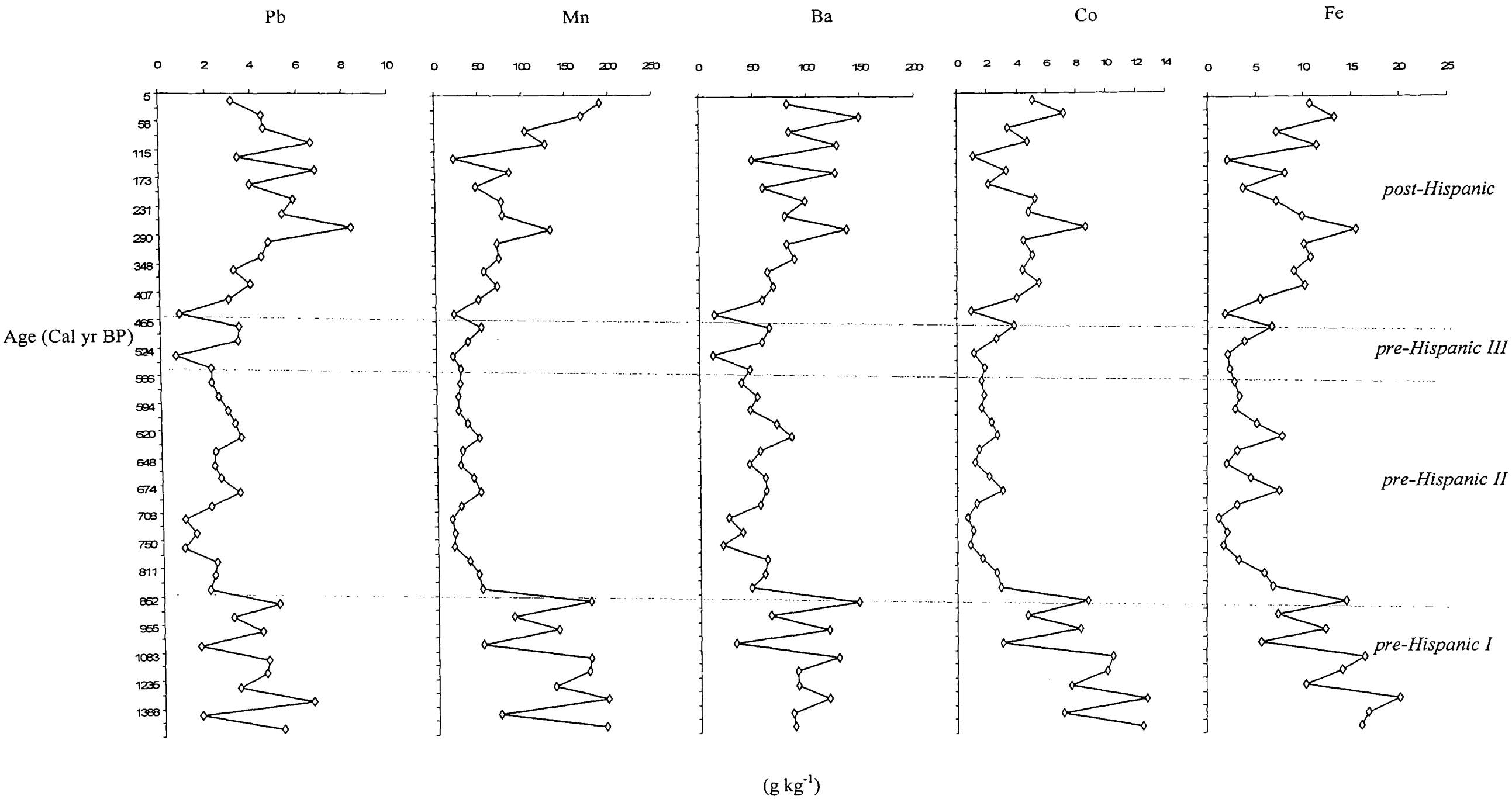


Fig. 5.4. Geochemical dynamics for some elements in a cloud forest of West-Central, Mexico.

5.4.4. Cyclic Dynamics

A cyclicity at every 64 years is apparent in the dataset for trees and shrubs (*Pinus, Quercus, Parathesis, Rubus, Carpinus* and *Clethra*), as well as for Poaceae and epiphytes (Polypodiaceae and Aspleniaceae). There is also a cycle apparent at 95-year for Polypodiaceae and Hymenophyllaceae. (Fig. 5.5). Others cycles at 115 and 120-year are also apparent for the cultural taxa Asteraceae and Poaceae. For *Magnolia, Fraxinus, Tilia* and *Carpinus* peaks are revealed at 170, 175, 213 and 405-years respectively. A 65-year cycle similar to some of the taxa is also detected for charcoal, Na and Ba. Peaks from 70-80 years are evident in Ca, Cu, V, Cr, Mn, Mg, Pb and Magnetic susceptibility. Al and Fe have peaks at 125-years (Fig. 5.6).

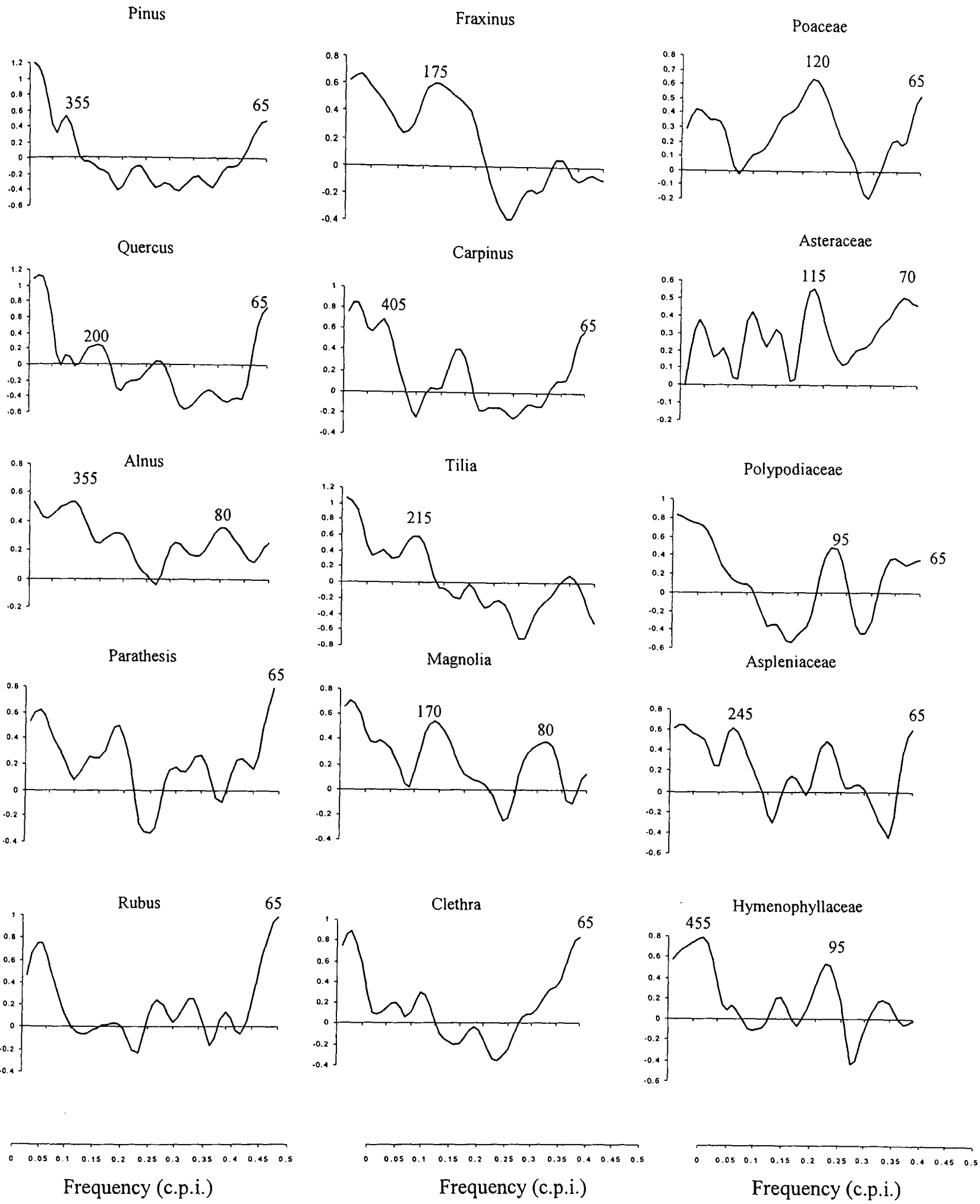


Fig. 5.5. Power spectra of pollen abundance in cloud forest of West-Central Mexico for the last ~1635 years. Vertical axes give spectral power in arbitrary units; horizontal axes give frequency in cycles per interval (c.p.i.); they represent the following periods in years; 0.1 = ~ 320, 0.2= ~160, 0.3= ~100, 0.4= ~ 80, 0.5= ~65; some specific periods are expressed at the highest peak.

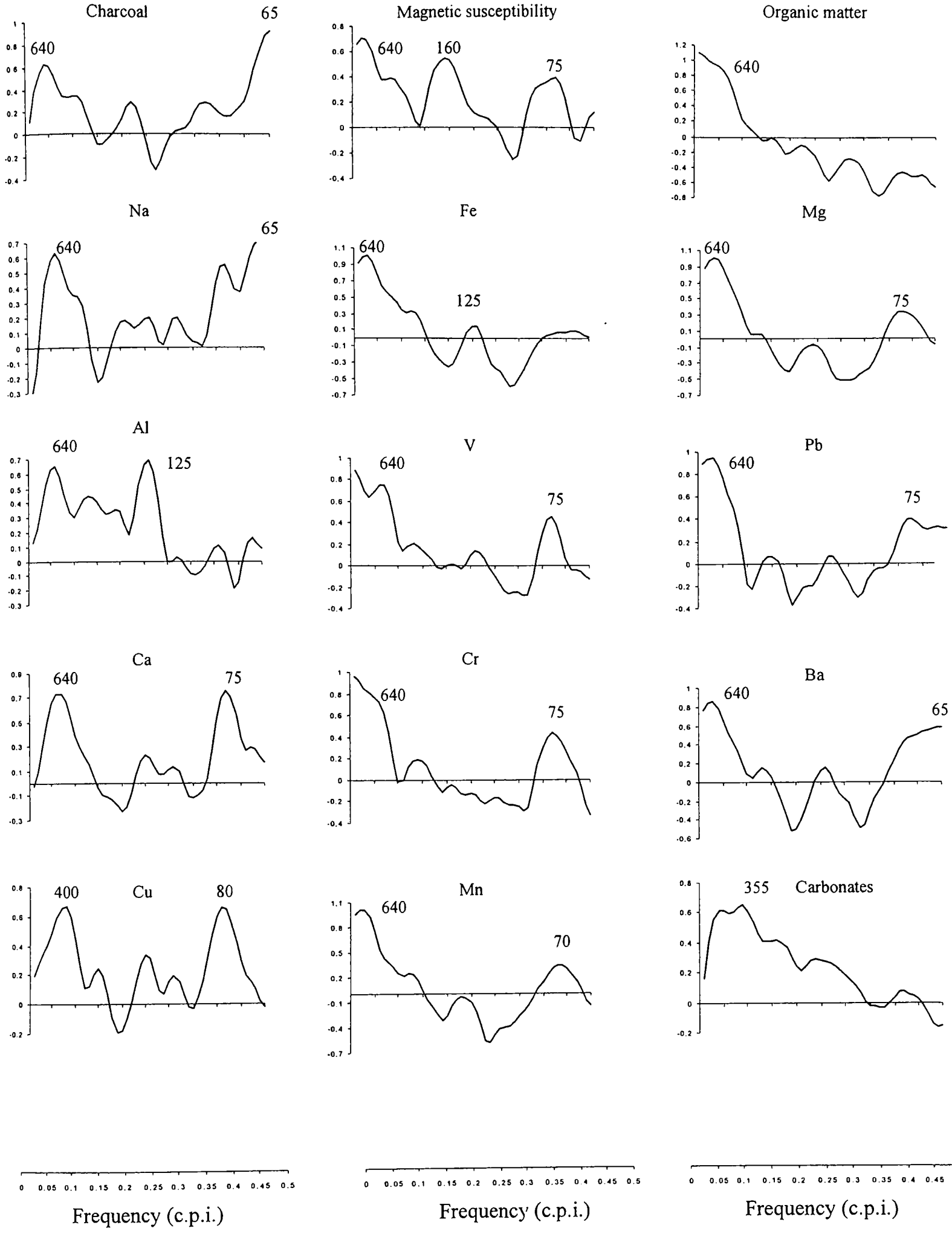


Fig. 5.6. Power spectra of some environmental variables in cloud forest of West-Central Mexico for the last ~1635 years. Vertical axes give spectral power in arbitrary units; horizontal axes give frequency in cycles per interval (c.p.i.); they represent the following periods in years; 0.1 = ~ 320, 0.2= ~160, 0.3= ~100, 0.4= ~ 80, 0.5= ~65; some specific periods are expressed at the highest peak.

5.5. Discussion

5.5.1. Temporal taxa turnover

A cloud forest dominated by *Quercus, Tilia, Carpinus, Fraxinus, Magnolia* and *Ilex* has been present in the region over the last ~1400 yrs. These taxa are common to most of the cloud forest studied in Mexico (Alcantara & Luna 2001, Cartujano et al. 2002, Mejía-Rodríguez et al. 2004, Sánchez-Rodríguez et al. 2003) whose structural performance of big heights and diameters enabled them to thrive in the upper stratum. However, it is known from present-day studies that cloud forest is much more diverse than this, usually containing up to 100 different arboreal species (Cuevas-Guzmán et al. 2004).

Some of these types are present in the pollen sequence but the majority of these arboreal taxa, indicative of current cloud forest in the Sierra de Manantlan Biosphere Reserve (Table 5.2), have low pollen percentages or are absent from the record. This is most likely as a result of the pollen representation of these types as they are trees mostly dispersed by animals.

In tropical forests seventy percent of Neartic forest taxa (e.g. *Pinus, Alnus, Quercus*) are anemophilous while most of the Neotropical taxa are entomophilous given the possibility for under-representation of pollen from Neotropical origin and consequently over-representation of the Neartic one (Bush 2002).

In view of the insufficient arboreal pollen representing cloud forest, epiphytes are regarded as main indicators for this community (Figueroa-Rangel et al. *In preparation*, Figueroa-Rangel et al. *In preparation*). Epiphytes embody the most diverse group (more than 30% of all species)

in the cloud forests of Mexico (Rzedowski 1996) displaying a great endemism and used as a good surrogate for changes in diversity (Williams-Linera et al. 2005). In this study Aspleniaceae displays percentages similar to the most abundant trees (*Pinus* and *Quercus*) while Polypodiaceae, considered the second most diverse family (47 genera) in cloud forest of Mexico (Rzedowski 1996), resembles abundances to that of *Carpinus, Tilia* and *Alnus*. The rest of the epiphytes, recognized to the genus level (*Adiantum, Anograma, Botrichium, Cheilanthes, Dryopteris, Equisetum* and *Pteridium*), show limited numbers.

Analysis of variance show non-significant differences among the four zones indicating that richness has been constant along ~1400 years even when palynological richness has apparent minimum and maximum values in different zones of the sequence. However, there has been turnover in the canopy as evidenced through the different temporal cycles displayed by the taxa, which vary from two centuries to less than a century. There is also an important shift in dominance, some genus *Cleyera, Fraxinus, Ilex* and *Tilia* dominate in the post-Hispanic zone (436-cal. yr BP to present) while others, *Carpinus, Clethra* and *Meliosma*, predominate in the pre-Hispanic II zone (810-565 cal. yr BP). Expansion and contraction periods in epiphytes differ among the zones reinforcing the statement of taxa turnover along the sequence. Differences in life-intervals for canopy dominants have been reported in tropical forests (Bush and Colinvaux 1994), acknowledging that some trees need a century or less to become mature while for others it may take up to three centuries. In addition, cloud forest taxa need particular microhabitat conditions to survive (Hietz & Briones 1998), so a temporal division of the resources is taking place through temporal niche partitioning. It is suggested that this is playing an important role in the alternating occurrence of the taxa; as a result there is a

heterogeneous canopy composition with low abundances per taxa along the fourteen decades that this sequence represents.

Pinus and *Quercus* are the leading genera with the highest pollen percentages in the sequence even surpassing epiphytes. Of particular significance is the drop in *Quercus* abundance at about ~555 cal yr BP (1400 A.D.) and remaining to present times. This genus is one of the canopy dominants in most cloud forests in Mexico with high importance values in density and basal area (Mejía-Rodríguez et al. 2004, Sánchez-Rodríguez et al. 2003) and with high number of species even exceeding very diverse herbaceous families (Alcantara & Luna 2001). The *Quercus* decline could therefore be an indication of a cloud forest decline from the end of the pre-Hispanic III to present. Opposite to this pattern is the signal of *Pinus* and charcoal whose increase are simultaneous to the reduction in *Quercus*.

The increase in *Pinus* dominance could be also the origin of the cloud forest decline due to the strong competition among canopy dominants. *Pinus* individuals are shade-intolerants competing and thriving better against shade-tolerants such as *Quercus, Tilia, Carpinus* and *Magnolia*.

In summary it is difficult to identify a specific cloud forest assemblage constant along the sequence. The spatial heterogeneity reported for high-altitude forests in this region (Olvera Vargas et al. 2006), in concert with high beta diversity (Vazquez-Garcia & Givnish 1998), is a manifestation of the high temporal variability in species composition for these forests. The assemblage therefore is not evolving as a complete entity but its components are highly dynamic following different trends, a tendency common to many biological communities (Lovejoy 2006) with each taxon displaying an individualistic response.

5.5.2. Underlying causes of temporal taxa turnover

Cloud forest conservation is critical as it shelters arboreal dominants of different phytogeographical affinities, as well as herbs and epiphytes with particular requirements. Results from this study indicate that these components are responding at different temporal cycles, possibly as an individual reaction to climate change or to human disturl ınces, but to what extend are both affecting the existence of this threatened woodland?

5.5.2.1. Climate change

In this study the organic and inorganic proxies, are providing evidence of climate change in West-Central Mexico spanning the last ~1400 years. The pattern observed resulted in two wet periods with a dry period in-between. Indicators of wet intervals are the lower values of inorganic geochemical element (Fig. 5.4) probably indicating a reduction in topsoil erosion into basin.

A specific dry period can be observed in the second half of pre-Hispanic I zone (~1200-810 cal. yr BP) with high values of geochemical elements and magnetic susceptibility while organic matter and carbonate content expresses minimum values. A similar high concentration of some geochemical elements has been related to climate factors, particularly to droughts. Increases of Na have been reported as a response to hotter and drier events in the Holocene of lowlands in Southern Mesoamerica (Neff et al. 2006) while in England and Scotland an increase in Mg, Al, Ca, Ni, Cu, Zn, Cd and Pb could be observed following periods of

droughts (Tipping et al. 2003). A decrease in carbonate content has been also related to drought periods in North America during the last 4500 years (Brown et al. 2005).

During this dry interval there is a decrease in the cloud forest and change in vegetation with high values in Poaceae, Hymenophyllaceae and Polypodiaceae. The increase in Poaceae confirms an open canopy where the incidence of sunlight into the forest has been related to arid periods (Bush 2002). Hymenophyllaceae family is recognized for its high tolerance to desiccation as a consequence of sunlight thriving well with alternating wet and dry periods (Proctor 2003). Polypodiaceae fluctuates enormously according to saturation deficit (Benzing 1998) and some species have been reported as desiccation-resistant ferns (Andrade & Nobel 1997, Muslin & Homann 1992, Proctor 2003). The coincident cycle at 95-year for Polypodiaceae, Hymenophyllaceae and *Alnus* may be a response to simultaneous dry and wet periods due to their high climate sensitivity. Another line of evidence is the first appearance of maize occurred during the dry interval. It is likely that people in that time started maize cultivation in the highlands as a consequence of the scarcity of water in the lowlands.

The dry period reported in this study encloses the period when drier conditions have been reported for Mexico (800-1000 A.D.) (Haug et al. 2000, Hodell et al. 2001, Metcalfe et al. 2000) and elsewhere (Chu et al. 2002, Neff et al. 2006, Russell & Johnson 2005). Particularly in the Mayan region (Yucatan Peninsula), palaeoclimatic records of precipitation in the past 2600 years have demonstrated correlations with solar forcing influences revealing a 208 years periodic pattern of drought composed of multiple ~ 50 years oscillations (Hodell et al. 2001). During the subsequent wet periods reported in this study, maize occurrence is disperse and nearly absent in the pollen spectra.

An important peak at 100-year was also detected in that study which coincide with our peak at 96-year. For Central Mexico an analogous dry period has been also accounted (Almeida-Lenero et al. 2005, Arnauld et al. 1997, Ludlow-Wiechers et al. 2005, Metcalfe & Hales 1994, Metcalfe 1995, Metcalfe et al. 2007, O'Hara & Metcalfe 1997). After the unique dry period (from 811 cal. yr BP to present) reported for cloud forest in this study, wet conditions have prevailed coinciding with other studies in different regions of Mexico (Almeida-Lenero et al. 2005, Curtis et al. 1996, Ludlow-Wiechers et al. 2005, Vazquez-Selem 1997).

5.5.2.2. Human disturbances

Archaeological evidence suggests that there has been human activity in the Sierra de Manantlan region over the past 1400 years. For example, archaeological excavations in Autlan, the locality closest to the Sierra de Manantlan (Fig. 5.1), have reported that by 1525 A.D. the area was an urban population reliant upon intensive agriculture and irrigation (Kelly 1945). So what impact did these people have on the cloud forest? It is highly likely that they would have carried out small-scale agriculture, clearance through burning and also logging. Evidence for each will be considered in turn:

Logging and Fires

The 65-year cycle reported for arboreal and non-arboreal taxa could be related to the forest logging rotation periods used for timber extractions in cloud forests. The open areas left after tree-cutting operations were probably regenerated promptly but the forest recovery was completed in ~ 65 years.

In the Manantlan region, it takes 120 years for a fully recovered of the forest dominated by *Quercus*, a genus with slow-growth individuals and average diameter of 45 cm (Olvera Vargas & Figueroa-Rangel 1998). Some secondary rain forest stands in Latin America can regenerate in 8-80 years (Finegan 1996). It has been reported that soil macro-invertebrate community composition of a cloud forest in southern Mexico recovered completely in 100 years after logging (Negrete-Yankelevich et al. 2007); while in an abandoned pasture in Veracruz, Mexico, cloud forest re-established in 40-50 years after disturbance (Muniz-Castro et al. 2006).

The decline of *Quercus* in the cloud forest of Manantlan from ~ 555 cal yr BP to present may also be due to human activity, which resulted in the simultaneous increase in *Pinus*. Similarly the expansion of *Pinus* in southern Mexico in recent times has been widely attributed to the influence of human activity, in particular to the extraction of *Quercus* trees (Ramirez-Marcial et al. 2001).

Agriculture and Fires

The principal method of agriculture in Mexico is the slash and burn system (Castellanos et al. 2001, Ellingson et al. 2000, Negreros-Castillo et al. 2003, Ochoa-Gaona 2001). This consists of clearing the land followed by burning. This land is cultivated and then left fallow for a certain period of time before cultivating again (Pascual 2005).

The 65-year cycle in cultural taxa (Poaceae and Asteraceae families) may also therefore be an expression of forest clearance activities in Manantlan. We argue that the forest clearance in the area may be the result of either logging operations or vegetation fallows left after intensive

cultivation. Similar cycles of charcoal and certain geochemical elements (Na, Al, Ca and Cu) support our argument indicating that the burning of cloud forests and the cycles of the geochemical elements are closely linked to the cycles of cultural taxa.

Similarities in vegetation as well as in environmental dynamics between the pre-Hispanic I and the post-Hispanic zones are obvious. The decline of cloud forest and the consequent dominance of *Pinus* is particularly similar between the two zones. Some of the geochemical elements also reach their highest values in these two zones. Although these coincidences seem to be the result of climate change events rather than to a higher human disturbance, the human disturbance and climate change are intricately linked in this part of the world (Metcalfe et al. 2000, Williams 2003) .

Conflicting evidence supports the link between human land use and reduction in forest vegetation before and after the Spanish Conquest. Increases in *Zea* pollen and burnt grasses, together with a decrease in arboreal pollen have been related to agricultural erosion (Beach et al. 2006). On the other hand, a study developed around a highland lake in Central Mexico revealed that plough agriculture initiated by the Spanish was less aggressive than the traditional agricultural methods (O'Hara et al. 1993). The landscape changes in the post-Conquest regions of West-Central Mexico are suggested to have been the result of land tenure changes imposed by the Spanish administration rather than by the nature of the land use (Endfield & O'Hara 1999). Finally the Native American landscape before the 16th century was an already humanized land with a modified forest composition, disturbed wildland and severe erosion where the pristine vision was more a myth than a reality. In summary, we suggest that the main changes in vegetation in the cloud forest of Manantlan over the past 1400 years are tied to human disturbances coupled with climate changes (Denevan 1992)

5.6. Conclusions

The cloud forest assemblage in West-Central Mexico has been fluctuating during pre- and post- Hispanic times until present. A flourishing stage is apparent in the pre-Hispanic II zone (~ 810-565 cal. yr BP) and the beginning of the pre-Hispanic III zone (~555-465 cal. yr BP). A high temporal turnover of taxa is apparent with shifts in cloud forest taxa, epiphytes and *Pinus*. *Pinus* expands from the pre-Hispanic III zone to present times when *Quercus* contracts. It is also possible that the extraction of timber taxa such as *Pinus and Quercus* has dictated the temporal turnover of taxa in periods shorter than 150 years. Burning is constant through the whole sequence linked to the forest clearance and the slash-and-burn system of agriculture. At present the high beta diversity, few individuals per species and the fragmented character of cloud forest make it difficult to conceive the idea of a constant assemblage over centuries. In this respect, to maintain a constant cloud forest assemblage, it is important to avoid excessive logging in these stands. Otherwise a selective extraction scheme for timber species has to be designed depending on the composition of the canopy taxa and the structure of the present-day vegetation. The vulnerability of cloud forest in response to climatic change and to anthropogenic influences in different cycles provides crucial information for the continuous preservation of this important forest type. The present results fully support the actual protection scheme for cloud forests in West-Central Mexico where areas are kept in exclusion zones, namely the core areas of the Sierra de Manantlan Biosphere Reserve. In these areas timber extraction, grazing and agricultural activities are excluded. Our results confirm that these are the best conservation strategies for the long-term maintenance of the cloud forest dynamics.

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6. PAPER 4

Successional stages in a transitional montane forest in the Mexican Neotropic during Late Holocene

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Abstract

The determination of past successional stages, as well as the factors triggering succession, is crucial in the understanding of forest dynamics for the adequate design of current and future management and conservation strategies. The trajectories followed in a succession can take decades or even centuries to occur due to the longevity in trees; therefore palaeoecological studies are important tools for their study. The present research involves the palaeo-reconstruction of a transitional forest dominated by *Pinus-Carpinus-Quercus* in West-Central Mexico over the last 1200 years, an interval of significant climate change and human disturbances in Mexico. The proxies employed include fossil pollen, microfossil charcoal, magnetic susceptibility and sediment geochemistry evaluated through multivariate techniques and time-series analysis.

The findings reveal that a stage classified as cloud forest developed from 1230 to 1045 cal. yr BP associated with a wet environment. This stage was interrupted during ~400 years (during ~10-12th century A.D.) when a drier climate turned the forest into an open canopy landscape dominated by herbs and cultural taxa such as Asteraceae, Poaceae, *Plantago* and *Zea*. The cloud forest, following cyclical succession, returned from 655 cal yr BP with a highest diversity. Temporal heterogeneity through niche partitioning has maintained diversity in this forest with a high taxa turnover. Given the predicted conditions of local and global warming, it is plausible that this forest might be converted into an open canopy with herbaceous and cultural taxa domain as that described for the 10-12th century A.D.

Key words: climate change, cloud forest, cyclic succession, fire, human disturbance, West-Central Mexico.

6.1. Introduction

Historical factors are of prime importance (Motzkin *et al.*, 2003; Myster and Pickett, 1990; Swetnam *et al.*, 1999) in the determination of forest change. Knowing the modes of forest succession over past decades, as well as the mechanisms involved in those changes, is essential for forecasting the future development of the forest with predicted global change. Succession is the modification of the actual plant assemblage into a different state either in composition or structure through time following a perturbation (Davis *et al.*, 2005). Several modes of forest succession have been described including the cyclic model first developed by Watt (1947). In this model is it suggested that following a perturbation an initial stage turns

into one or several intermediate stages to finally reset to the original stage (Frelich, 2002). The conversion to intermediate stages can be triggered by internal and/or external factors such as competition and disturbance (Rogers and Hartnett, 2001). With the creation of new spaces for colonization during succession, it minimizes or enhances species dominance over time involving temporal niche partitioning (Fargione and Tilman, 2005; Mamolos, 2006). If fire is the disturbance factor triggering succession, competition between thermophilous and non-thermophilous species is involved (Bataineh *et al.*, 2006; Carrion *et al.*, 2003; Carrion and van Geel, 1999). In other cases where climatic factors such as precipitation and temperature are engaged, turnover between wet and dry-resistant species is implicated (Guarin and Taylor, 2005; Parmesan and Yohe, 2003).

There are few palaoeoclimatic or palaeoecological records for West-Central Mexico and the majority of the records that exist are focused predominantly in Central, South and North Mexico documenting that climate change has impacted the Mexican territory over the last millennia causing changes in different plant assemblages (Almeida-Lenero *et al.*, 2005; Arnauld *et al.*, 1997; Hodell *et al.*, 2005a; Metcalfe *et al.*, 2000). In those regions there is evidence for human-induced vegetation change, transforming the land into fallows or open grassland through clearing and burning over several millennia (Almeida-Lenero *et al.*, 2005; Beach *et al.*, 2006; Conserva and Byrne, 2002; Lozano-Garcia and Vazquez-Selem, 2005; Ludlow-Wiechers *et al.*, 2005; McClung de Tapia, 2000; Pope *et al.*, 2001; Sluyter and Dominguez, 2006; Xelhuantzi-Lopez, 1994a).

In this region there is known to have been an interval of important climatic changes (Figueroa-Rangel *et al.*, In preparation-c). It is also known from previous studies that there has been human impact upon the landscape (Figueroa-Rangel *et al.*, In preparation-b; Kelly, 1945).

Here we present the development of successional stages in a transitional forest over several decades (last ~1200 yrs) using palaeoecological methods through a variety of proxies including fossil pollen, microfossil charcoal, magnetic susceptibility and sediment geochemistry.

The transitional forest is located in the Sierra de Manantlan and is it thought to represent an intermediate development stage among different forest types such as Pine, Pine-Oak and Cloud. These three forest types are highly diverse and with respect to Pine and Pine-Oak forests they are a major economic resource for the timber that they provide; the cloud forest is one of the most biodiverse forests in Mexico (Rzedowski, 1996). It is unclear, however, the stages in succession that lead to the development of these three different forest types and the impact of climate change upon this process of succession. This study therefore aimed to reconstruct the dynamics of the transitional forest in response to past climate change in order to determine the successional paths leading to the development of pine, pine-oak and cloud forests. Key questions addressed included what are the main drivers for forest succession either human-induced or climate-induced disturbances? How long did succession take? Such questions provide fundamental tools for the design of forest management and conservation strategies and will contribute to filling an information gap on palaeo-studies of the West-Central region of Mexico.

6.2. Study Area

The study site is a transitional forest with the association *Pinus-Carpinus-Quercus* in the Sierra de Manantlan Biosphere Reserve. It is located in the Sierra Madre del Sur physiographic province in West-Central Mexico lying between 19°, 35 '134'' N and 104°, 16' 460" W at 1880-2100 m asl (Fig. 6.1). It is predominantly comprised by igneous rocks from the Cretaceous and early Tertiary (Quintero A. and Martinez R., 1993). The climate, according to Köppen modified by Garcia (1987) is temperate subhumid with mean yearly temperature between 5°C and 18°C and average rainfall of 1500 mm.

This forest represents a Transitional stage between a pine, pine-oak forest and cloud forest. *Pinus douglasiana* dominates the canopy with an average height of 18±2 m, 62% in density and 91.6% in basal area. *Carpinus tropicalis* follows in dominance (10±2m height; 5% basal area) and abundance (17.2% in density) while *Quercus* species (*Q. candicans, Q. praineana* and *Q. scytophylla*) do with 10±1 m height, 2.1% basal area and 11.8% density. Other species associated to the main dominants are *Alnus jorullensis, Clethra vicentina, Cornus disciflora Prunus cortapico, Tilia americana var. mexicana* and *Buddleja* sp. (Table 6.1). Main herbs include *Senecio salignus, Stevia* sp., *Euphorbia schlechtandalii, Festuca breviglumis, Melinis minutiflora, Muhlenbergia dumosa, Zea* sp., *Castilleja arvensis* and *Solanum sp.*

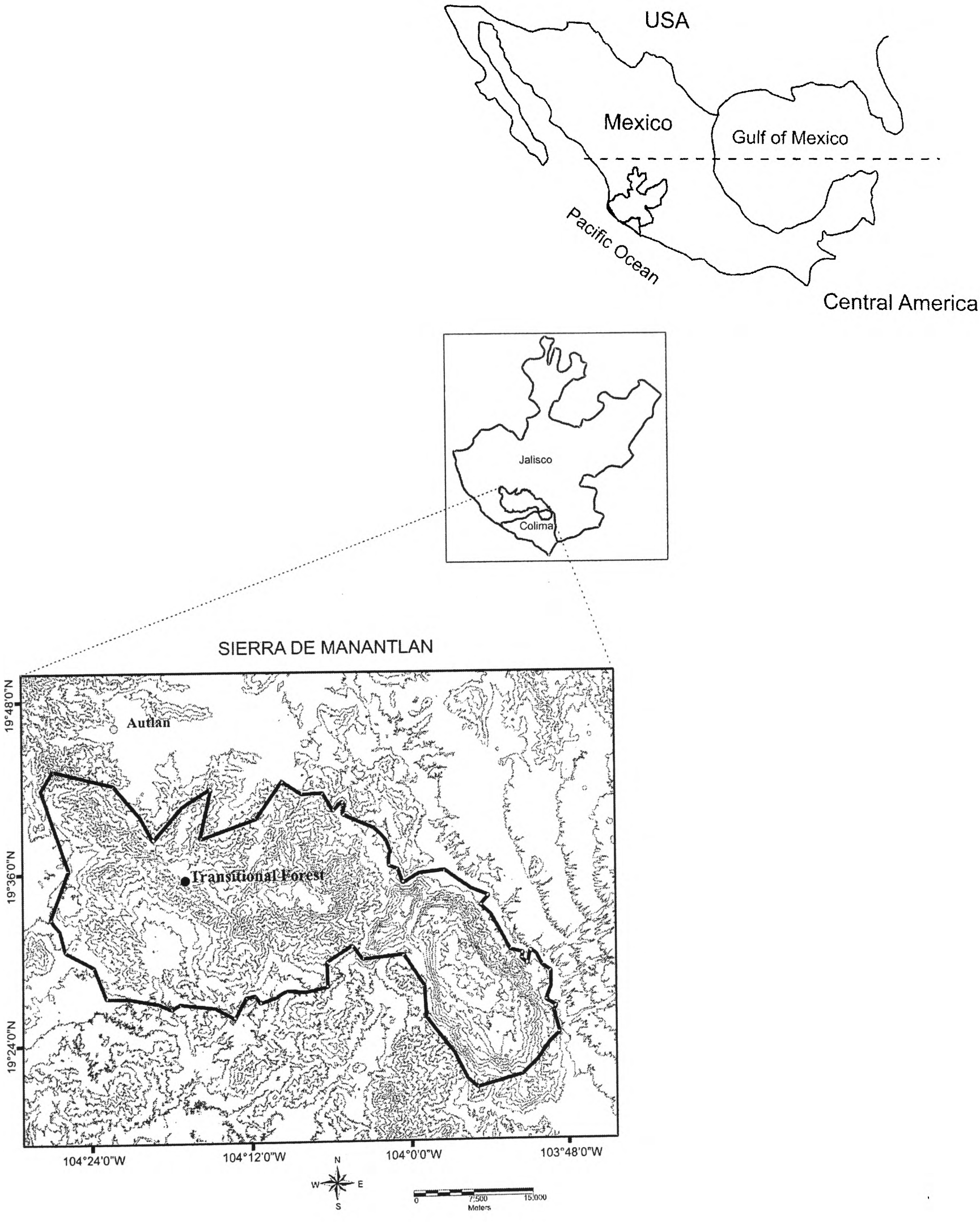

Fig. 6.1. Map of the study area with the location of the transitional forest dominated by *Pinus-Carpinus-Quercus*.

Table 6.1. Relative density and Basal Area for the present-day arboreal component of the *Pinus-Carpinus-Quercus* forest.

Family	**Species**	Relative Density (%)	Relative Basal Area (%)
BETULACEAE	*Alnus jorullensis*	1.8	0.1
	Carpinus tropicalis	17.2	5.0
BUDDLEJACEAE	*Buddleja sp.*	0.9	0.3
CORNACEAE	*Cornus disciflora*	1.3	0.09
CLETHRACEAE	*Clethra sp.*	0.9	0.08
FAGACEAE	*Quercus candicans*	0.9	0.04
	Quercus praineana	7.2	1.1
	Quercus scytophylla	3.6	0.9
MIMOSACEAE	*Calliandra longipedicellata*	1.3	0.1
PINACEAE	*Pinus douglasiana*	62.2	91.6
ROSACEAE	*Prunus cortapico*	1.8	0.2
TILIACEAE	*Tilia americana var. mexicana*	0.9	0.4

6.2.3. Archaeology and culture

Human occupation previous was revealed in archaeological sites around the coring place in the Autlan and the Tuxcacuesco-Zapotitlan Zone (Fig. 6.1) (Kelly, 1945). Around ~1200 A.D, Autlan, one of the closest cities to the coring site, 19°, 46 '05'' N, 104°, 21' 59" W, is described as a highly civilized region of agricultural activities and ceramic complexes.

6.2.4. Climate change

Paleoclimatic records for West-Central Mexico do not exist at present. Studies in this discipline have focused in the Central region (Almeida-Lenero *et al.*, 2005; Arnauld *et al.*, 1997; Lozano-Garcia *et al.*, 1993; Ludlow-Wiechers *et al.*, 2005; Metcalfe *et al.*, 2000; O'Hara and Metcalfe, 1995; O'Hara and Metcalfe, 1997) and the Yucatan Peninsula (Beach *et al.*, 2006; Curtis *et al.*, 1996; Hodell *et al.*, 2005a; Hodell *et al.*, 2001; Hodell *et al.*, 2005b; Hodell *et al.*, 1995) and very scarce on the Northern (Cheshire *et al.*, 2005; Metcalfe *et al.*, 2002), Southern (Berrio *et al.*, 2006) and Eastern Mexico (Conserva and Byrne, 2002). Reports over the last 5000 years demonstrate that wet and dry periods have occurred in Mexico. The dry periods, in particular, have occurred around 1000 yr BP for Central Mexico (Metcalfe *et al.*, 2000) and between ~1200 and 800 yr BP for the Yucatan Peninsula (Hodell *et al.*, 2005a; Hodell *et al.*, 2001).

6.3. Methods

6.3.1. Field and Laboratory techniques

A 152 cm sediment core was recovered from a hollow (27m x 11m in diameter) located in the transitional forest of the Sierra de Manantlan Biosphere Reserve using a modified Livingstone corer (Moore *et al.*, 1991). Two sequences were collected from adjacent holes ensuring that any gap in the first sequence was covered in the overlapping samples. The core was described in the field, wrapped in cling-film and aluminium foil to create anaerobic conditions. Samples were analysed throughout the sequence for pollen, microfossil charcoal, magnetic susceptibility and sediment geochemistry (organic matter and carbonate content). One cubic centimetre sub-samples were used for pollen extraction through the standard acetolysis method described by Bennett and Willis (Bennett and Willis, 2001). A known quantity of the exotic spore *Lycopodium* was added to each sample in order to estimate pollen (pollen grains cm^{-3}) and charcoal concentration (charcoal cm^2 cm^{-3}) (Stockmarr, 1971). Pollen and spores were identified using comprehensive pollen and spore reference collection prepared with regional material specific to the study area and the reference collection of the *Oxford Long-term Ecology Laboratory*.

Microfossil charcoal abundance was quantified in each level by the point count method (Clark, 1982) using the pollen slides. This was considered as a proxy for fire incidence within the pollen source area (Figueiral and Mosbrugger, 2000; Moore, 2000). A vegetation survey was undertaken in circular plots $100m^2$ (5.7 m radius) around the coring site according to the forest inventory procedure suggested by Olvera Vargas (1996). For stand-age determination a tree core was extruded from pine individuals in each $100m^2$ plot using a using a Presler increment

borer. Two increment cores were taken in each pine tree at 1.3 m height above the ground level in two different directions (Pazdrowski and Szaban, 2005).

6.3.2. Data Analysis

Core chronology was determined by AMS ^{14}C dating (Poznań Radiocarbon Laboratory, Poland) and ^{210}Pb dating (*Ortec* Coaxial Well Photon Detector in the Oxford Long-Term Ecology Laboratory). Results were calibrated using the CALIB v5.02 and INTCAL04.14 programs (Stuiver and Reimer, 1993). For ^{210}Pb dating the top of the core was measured applying the constant rate of supply (CRS) model (Appleby and Oldfield, 1978). The age-depth model was developed using linear interpolation including radiocarbon and ^{210}Pb dates (Bennett, 1994). Stand age was estimated on the basis of the increment cores in every pine tree present in the site.

Pollen percentages were plotted and analysed using PSIMPOLL 4.25 and PSCOMB 1.03 software (Bennett, 2005). Zonation was undertaken by optimal splitting and significant zones were resolved using a broken-stick model (Bennett, 1996; Bennett, 2005). Rarefaction analysis (Birks and Line, 1992) was applied to provide an estimate of the palynological richness in each sample.

The coefficient of variation was estimated to determine the variability of organic matter, magnetic susceptibility and microfossil charcoal along time. This parameter represents the ratio of the standard deviation to the mean and is dimensionless allowing comparison of populations with significantly different mean values (Sokal and Rohlf, 1981).

Detrended Correspondence Analysis (DCA) was developed in order to detect trends in floristic composition over time and to locate the samples independent of depth in the ordination space

(HILL 1973, Hill 1980). A constrained ordination, Canonical Correspondence Analysis (CCA), was also developed considering the following environmental variables: microfossil charcoal, magnetic susceptibility, organic matter and carbonate content. Both analyses were computed in CANOCO 4.5 (ter Braak and Smilauer, 2002). Coefficient of variation was executed in SPSS v. 14.0.

Time-series analysis through spectral plots was used to detect peaks indicative of cyclical changes in pollen taxa as well as in microfossil charcoal, magnetic susceptibility and organic matter as described by Box and Jenkins (1970) using POLSTA v.7.0 software (Green, 1989). All estimates were done through a Bartlett window.

6.4. Results

6.4.1. Chronology

Sediment deposition in the basin occurred from approximately 1200 cal. yr BP with no hiatus. Deposition time was calculated according to the age-depth model indicating that 1 cm of sediment accumulates every eight years (Fig. 6.2). The average stand age corresponds to 34± 5 years consequently the pollen sampling resolution was determined at every 4 cm representing ~ 32 years. This gives a resolution that is appropriate for examining the successional stages in the transitional forest thus one sample every 32 years for the last ~1200 years.

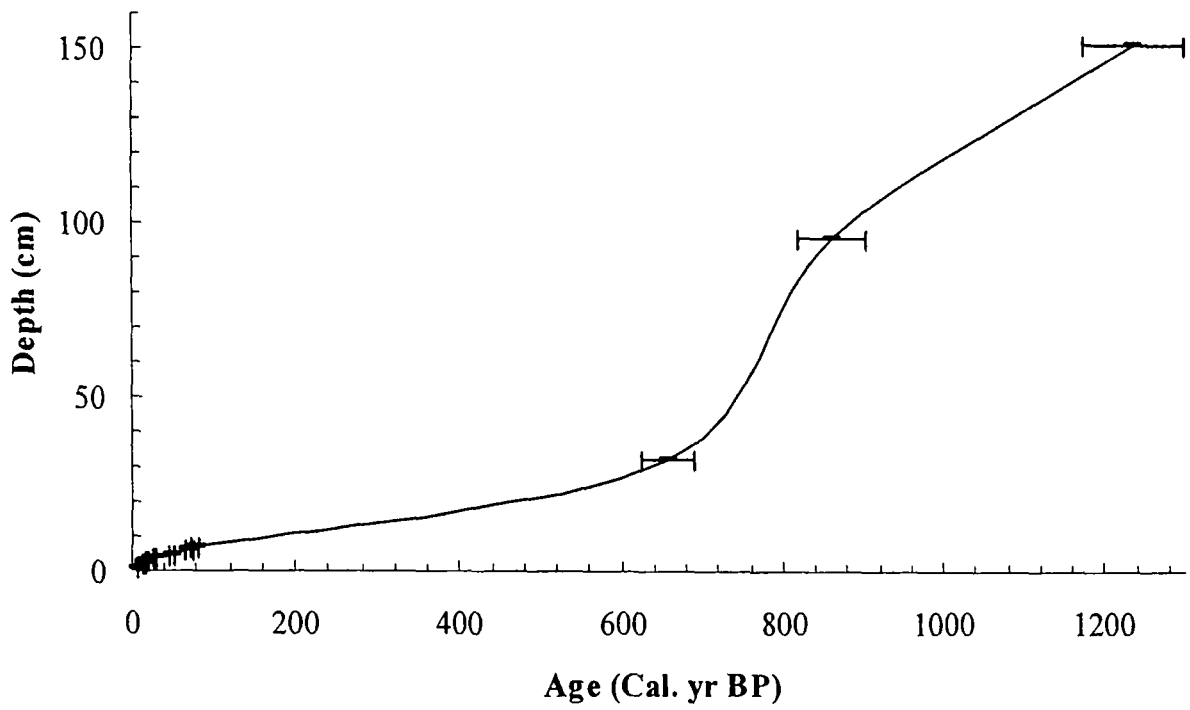

Fig. 6.2. Age-depth curve for the transitional forest (*Pinus-Carpinus-Quercus*) based on radiocarbon and Pb^{210} dates using linear interpolation. Error bars display the 95% confidence intervals for age determinations.

6.4.2. Pollen

Seventy-six taxa are recognized in the sequence. Nineteen trees and shrubs are predominant in the record (Fig. 6.3), the rest are infrequent taxa (< 5%) and therefore are not displayed in the pollen diagram though they are considered in analysis. *Pinus* dominates the arboreal component in both abundance and frequency while *Rubus* is the predominant shrub. Asteraceae and Poaceae are the clear leading herbaceous families. Chenopodiaceae is frequent but not abundant and *Plantago* is abundant in just one zone (Fig.6.4). For epiphytes, Aspleniaceae and Hymenophyllaceae stand out followed by Polypodiaceae and *Adiantum* (Fig. 6.4). Optimal division of the pollen data resulted in three zones (Figs. 6.3 and 6.4) as follows:

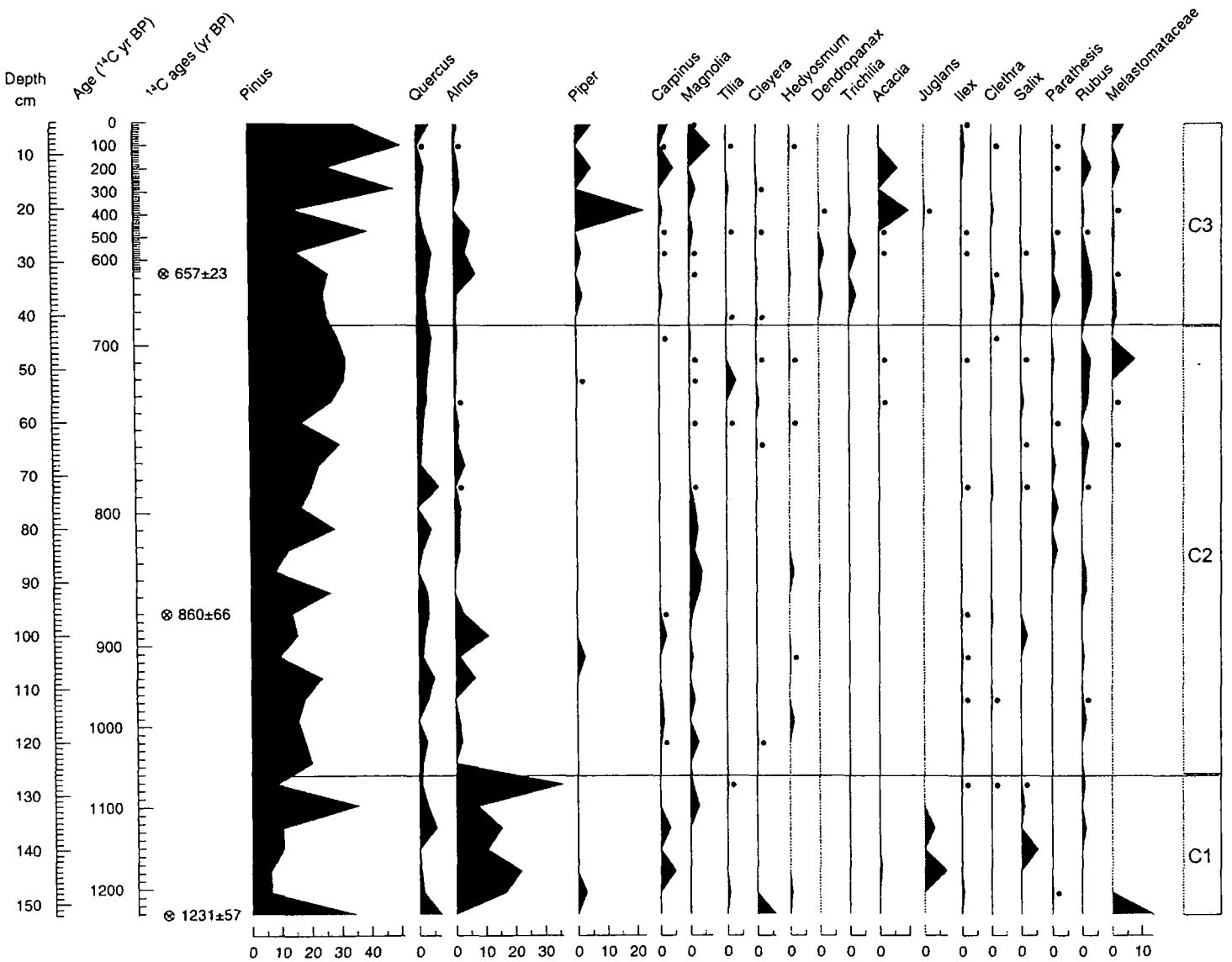

Fig.6.3. Pollen diagram for trees and shrubs in the transitional forest dominated by *Pinus-Carpinus-Quercus* in West-central Mexico. Ages are calibrated years BP.

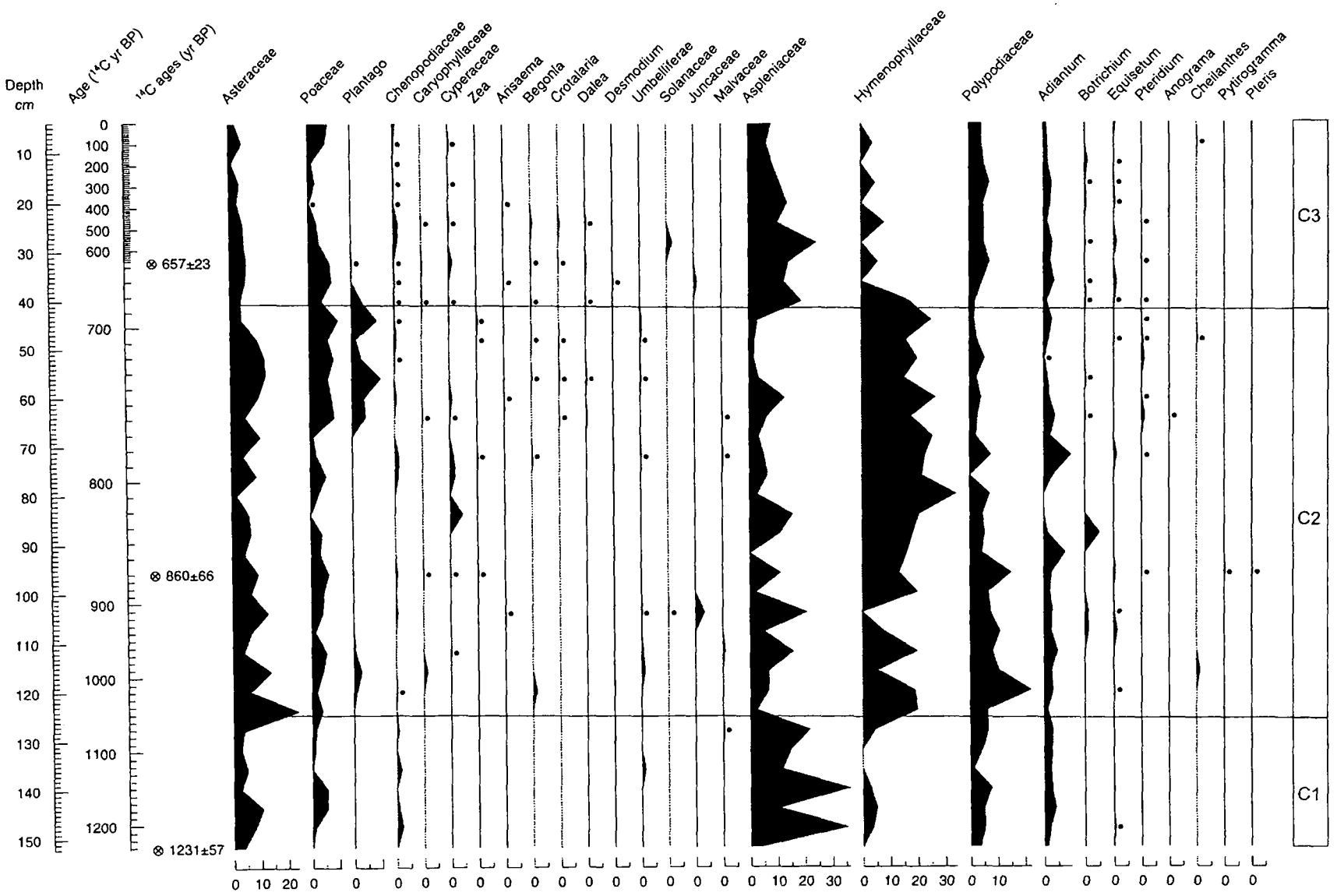

Fig. 6.4. Pollen diagram for herbs and epiphytes in the transitional forest dominated by *Pinus-Carpinus-Quercus* in West-central Mexico. Ages are calibrated years BP.

Zone C-1 (152-124 cm, 1230-1045 cal. yr BP)

A high *Pinus* abundance is evidenced in the first zone followed by a remarkable decrease (to the lowest values in the sequence). *Pinus* then recovers its abundance to the same level showed previously. *Quercus* performs the same pattern of abundance as *Pinus* (Fig. 6.3). The *Pinus* decline is coincident with two subsequent increases in *Carpinus* and *Juglans* and one in *Salix*. *Alnus* portrays its highest dominance in this zone jointly with Aspleniaceae. In contrast spores from the epiphytes Hymenophyllaceae and Polypodiaceae are scant (Figs. 6.3 and 6.4). *Cleyera* and Melastomataceae are abundant in the first depth, similarly to *Pinus*, to be absent thereafter in the zone (Fig. 6.3). In this zone the highest pollen percentage of cloud forest taxa is apparent while a reduction in pollen representative of cultural taxa is evident (Fig. 6.5).

Zone C-2 (124-44 cm, 1045-695 cal. yr BP)

The herbaceous component (Chenopodiaceae, Caryophyllaceae, Malvaceae, Cyperaceae, Umbelliferae, *Begonia,* and *Crotalaria*) is prominent in this zone mainly through the cultural taxa (Asteraceae, Poaceae, and *Plantago*) (Fig. 6.4 and 6.5). *Zea* sp. is constrained to this zone with the first appearance at ~860 cal. yr BP. Hymenophyllaceae and Polypodiaceae indicate maximum values in this zone while Aspleniaceae performs the opposite (Fig. 6.4). The zone contains, in general, low palynological richness with the lowest at 1045 cal yr BP. Some taxa representative of cloud forest (*Juglans, Trichilia* and *Dendropanax*) are absent in this zone (Fig. 6.3 and 6.5).

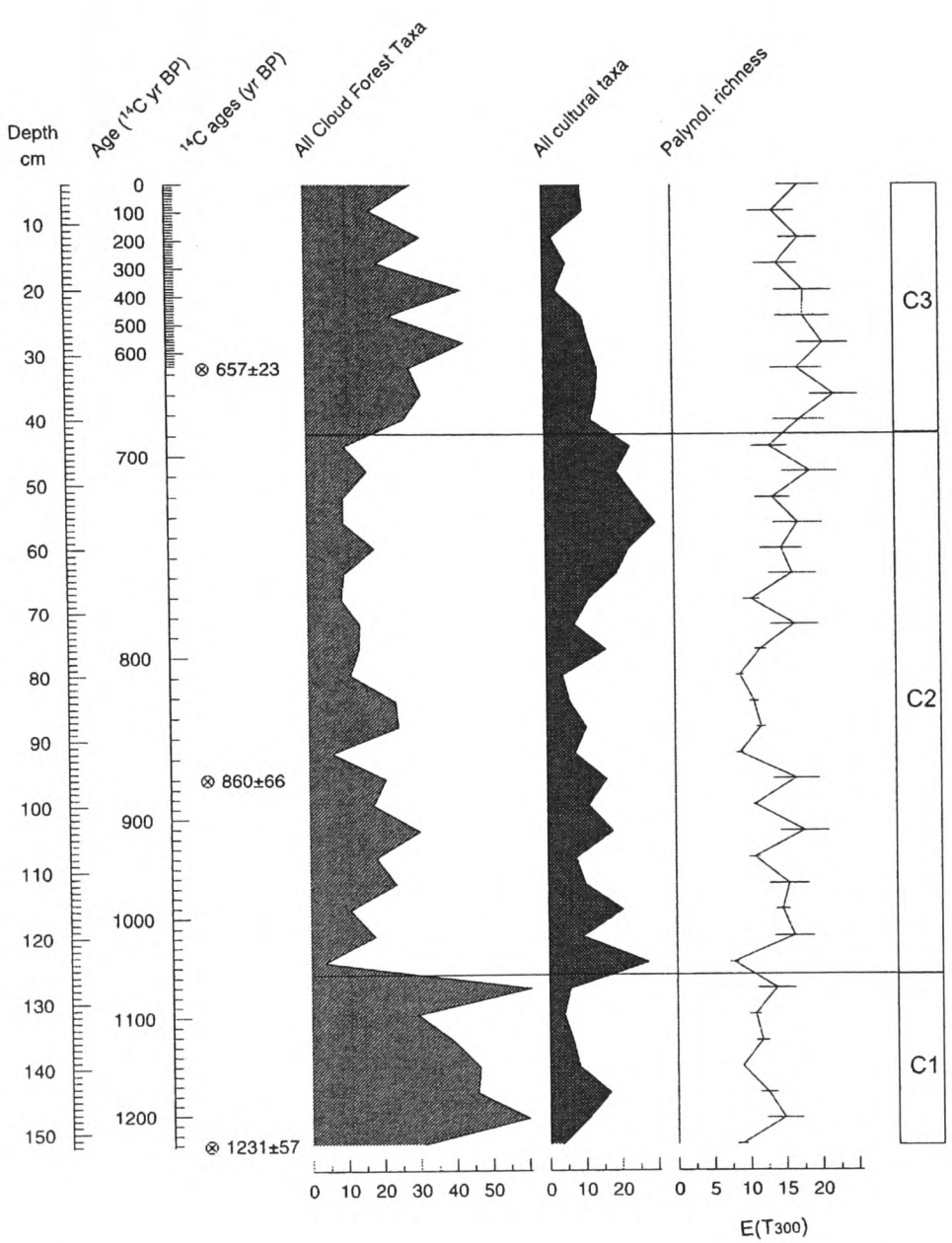

Fig.6.5. Sum of all taxa representative of cloud forest and sum of all cultural taxa (e.g. *Zea* sp., *Plantago*, Asteraceae, Poaceae) in the three different zones of the transitional forest in West-Central Mexico. Palynological richness is also displayed by zone.

Zone C-3 (44cm-0cm, 695 cal. yr BP to present)

Taxa specific to cloud forest (*Carpinus, Cleyera, Tilia, Dendropanax, Clethra, Trichilia, Piper*, *Ilex* and Melastomataceae) along this zone with a recovery in their percentages as compared with the previous zone (Fig 6.3 and 6.5). *Pinus* and *Acacia* reach their highest abundance in this zone as well. The greatest peak in palynological richness occurs at 670 cal. yr BP (Fig. 6.3 and 6.5). Cultural taxa decline in percentages when compared to the previous zone (Fig 6.5). Hymenophyllaceae, Polypodiaceae and *Adiantum*, are reduced but Aspleniaceae experiences a recovery. *Zea* sp. is entirely absent (Fig. 6.4 and 6.5).

6.4.3. Indirect Ordination

Detrended Correspondence Analysis (DCA) reveals three groups clustered according to the temporal sequence that nearly correspond to the three zones (C-1 to C-3) displayed by optimal splitting. Few samples are intermixed into different groups, e.g. one sample dated 1230 cal yr BP is assigned to Group A whose ages are from 695 cal yr BP to present. Six samples do not correspond with the ages in Group B; 1045-695 cal yr BP) (Fig. 6.6). It is not possible to discern a compositional pattern involving the three groups lined along the two axes. Group A and B are closer in axis 1 while Group A and C are in axis 2.

In order to detect a delineated taxa composition by group and, to discern successional stages along time, a DCA was undertaken in each group including the rare or infrequent taxa as followed:

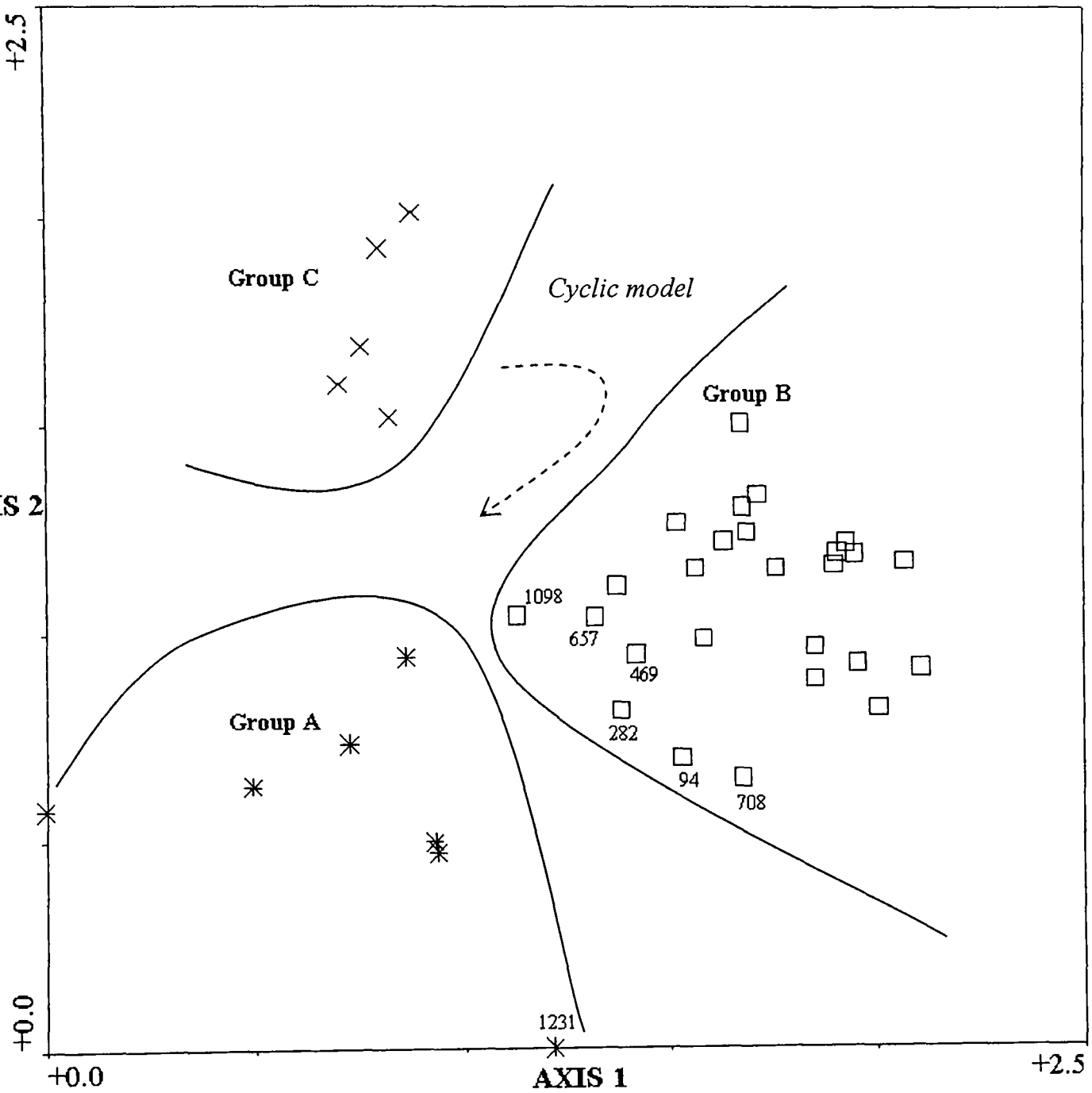

Fig.6.6. DCA ordination of the pollen data with sample (ages) distribution. Group A (star) mostly represents samples with ages from 695 cal yr BP to present, except the one marked in the graph with its age, Group B (squares) ages from 1045-695 cal. yr BP except the ones with the labels. In Group C (cross) all ages are from 1230 to 1045 cal yr BP.

Group C (ages from 1230 to 1045 cal. yr BP) contains the more frequent cloud forest taxa separated in three different clusters. One cluster is located in the upper right hand (*Piper, Hedyosmum, Tilia, Ilex* and *Fraxinus*), other in the middle left (*Carpinus* and *Juglans*) and another at the center (*Clethra* and *Magnolia)*. *Quercus* and *Pinus* are distant from the clusters while cultural taxa are dispersed and *Salix* stands alone at the bottom right of the diagram (Fig 6.7a).

Group B (ages from 1045 to 695 cal. yr BP) shows a less apparent demarcation in taxa composition. *Pinus, Quercus* and *Alnus* are closer to each other while cloud forest taxa are intermixed but mostly in the right side. Cultural taxa are clearly exposed to the left (Fig. 6.7b).

Group A (ages from 695 cal. yr BP to present) encompasses cloud forest taxa dispersed and intermixed on the diagram. Cultural taxa are at the right and closer to *Pinus, Quercus* and *Alnus* (Fig. 6.7c).

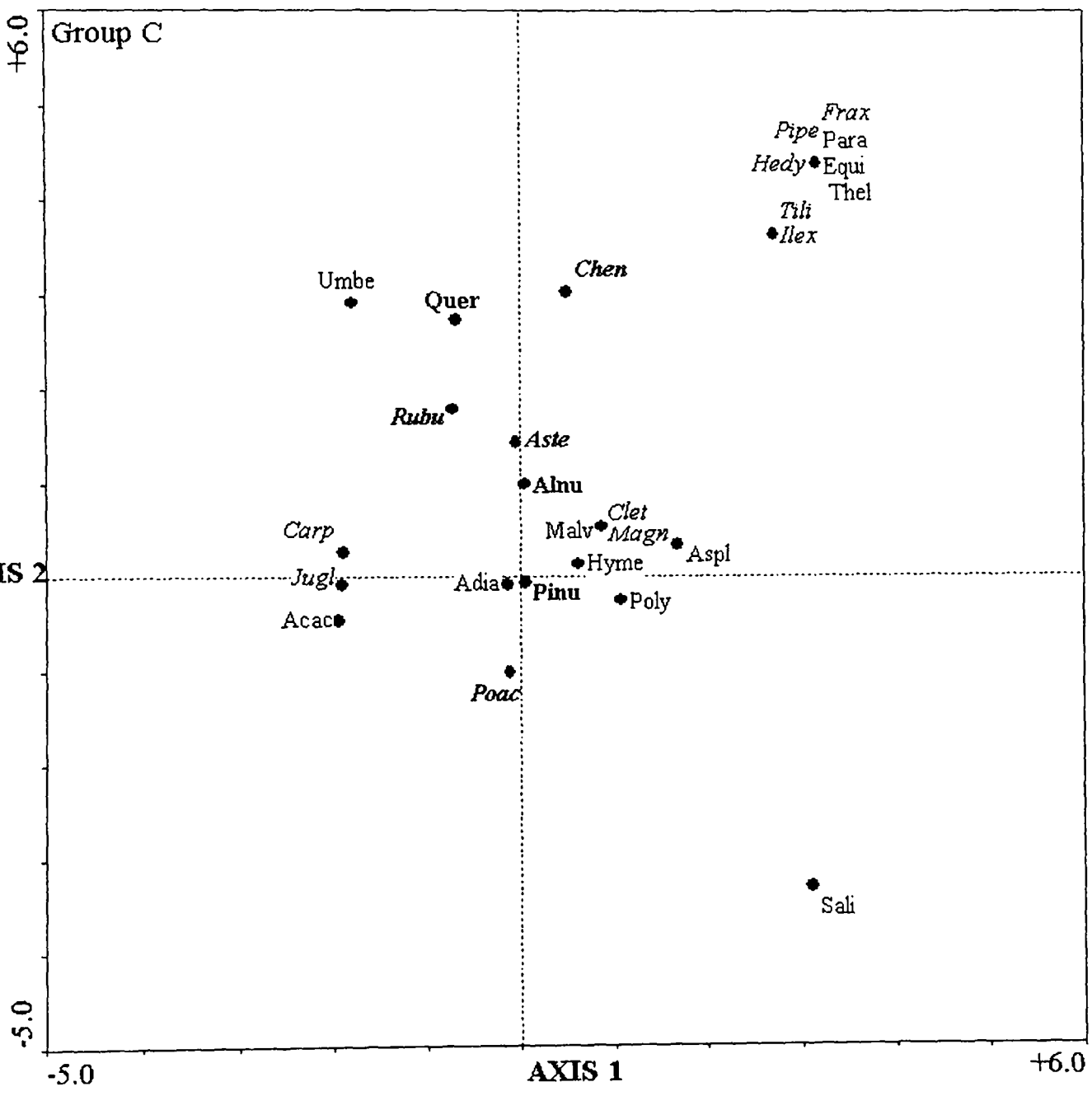

Fig. 6.7a. DCA ordination for the pollen taxa included in Group C (ages from 1230 to 1045 cal yr BP). Taxa in bold represent *Pinus, Quercus* and *Alnus*; italics include cloud forest taxa and bold italics cultural taxa. Taxa names in Appendix 1.

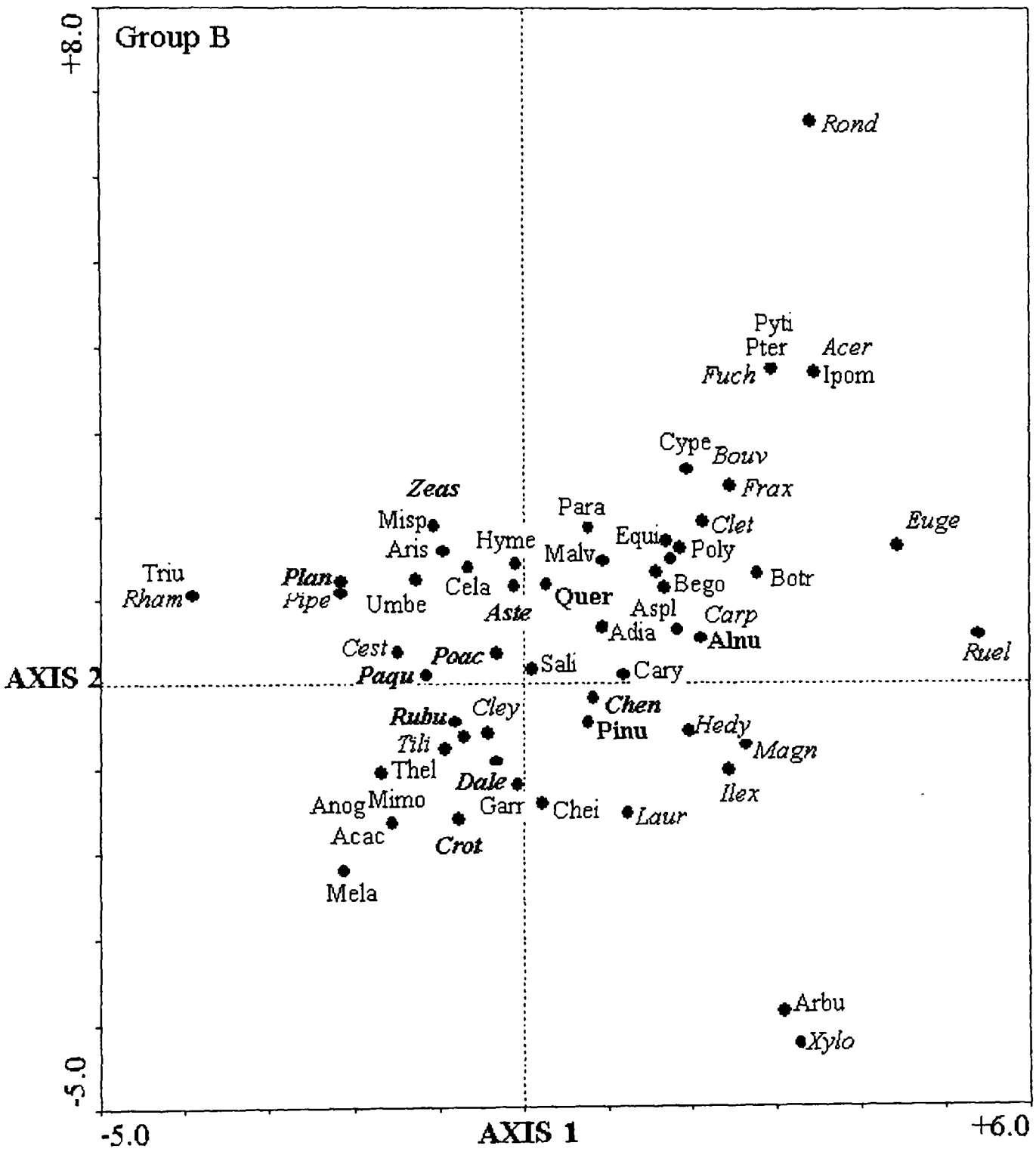

Fig. 6.7b. DCA ordination for the pollen taxa included in Group B (ages from 1045-695 cal. yr BP). Taxa in bold represent *Pinus*, *Quercus* and *Alnus*; italics include cloud forest taxa and bold italics cultural taxa. Taxa names in Appendix 1.

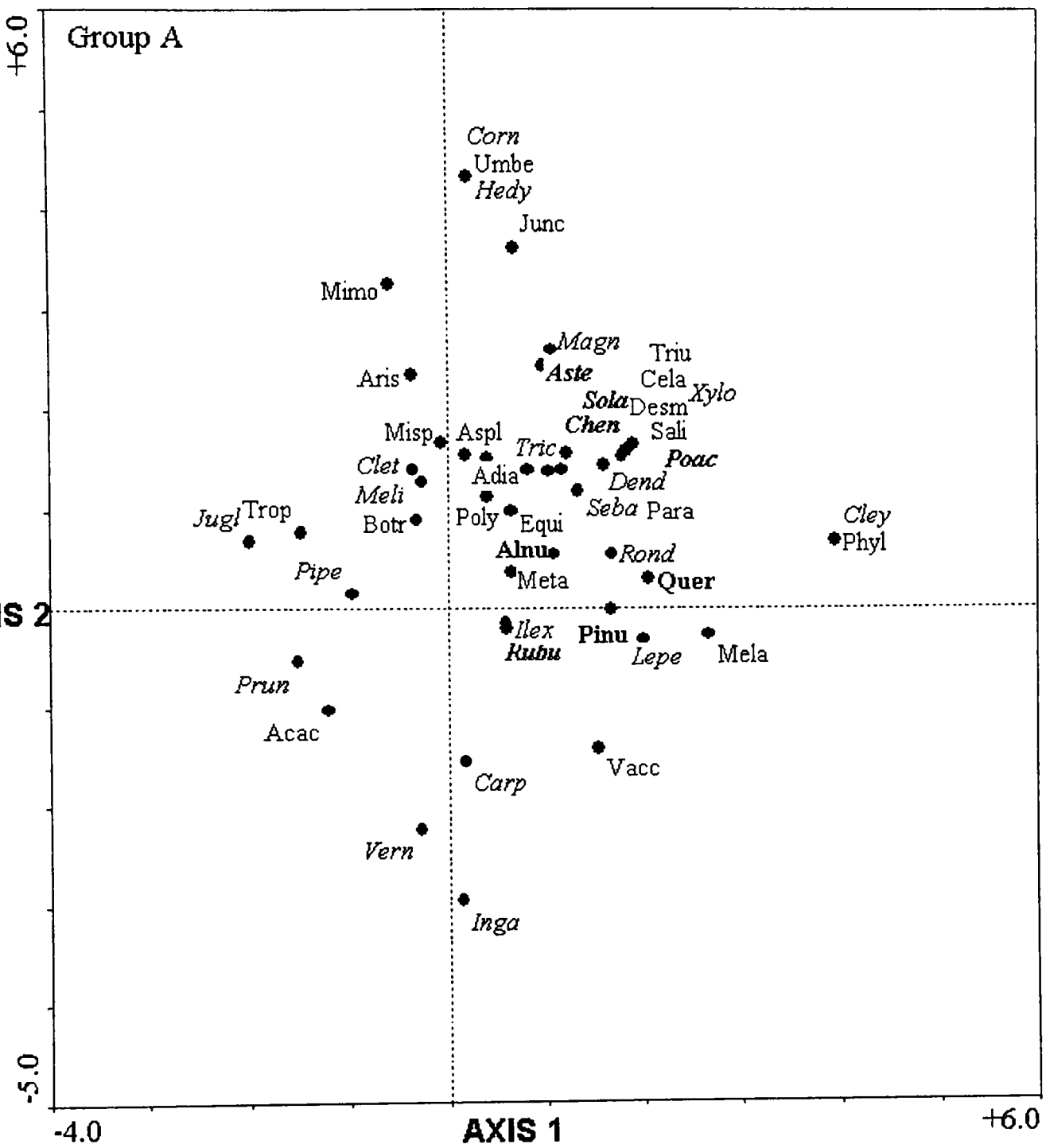

Fig. 6.7c. DCA ordination for the pollen taxa included in Group A (ages from 695 cal yr BP to present). Taxa in bold represent *Pinus, Quercus* and *Alnus*; italics include cloud Forest taxa and bold italics cultural taxa. Taxa names in Appendix 1.

6.4.4. The Environment

Results from the three different proxies (organic matter, magnetic susceptibility and microfossil charcoal) indicate variable responses over the 1200 years of the sedimentary record (Fig. 6.8). Magnetic susceptibility performs the highest coefficient of variation (74%) followed by microfossil charcoal (55.5%) and organic matter (27.7%).

Magnetic susceptibility experiences an abrupt change going from around 1020 cal. yr BP then dropping at 720 cal yr. BP and raising at 375 cal. yr BP. Microfossil charcoal is very irregular through the sequence but displays a maximum value at ~565 cal. yr BP. Organic matter shows the most substantial raise at 720 cal. yr BP (Fig. 6.8).

6.4.5. Direct ordination

Canonical Correspondence Analysis reveals a highly dispersed pattern of taxa composition (Fig. 6.9) elucidated by the set of environmental variables. Axis 1 explains 13.1% of the variance with magnetic susceptibility as the main explanatory variable (according to the t-values of the canonical coefficients which must be greater than 2.1 with $p<0.05$ (ter Braak and Smilauer, 2002)), while Organic matter is more important in axis 2 explaining 17.9% of the total variance.

In axis 1, those taxa closely associated to microfossil charcoal such as *Cornus* (Corn); *Arisaema* (Aris), Mimosaceae (Mimo), Solanaceae (Sola) and Juncaceae (Junc) are present at ~915 cal yr BP where a peak in charcoal arises (Figs. 6.7 and 6.8). *Piper* (Pipe) and *Acacia* (Acac) are related to magnetic susceptibility, occurring with their highest abundance at 375 cal. yr BP (Fig. 6.8).

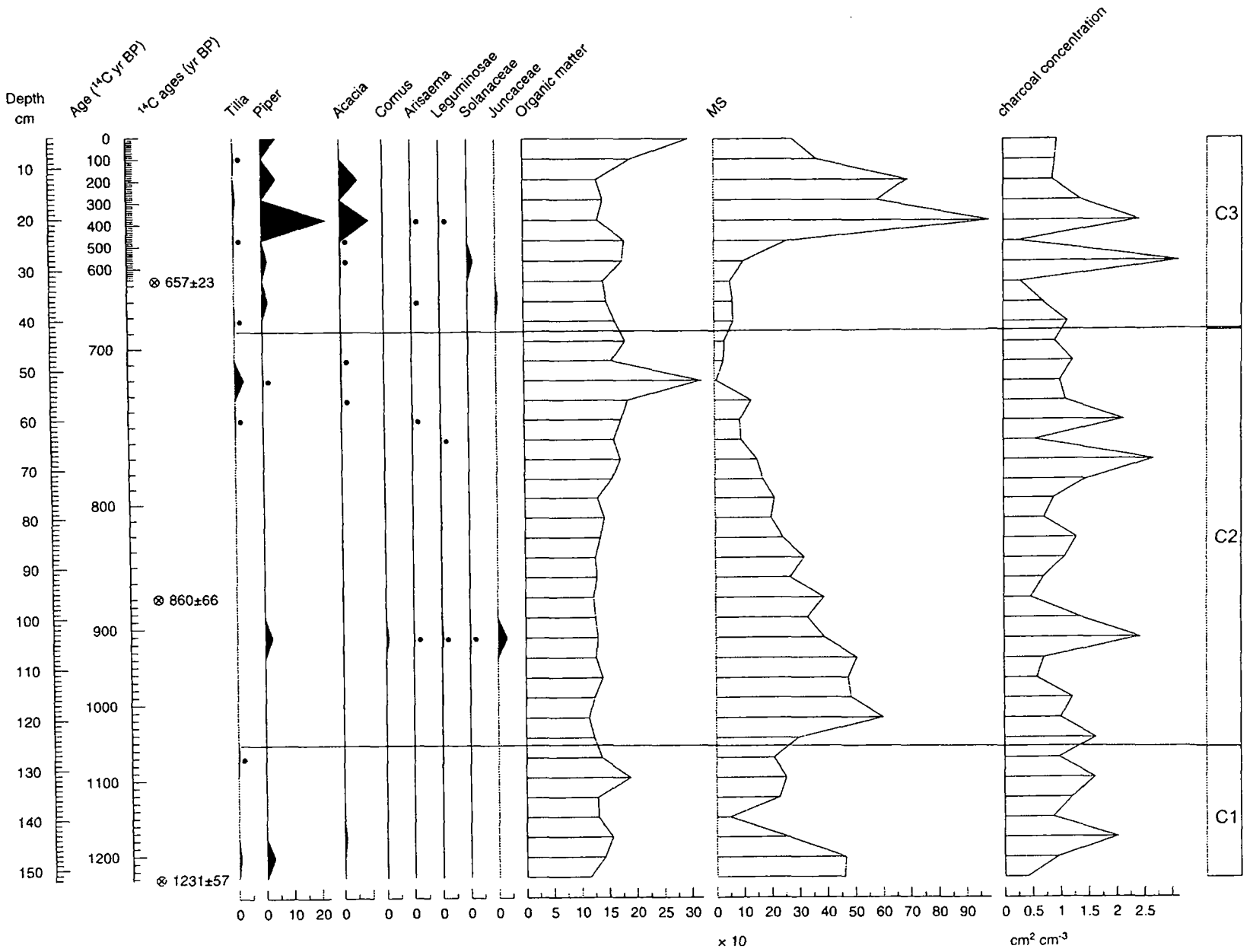

Fig. 6.8. Comparative sequence for sedimentary geochemistry and some taxa in the transitional forest dominated by *Pinus-Carpinus-Quercus* in West-central Mexico. Ages are calibrated years BP.

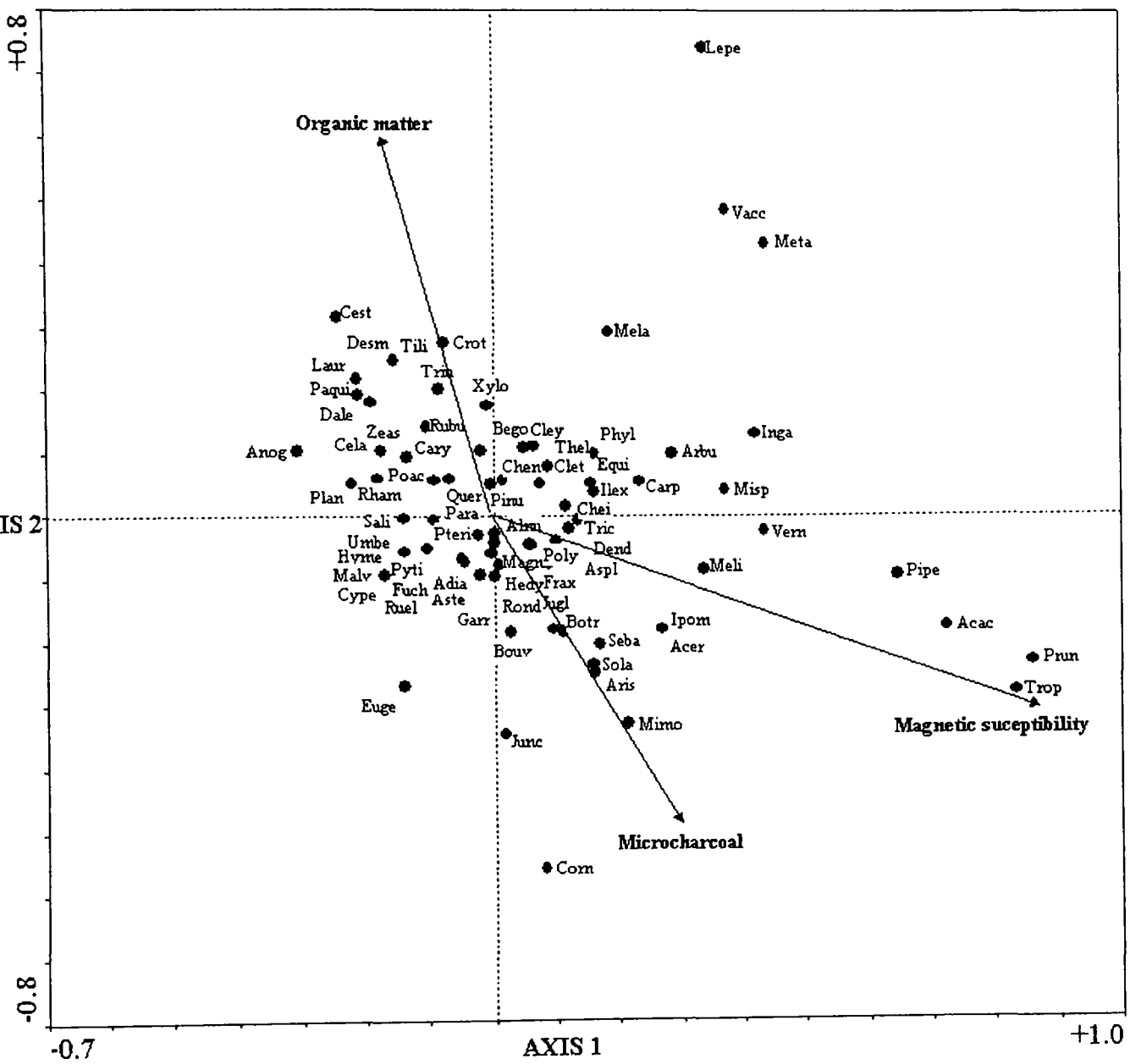

Fig. 6.9. CCA biplot of pollen taxa and environmental variables. Taxa names in Appendix 1.

In axis 2, *Tilia* (Tili) runs along the organic matter arrow experiencing its greatest abundance at 720 cal. yr BP where the highest value in Organic matter takes place (Figs. 6.8 and 6.9).

6.4.6. Spectral analysis

The highest power (displaying the strongest temporal cycle in the dataset) is reached at 80-years for cultural taxa Asteraceae and Poaceae, as well as for *Pinus* and. Microfossil charcoal and organic matter have peaks at different cycles, some coinciding with those present in vegetation (e.g. the highest peak in charcoal concurs with the one at 80-years in cultural taxa, *Pinus* and *Alnus*). Organic matter and Polypodiaceae peaks agree at 95-years while Aspleniaceae has a high power at 85 years (Fig. 6.10).

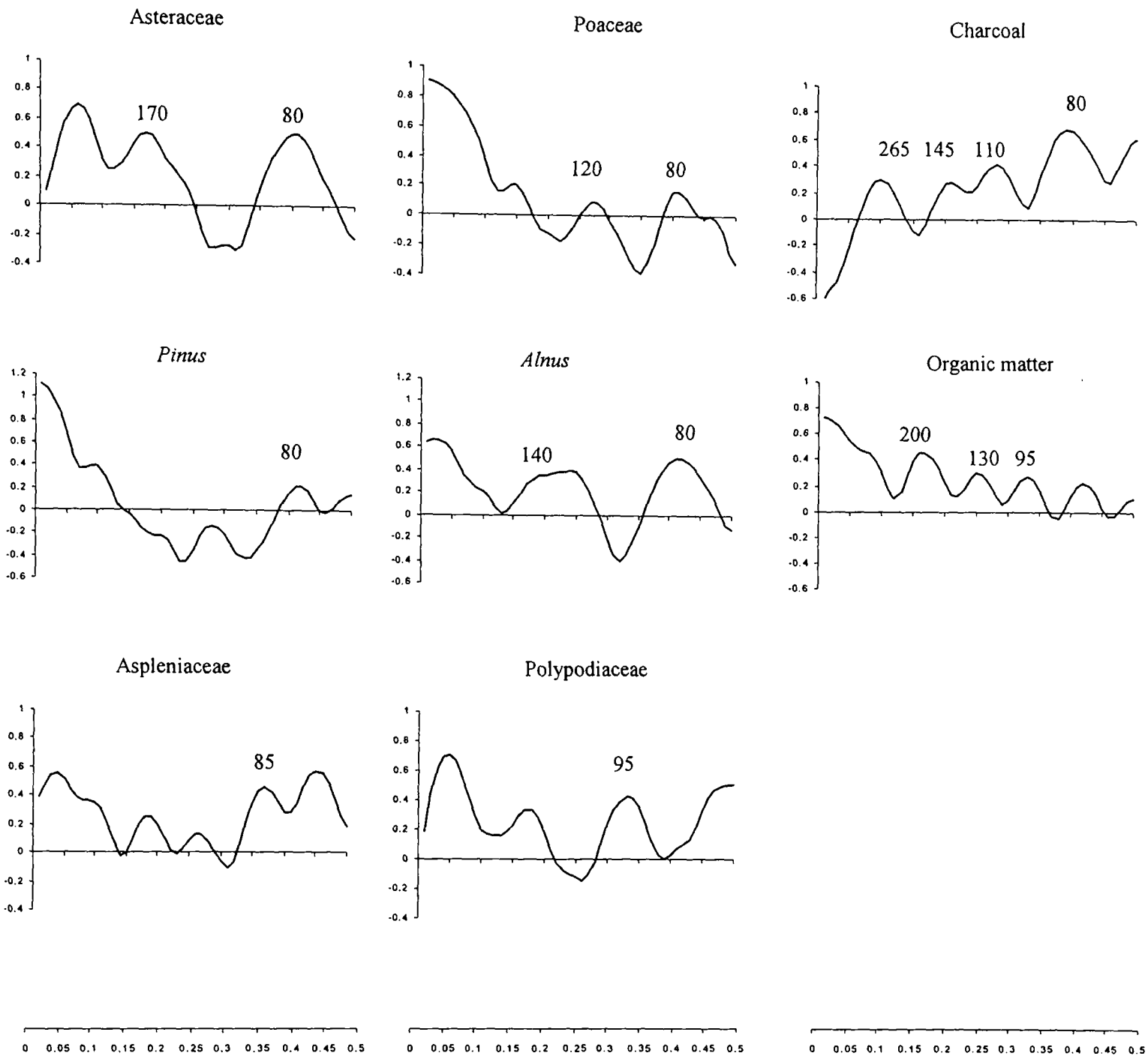

Fig. 6.10. Power spectra of pollen abundance in the transitional forest of West-Central Mexico for the last ~1231 years. Vertical axes give spectral power in arbitrary units. Horizontal axes give frequency in cycles per interval (c.p.i.). They represent the following periods in years; 0.1 = ~ 320, 0.2= ~160, 0.3= ~100, 0.4= ~ 80, 0.5= ~65; some specific periods are expressed at the highest peak.

6.5. Discussion

6.5.1. Successional stages in a transitional forest

Three successional stages can be discerned along ~1200 years of vegetation change in the transitional forest of the Sierra de Manantlan. These include an initial cloud forest stage (Group C or Zone C-1), a human-induced stage with open canopies and cultural taxa (Group B or Zone C-2) and the return of a cloud forest stage (Group A or Zone C-3) with an elevated number of taxa though with low frequencies and abundances as it can be observed in the lower pollen percentages of cloud forest taxa when compared to the initial cloud forest stage (Fig 6.3, 6.5 and 6.6). The pattern of succession resembles a cyclical model similar to that proposed by Watt in 1947 (Frelich, 2002). This consists in the transition of an initial assemblage into intermediate ones after a disturbance event. The cycle is completed when the initial assemblage is recovered. In the ordination space Group C and Group A, which correspond to the same assemblage (cloud forest), are situated in the same position in axis 1 expressing their similarities in taxa composition even though they are separated by ~ 400 years. We suggest that the trigger for this change is human activity but linked to climate change; the drier period is reported in the human-induced stage and the wet periods coincide with the cloud forest stages.

6.5.1.1. The earliest cloud forest stage

A cloud forest stage is evidenced from ~1230 to 1045 cal yr BP contained trees such as *Alnus, Carpinus, Salix* and *Juglans* and epiphytes represented by Aspleniaceae family. Other less abundant arboreal elements, *Cleyera, Piper, Magnolia* and Melastomataceae, were also

present and are presently indicators of this assemblage as well. The absence of most of the herbaceous (e.g. Caryophyllaceae, *Begonia, Crotalaria, Dalea, Desmodium*) and cultural taxa (Solanaceae, *Zea* and *Plantago*), along with the low abundances of other herbs families (Asteraceae and Poaceae) is typical of forest with closed canopies verifying the existence of a cloud forest stage.

In the ordination plot (Fig. 6.7a) of the first zone (Group A) the cloud forest taxa are demarcated into three separated clusters. This indicates a temporal heterogeneity in the cloud forest. Taxa in the same cluster (e.g. *Carpinus* and *Juglans*) were present during the same time interval. This behaviour can be explained through niche differentiation hypothesis (Fargione and Tilman, 2005), particularly by temporal niche partitioning. Temporal variability in resource accessibility has been acknowledged as a driver affecting diversity where species composition may vary and respond to the changing environment (Brown *et al.*, 2001). This mechanism is allowing cloud forest taxa to thrive better during particular time intervals when certain environmental conditions favour their development. (Mamolos, 2006) found that a moisture increment in the soil during wetter years enhance the growing period of some species, increasing their abundance.

6.5.1.2. The Human-induced stage

A human-induced stage is predominant from ~1045 to 695 cal yr BP (Group B). The high number of herbs and, particularly the high abundance of cultural taxa such as Poaceae, Asteraceae and *Plantago* suggest the opening up of the canopy (Brown and Hebda, 2003; Bush *et al.*, 2004). The presence of *Zea* sp., which is only found in this zone, emphasizes that humans must be closely associated to vegetation changes in this stage. An endemic perennial

teosinte or "wild maize", *Zea diploperennis*, was discovered in Manantlan more than two decades ago (Iltis *et al.*, 1979). Teosintes are considered ancestors of maize (Bennetzen *et al.*, 2001) contributing to its domestication through human selection (Eubanks, 2001; Hubbard *et al.*, 2002; Iltis, 2000; Wang *et al.*, 1999). Even when *Zea* pollen was not identified to species level, evidence of maize is unquestionable in this stage, either by *Zea diploperennis* or *Zea mays*.

The ordination diagram corroborates the cultural domain in Group B accommodating cultural taxa on the left of the plot such as *Rubus, Dalea, Crotalaria, Plantago, Zea*, Asteraceae, Poaceae and the fern *Pteridium aquilinum* (Fig. 6.7b) which is usually a post-disturbance colonizer (Engelman and Nyland, 2006; Whittle *et al.*, 1997). In association with these cultural indicators there is a decline in Aspleniaceae (considered as indicators of cloud forest assemblage (Figueroa-Rangel *et al.*, In preparation-a) and in some cloud forest trees. This is probably due climate change rather than direct human activity (discussed below). In contrast Polypodiaceae and Hymenophyllaceae indicate maximum values. Hymenophyllaceae family is known for its high tolerance to dryness (Proctor, 2003) and some Polypodiaceae elements are also desiccation-resistant ferns (Andrade and Nobel, 1997; Muslin and Homann, 1992) suggesting that this period was drier than the previous one. A drier period is known to have occurred between 800 to 1000 A.D. in Mexico Hodell *et al.* (2001) which coincides with the ages (~905-1255 A.D) reported in this stage.

Burning episodes are very heterogeneous and no correlation of higher charcoal concentration is found in this human-induced stage, however the charcoal peak at around 915 cal. yr BP matches with a peak in *Piper* and the presence of infrequent taxa such as *Cornus, Arisaema*,

Mimosaceae, Juncaceae and Solanaceae (Fig. 6.8 and 6.9). The existence of this fire event appears to be triggering turnover composition allowing the establishment of species that only appears related to changes in the environment, in this particular case linked to fire. Fire is seen as a consumer control of species composition (Bond and Keeley, 2005) and, according to Buhk *et al.* (2006), herbaceous plants are favoured by abundant light and nutrients after fire, a situation that increase their abundances. Keeley *et al.* (2005) also reported this pattern particularly associated to Mediterranean shrublands where diversity peaks after a fire although with a later decrease in species richness. Different peaks in charcoal are expressing the irregular pattern in fire events. Of note, however, is an apparent cyclicity at 80-year which is concurrent to the peaks in Poaceae, Asteraceae, *Pinus* and *Alnus* possibly suggesting a periodicity related to human influences.

6.5.1.3. The recent cloud forest stage

The cloud forest stage recovered in this region from ~695 cal yr BP to present, with a greatest palynological richness indicating a higher number of cloud forest taxa in comparison with the first cloud forest stage recorded from ~1230 to 1045 cal yr BP, and the more numerous infrequent or rare taxa in the whole sequence. It is important to note that a lower percentage of pollen coming from cloud forest is expressed in this zone than in the previous cloud forest stage with the highest contribution to the total pollen sum given by epiphytes Aspleniaceae. A different sort of cloud forest taxa (*Piper* and *Magnolia*) dominates this period and human disturbances are more evident in this stage. These include maximum abundance in *Pinus*, more open canopies supported by the superior number of herbs, bigger peaks in charcoal and the highest magnetic susceptibility. Essentially the last two events are concentrated at 375 cal.

yr BP (~1575 A.D.) after the Spanish Conquest (1521 A.D.). Interestingly this episode triggers the abundance in *Piper* and *Acacia* (Fig. 6.8 and 6.9). The last genus characterizes Pine-Oak and Oak forest in the region and elsewhere (Greenberg and Bichier, 2005; Vazquez-Garcia *et al.*, 1995), it is also a taxon related to disturbed sites (Purata *et al.*, 1999) and it is primarily associated to grazing land for livestock (Greenberg *et al.*, 1997).

Again in the DCA ordination of this zone (Group C) cultural taxa are grouped on the right of the ordination diagram together with *Pinus, Quercus* and *Alnus* reaffirming this stage is more associated to human interventions than the earlier stage. *Pinus, Quercus* and *Alnus* characterize many high-altitude ecosystems in Mexico (Rzedowskii, 1981), all three have Holarctic phytogeographical affinity and prevail in pine, pine-oak and cloud forest in the West-Central region of Mexico and are closely associated to fire (Agee, 2000; Brown and Hebda, 2003; Carrion *et al.*, 2000).

Taxa related to charcoal and magnetic susceptibility in the CCA plot include *Cornus*, Mimosaceae (including *Acacia* from the same family) and *Prunus*. Some of these taxa are dominant in the present-day vegetation (Table 6.1) and results from this study indicate that fire may be determining their successional trajectories in high-altitude forest in West-Central Mexico.

6.5.2. Factors triggering succession in a transitional forest

The cloud forest assemblage established from ~1230 to 1045 cal yr BP turned into a less closed canopy type during ~400 years to recover from ~695 cal yr BP and continues to

present. We suggest that the drivers involved in the interruption of the cloud forest succession were climate change and human disturbance. The impact of each will be discussed in turn:

6.5.2.1.Climate change

Previous studies have indicated that there was a particularly dry period (~1045 to 695 cal yr BP; 904-1255 A.D.) in Central and Southeastern, as well as in North Mexico. In the North the driest years were 936, 1034, 1150, 1253 A.D. (Cook *et al.*, 2004) with evidence for a ~400 year interval of general aridity from 900 to 1300 A.D. with atypical warmth conditions. A similar arid interval has been determined for Central Mexico around 1000 yr BP (Arnauld *et al.*, 1997; Metcalfe and Hales, 1994; Metcalfe, 1995) and for the Yucatan Peninsula from ~800 to 1000 A.D. (Hodell *et al.*, 2005a; Hodell *et al.*, 2001; Hodell *et al.*, 1995). In the Yucatan Peninsula, the main causes are related to solar forcing which acts on a centurial scale. Paleoclimatic records of precipitation in the past 2600 years have demonstrated correlations with solar forcing revealing a 208 years periodic pattern of drought analogous to the 206-year phase in records of cosmogenic isotopes ^{10}Be and ^{14}C which are inversely related to solar activity (Hodell *et al.*, 2001). The study on cosmogenic isotopes revealed that solar activity was high from A.D. 1100 to 1250 (Beer *et al.*, 1996) a period coincident with the drier period found in this study from 905-1255 A.D. The close temporal correlation between the reduction in cloud forest and the rise of drought resistant epiphytes evidenced in our study is in accordance with these palaoeoclimatic reconstructions suggesting that a similar dry interval was occurring in this region.

This evidence therefore suggests that climate change at a regional scale was also affecting succession in the transitional forest in West-Central Mexico. But how was the human activity affecting successional trends in the transitional forest? Some possible explanations follow:

6.5.2.2. Human disturbances

Considering that the first appearance of maize and/or teosinte in the sequence dates back to 710 cal. yr BP (1240 A.D.) is prudent to believe that people must have already inhabited Manantlan practising agriculture and focusing on maize crops before the Spanish Conquest. Manantlan is mentioned in Kelly's (1945) work as a site with human occupation in a valley between hills and the environs extensively terraced. The earliest ceramic complex found for the Autlan zone (~25 km from the coring site) is *Cofradia* related to a pre-Conquest horizon particularly to *Aztecs* time (referred as *Aztec I-Chichimec*)(Kelly, 1945). *Aztec* refers to the Nahuatl-speaking people of central Mexico during the Late Postclassic period (from the 12th century A.D.) until the Spanish invasion of the 15th century (Hodge, 1998).

It is highly likely that the drier period would have caused scarcity of water resources in the lowlands inducing people to undertake agriculture in the relatively more humid highlands. In Kelly's (1945) work there is also a recurrent allusion of the insufficient water supply in the Autlan valley tied to the frequent lost of maize crops over the years. So even in wet years water was an important issue for people in the valley.

Land rotation or shifting cultivation in Mexico is an ancient agricultural method (Mendoza-Vega and Messing, 2005) based on the natural recovery of the soil. The land is used for cultivation in variable periods, after that time the soil is allow to recover naturally under the effect of a fallow vegetation (Bravo-Garza and Bryan, 2005). With agricultural practices

forest-clearing increases allied to slash-and-burn activities. We suggest that this is reflected in the 80-year for charcoal and cultural taxa as well as for *Pinus* and *Alnus*. *Pinus* is a thermophilous taxa favoured by fire (Agee, 2000) while *Alnus* is recognized as a shade-intolerant, early seral taxa easy to establish in open habitats and a good indicator of disturbance, particularly fire (Brown and Hebda, 2003). The cycles in the vegetation reported in this study are therefore possibly coupled to the different fallow periods that people in the past used to recover their lands for agricultural purposes, an indispensable time for the forest recovery as well. Other studies have documented decadal periods between 40-100 years for the recovery of Neotropical forest in a vacant land after disturbance events namely grazing, logging and agriculture (Finegan, 1996; Muniz-Castro *et al.*, 2006).

6.6. Conclusions

Disturbance regimes regulated by humans and climate have been influencing successional trajectories of the present-day transitional forest in West-Central Mexico for at least the past 1200 years. In the study region, a cloud forest assemblage dominated from ~1230 to 1045 cal. yr BP, to be interrupted by an interval of aridity from ~1045 to 695 cal. yr BP (10-12th century) when an open canopy and higher herbaceous and dry-resistant epiphytes became abundant in the area. After ~400 yrs (from 695 cal. yr BP), the cloud forest assemblage returned and the current transitional assemblage of *Pinus-Quercus-Carpinus* forest became established. Temporal heterogeneity through niche partitioning has maintained diversity in this forest with a high taxa turnover. Evidences of human disturbances were also higher during the drier period when cultural taxa such as Poaceae, Asteraceae and *Zea* sp. were predominant. Periodicities in cultural taxa, microfossil charcoal and taxa related to human interventions

such as *Pinus* and *Alnus* are around 80 yrs. Local farmers took advantage of the more open canopy and possibly the slightly more humid conditions in comparison to the lowlands to undertake agriculture in this region during this period of climate change between ~ 905-1255 A.D.(~1045 to 695 cal yr BP).

Even when the cloud forest assemblage returned to the region after ~400 years, there was a turnover of taxa where *Pinus* and herbs in this community increased. We suggest that this is evidence of continued human activity. Increased fire occurrence and palynological richness also support this suggestion of a higher human occupation from 695 cal yr BP to present times, therefore a fire human-induced environment is driving the direction of succession in this high-altitude forest in West-Central Mexico. Considering the prediction of global warming, it is highly probable that this forest could return to an open canopy forest with herbs and cultural taxa as observed in the 10-12th century A.D.

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7. General Conclusions

The present research evaluated the long-term forest dynamics in high-altitude mountains of West-Central Mexico. Three forest types were evaluated; pine forest, cloud forest and transitional Forest over ~4200, 1400 and 1200 cal yr BP respectively. It appraised vegetation responses at stand level including trees, shrubs, herbs and epiphytes supporting the individualistic concept in plant species distribution.

The main drivers of change were climatic fluctuations and disturbance events induced by humans such as fires and land clearance mainly through logging and agriculture on timescales of decades to centuries (Table 7.1). The main ecological mechanisms underlying the long-term dynamics were secondary succession, taxa turnover and minor variation in diversity (Table 7.1). These results support the view that species not only depend on their dispersal capacity (neutral theory) but also on the availability of temporal adequate spaces for establishment (niche theory).

Conclusions are arranged according to the research questions posed in the introduction. First is the account of the modern pollen signature; second a perspective of the environmental heterogeneity; third the main aspect of vegetation changes; fourth the two main drivers of forest dynamics and finally some strategies for the conservation and management of the three forest types.

7.1 Modern Pollen and Forest Assemblages

The three forests differed in terms of pollen abundance and composition. Cloud forest produced more grains per cubic centimeter followed by pine forest and the transitional forest. Despite *Pinus* pollen dominating the spectra in the three forests, every forest type (i.e. cloud forest, pine forest and transitional forest) had a unique taxa composition. In pine forest, *Pinus, Alnus* and *Fuchsia* were predominant in the arboreal component and Asteraceae family in the non-arboreal. In cloud forest *Quercus* and Melastomataceae, Aspleniaceae and Polypodiaceae were predominant representing the indicator taxa for the existence of cloud forest. In the transitional forest they were *Carpinus, Clethra* and *Magnolia* together with Poaceae, Chenopodiaceae and Hymenophyllaceae.

Modern pollen composition expressed accordance with the actual vegetation. Types dominating the modern pollen assemblage in every forest were the same taxa leading the canopy. In pine forest, *Pinus* and *Alnus* were both present in the actual vegetation and the modern pollen. In the transitional forest *Carpinus,* the second canopy dominant tree (either in density or in basal area), was also leading the pollen sum. In cloud forest, *Quercus* was the second most productive tree in terms of pollen grain percentages having a good species representation in the actual vegetation. This included three oak species, *Quercus candicans, Q, castanea* and *Q. xalapensis*.

Pollen production was strongly connected to the structural performance of the species. Results indicated that more than one structural variable is necessary to express taxa dominance allied to pollen production; e.g. basal area alone could not convey *Zinowiewia concinna* dominance

in transitional forest because density was considerable reduced. Considering just frequency was ineffective when comparing *Carpinus tropicalis* and *Pinus douglasiana* in cloud forest, they had the same frequency but basal area was reduced fifty times in the first taxa.

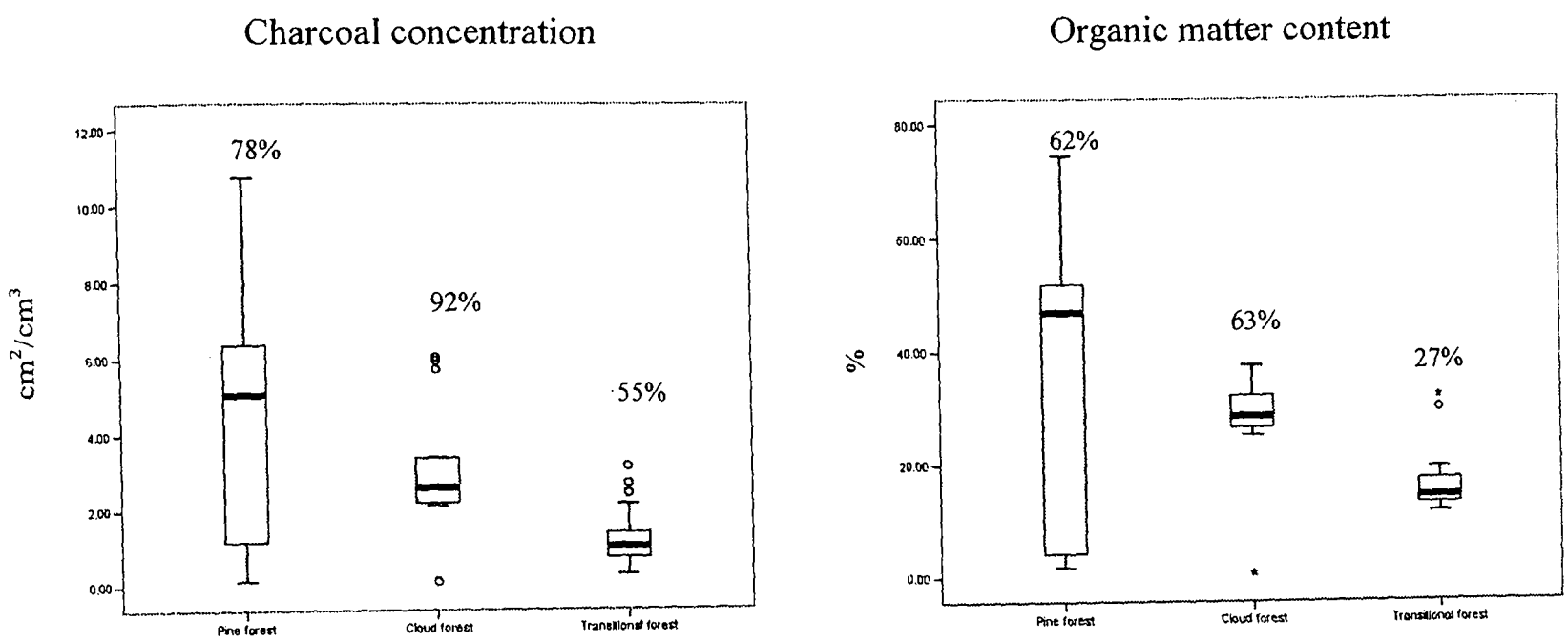
In addition taxa composition was also determining differences in pollen production among forest types. This behavior was mostly perceived in the cloud Forest where the three *Quercus* species exhibited a masting year producing more pollen grains per tree than those in transitional forest, even when basal area and number of trees per ha surpassed in transitional forest.

In summary, the structural particularities and compositional divergences in high-altitude forests of West-Central Mexico should be considered when studying modern pollen and forest assemblage relationship.

7.2. Environmental heterogeneity through time

The environment surrounding the three forest types depicted an irregular pattern through time (Fig. 7.1). For microfossil charcoal, that is an expression of fire occurrence, pine forest demonstrated the highest range and value representing the most burned type, followed by cloud and the transitional forest. However according to the coefficient of variation (regarded as the best estimate in determining variability and allowing comparison of populations with significantly different mean values), Cloud forest was the most variable whereas the transitional forest was the less variable (Fig. 7.1). This suggests irregular fire events affecting cloud forest, possibly as a result of its high vulnerability to fire.

Fig. 7.1. Descriptive statistics for environmental variables in pine-dominated forest, cloud forest and transitional forest. Coefficient of variation for each variable in the top of the box-plots.



The same pattern observed for microfossil charcoal applied to organic matter content probably as a result of the deposition of organic components tied to burning occurrences (Fig. 7.1). For magnetic susceptibility pine and cloud forest had very similar patterns while transitional forest had the highest range and coefficient of variation with the lowest value as well (Fig. 7.1). This result expressed that transitional forest, despite undergoing less burning through time, was more susceptible to soil erosion processes.

With respect to carbonates, transitional forest had once more the highest range but the highest value and the lowest coefficient of variation (Fig. 7.1). Contrastingly, pine forest had the smallest variation and the lowest value. This result agrees with the fact this forest was affected by more dry periods. This is in agreement with other studies which found a decrease in carbonate content related to drought periods (Brown et al., 2005).

Geochemical elements, though only estimated for cloud forest, showed the highest values during the drier period, indicating erosion related to climate change but also correlated to the period of major human disturbances. The increase in microfossil charcoal and organic matter, variables linked to fire occurrences, coincided both with the dry period in pine forest and only with organic matter in the transitional forest. The rest of the variables were not concurrent to either dry or wet periods (Table 7.1).

Accordingly some taxa behaved parallel to some of these variables, e.g. *Pinus* and *Alnus* appear to have responded similarly to microfossil charcoal and organic matter variation in pine forest while Hymenophyllaceae to magnetic susceptibility and carbonates in the transitional forest (Fig. 7.1 and 7.2a, 7.2c).

7.3 Taxa Turnover and Diversity

Even when diversity, explained through palynological richness, remained constant along the zones of the three forests, the most diverse was transitional forest with analogous values to those of cloud forest whilst the least diverse was pine forest. Temporal taxa turnover was an important pattern observed in this study. The taxa found along the sequence appeared and disappeared, particularly those of cloud forest (Table 7.1), partitioning a temporal niche and oscillating in similar cycles in the three forest types (Table 7.2). Diversity was then maintained through time even when taxa composition varied in response to the heterogeneous environment.

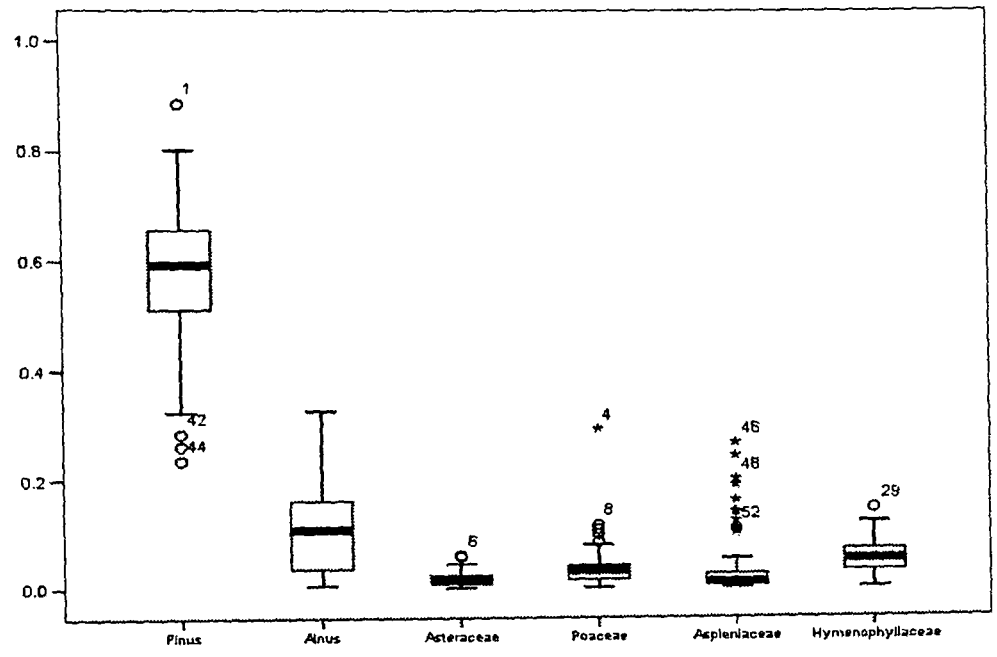
Pinus was expanding and contracting in a regular fashion in pine forest with the expansion period synchronized with the driest interval. *Alnus* did the same but in a reverse pattern to that of *Pinus* whereas *Quercus* was contracting during the wet periods.

Cloud forest taxa (e.g. *Tilia, Magnolia, Clethra, Fraxinus, Carpinus, Juglans*) only indicated increase during the wet intervals in the three forests (Table 7.1).

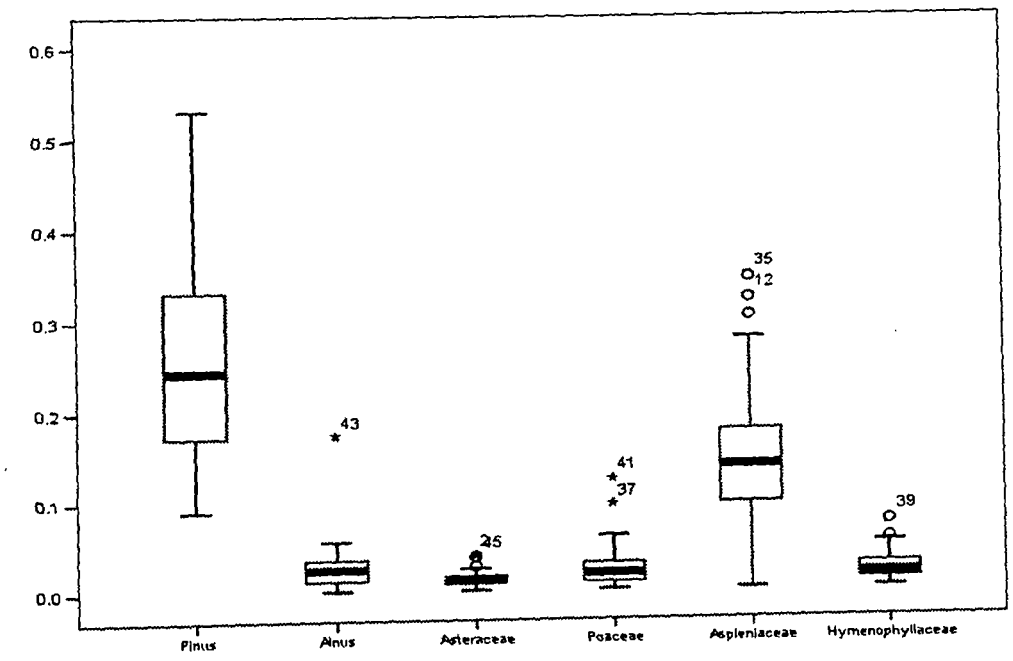
Cultural taxa (mainly characterized by Asteraceae and Poaceae) were higher during dry intervals with increased incidence of fire. Their cycles coincide in the three forests. Epiphytes (Aspleniaceae and Adiantaceae) differed from cultural taxa expanding during wet periods (Table 7.1 and 7.2).

Fig. 7.2. Descriptive statistics for the main taxa in a) pine-dominated forest, b) cloud forest and c) transitional forest.

a)

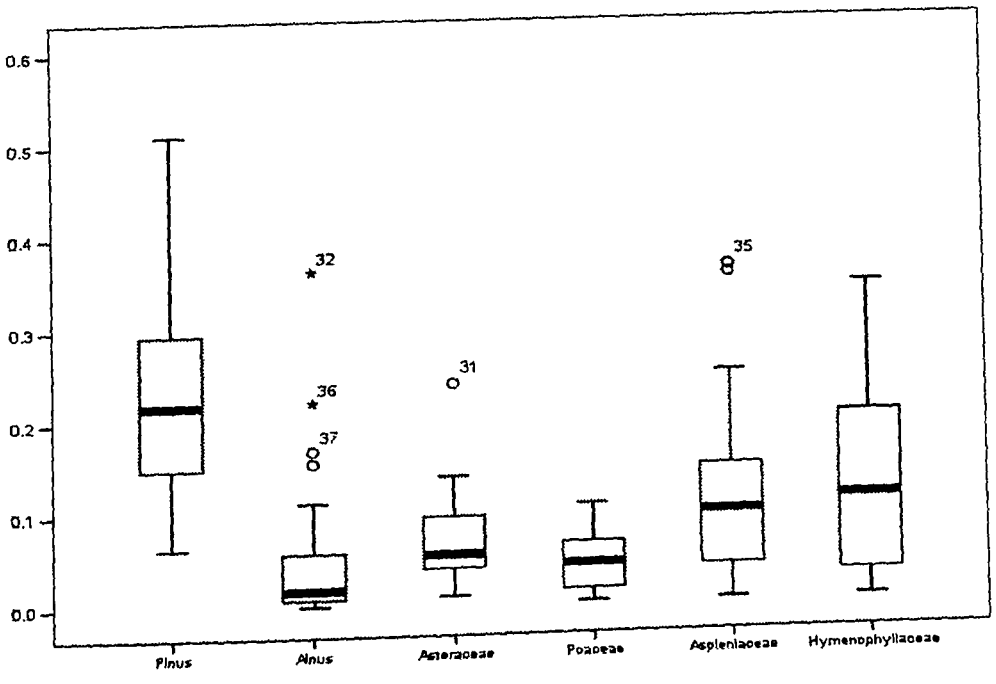


b)



Pollen percentages (x100)

c)



Actual Vegetation	*Pine-dominated forest*				*Cloud forest*				*Transitional forest*				*Concurrent Regional events*		
Time scale	Cal yr BP	Cli	Veg	Cul	Cal yr BP	Cli	Veg	Cul	Cal yr BP	Cli	Veg	Cul	Cli	Veg	Cul
0 100 200 300 400	**Z4**		Pinus ▲	Fire ▼except at 250 BP; Asteraceae, Poaceae Chenopodiaceae, Plantago ▲	**Z4**		Pinus, Tilia, Fraxinus ▲; Ilex, Cleyera, Quercus ▼	Fire ▲	**C3**		Palynological richness ▲; Pinus, Piper, Ostrya, Magnolia, Trichilia, Acacia ▲	Fire ▲	1b, 1g, 1h, 2a	Pinus ▲ 1b, 1g, 1k, 3a	Asteraceae▲ 3a Asteraceae▼ 3a
500			Pinus ▼; Alnus ▲		435 **Z3**		Pinus ▲;Quercus ▼; closed canopy; less human activities; Paly richness ▼	Poaceae, Asteraceae ▼; Fire ▼							
600 800 1000	510 **Z3**			Fire ▲; Maize ●	555 **Z2**		Pinus ▼; Ostrya, Clethra, Quercus, Meliosma ▲	Fire ▲	695 **C2**		Pinus ; Cloud forest taxa ; Aspleniaceae▼; Hymenophyllaceae ▲	Maize ● Poaceae Asteraceae, Plantago, Pteridium, Fire ▲; Palynological richness ▼	1b, 1c, 1d, 1e, 1f, 1g, 1j, 2a, 2b		
1200					811 **Z1**		Aspleniaceae ▼; Alnus, Hymenophyllaceae, Polypodiaceae, Dryopteris, Equisetum ▲; open canopies	Fire ▼; Poaceae ▲; Maize ●	1045						
1400	1260 **Z2**		Salix, Aspleniacea, Adiantaceae, Alnus▲; Pinus, Hymenophyllaceae, Polypodiaceae ▼; Quercus stable	Fire ▼; Asteraceae, Poaceae ▼	1390		Magnolia, Alnus, Clethra, Lauraceae ▲	Fire ▼	1230 **C1**		Alnus, Carpinus, Juglans, Magnolia, Salix, Piper, Cleyera, Melastomataceae Asplenia ceae ▲	Absence of most herbaceous; Asteraceae, Poaceae ▼		Mesophytic species ▲ 1a,1b	Maize, Chenopodiaceae, herbaceous species ▲1a, 1g, 1i, 1k
1600 1800 2000 2500													1a, 1b, 1d, 1e, 1i 2a, 4a		Maize ● 3a Maize ● 1g
3000 3500 4000 4500	2580 **Z1**		Pinus, Quercus ▲	Fire ▲; Rubus, Parathesis ▲									1d, 1e, 1f, 1g, 1j		Poaceae ▲ 1g Maize ● 1e Maize ● 5a,

Table 7.1. Main vegetation, climatic, and cultural changes in pine-dominated forest, cloud forest and transitional forest with concurrent regional events in Mexico over the last 4500 years. 1. Central Mexico a) (Gonzalez-Quintero, 1986), b)(Almeida-Lenero et al., 2005), c) (Metcalfe et al., 2007), d) (Metcalfe, 1995), e) (Arnauld et al., 1997), f) (Ludlow-Wiechers et al., 2005), g) (Metcalfe and Hales, 1994), h) (Vazquez-Selem, 1997), i) (Lozano-Garcia et al., 1993), j) (O'Hara and Metcalfe, 1997), k) (Brown, 1985); 2 Yucatan Peninsula a) (Curtis et al., 1996), b) (Hodell et al., 2005a; Hodell et al., 2001; Hodell et al., 2005b); 3. East a) (Conserva and Byrne, 2002); 4. North a) (Metcalfe et al., 2002); 5. Veracruz a) (Sluyter and Dominguez, 2006), b) (Goman and Byrne, 1998). The dotted line represents the Spanish arrival to the New World. Pattern in vertical lines indicates dry periods and diagonal lines wet periods.

Table 7.2. Cycles (express in years) gauge through spectral analysis for some taxa in pine-dominated forest, cloud forest and transitional forest.

		FOREST TYPES		
VEGETATION		**Pine-dominated forest**	**Cloud forest**	**Transitional forest**
Trees	**Taxa**			
	Pinus	80	65	65,80
	Alnus	80	355,80	140,80
	Quercus	250,135,95	200,65	
	Carpinus		406,65	65
	Magnolia		170,80	65
Shrubs	*Rubus*	155,80	65	
Herbs	Poaceae	200,135,80	120,65	120,80
	Asteraceae		115,70	170,80
Epiphytes	Aspleniaceae		245,65	85,70
	Polypodiaceae		95,65	95,65
MICROFOSSIL		110, 80	65	265,145,110,80
CHARCOAL				65
ORGANIC MATTER			640	200,130,95,70

Pine forest experienced the minimum turnover in taxa and transitional forest the greatest. The actual pine forest assemblage has been mostly alike over the last ~4200 years except from 2580 to 1260 cal yr BP, during a more humid interval in time. In that period *Pinus* decreased with an associated raise in epiphytes, taken to indicate an increase in cloud forest with *Alnus* and *Salix* (Table 7.1).

The present-day cloud forest has also persisted over the last ~1400 years with only minor changes in tree dominance. During the dry interval (~1200-810 cal yr BP), the assemblage was prolonged and only very sensitive taxa, e.g. *Alnus* and Aspleniaceae, were affected.

A highly evident successional process was detected in the transitional forest. At present this forest is dominated by *Pinus-Carpinus-Quercus*. However, this was a cloud forest from ~1200 to 1045 cal yr BP turning into an open stand dominated by herbs and cultural taxa from ~1045 to 695 cal yr BP (the driest period) to be reconverted in a cloud forest from ~695 to very recent times. The taxa turnover generated alternating patterns of dominance through a cyclical model according to (Frelich, 2002).

It is suggested from work in this thesis that niche partitioning through temporal habitat change was the main driving mechanism responsible for taxa diversification in the three forests. This mechanism was determining where and which taxa constitute the communities (Chesson, 1991; Chesson and Case, 1986; Norden et al., 2007), in opposition to the neutral theory (Hubbell, 2001) which supports the view that changes in species abundance through time are due to chance alone.

The process of taxa replacement, and the main cause of temporal patchiness in the three forests, involved human disturbances coupled to climate change events whose details follows.

7.4. Climate Change

Climate change has been impacting pine, cloud and the transitional forest performance over the last millennia imposing changes in vegetation. Cloud forest and the transitional forest had experience two wet and one dry period while pine forest had two dry and two wet periods (Table 7.1). The climate change episodes observed in these localities seem to be the effect of events occurring regionally in Mexico (Table 7.1).

Dry periods in pine and the transitional forest overlapped with the increase in fire occurrences while there was no discernable change in the burning regimes in the cloud forest during the dry period. One feasible explanation for this behaviour is El *Niño*-Southern Oscillation (ENSO) associated with extreme drought conditions where extensive fires are apparent as the vegetation dries up. The influence of ENSO varies according to vegetation status (Roman-Cuesta et al., 2003). Hence pine and transitional are more fire-prone communities and the availability of fuel to be ignited was greatest for that period in both forests. In the other hand cloud forest is situated at lower altitudes (1820-1890 m asl) than Pine (2510-2570 m asl) and transitional forest (1880-2100 m asl) and its microclimatic conditions such as a large amount of moisture, given by its location in a deeper ravine with very irregular topographies, sheltered it from fire incidences.

The dry period reported in Mexico has been extensively studied in Central Mexico and the Yucatan Peninsula but it has been also reflected in Central (Neff et al., 2006) and South America (Haug et al., 2003; Mohtadi et al., 2007). In Central Mexico the period has been reported in a range from ~1400 to 1000 BP (Almeida-Lenero et al., 2005; Arnauld et al., 1997; Ludlow-Wiechers et al., 2005; Metcalfe and Hales, 1994; Metcalfe, 1995; Metcalfe et al., 2007; O'Hara and Metcalfe, 1997) while in the Yucatan Peninsula mainly from ~1200 to 1000 BP (Curtis et al., 1996; Hodell et al., 2005a; Hodell et al., 2001; Hodell et al., 2005b).

The main causes are related to the seasonal shifts in the location of the Intertropical Convergence Zone (ITCZ) particularly to its southward displacement that is connected to dry conditions when precipitation diminished (Haug et al., 2003; Hodell et al., 2005a; Mohtadi et al., 2007). As it was indicated in a previous paragraph, these regional climatic events were pervasive influencing in larger geographical scales as the ultimate cause for the ITCZ shift was large-scale divergence in oceanic and atmospheric circulation explained by Holocene solar and orbital forcing (Bush, 2005; Hodell et al., 2001).

7.5. Human Disturbances

Human influences were evident in the three forests with an increase during the driest period. Maize first appearance (~ 1200 yr BP) coincided with this time (Table 7.1), supporting the interpretation that people underwent water shortage in the lowlands taking them to develop agricultural activities in the highlands and increasing forest clearance as a consequence. Agriculture with shifting cultivation and slash-and-burn activities set the scenario for vegetation change over the last millennia in high-altitude forests of West-Central Mexico. However, human activities did not appear to have any greater impact on the vegetation after

the Spanish Conquest (after ~1521 A.D.), assenting with scholars who have stated that Native Americans had already modified nature before the Spanish arrived to the New World (Lentz, 2000). This finding is supported by archaeological studies (Kelly, 1945; Kelly, 1980) in several localities around the coring site which have revealed a high civilization developing agricultural activities and ceramic complexes around 1200 A.D. The main constituents of a humanized period are an increase in cultural taxa (Asteraceae, Poaceae), dominance of taxa linked to disturbed sites such as *Pinus, Acacia, Rubus* and *Parathesis*, maize emergence and an increase in fire events.

Logging and agricultural activities are possibly influencing the cycles of occurrence for some of the taxa as well as for fire events. In pine forest and the transitional forest fire related taxa such as *Pinus, Rubus*, Poaceae and Asteraceae presented the same spectral powers than microfossil charcoal (Table 7.2).

Pine forest was the most burned type (Fig. 7.1) as a response to natural rather than to human factors including this was the most prone-to-fire community highly exposed to sunlight due to its location in an open high valley. As a result *Pinus* was related to fire increases during the last ~4200 years in the pine forest (Table 7.1). For the other two forest types, the relationship applied only for the last ~500 years.

7.6. Conservation and Management Strategies

One of the underlying objectives of this research was to derive information for the design of conservation and management strategies for each of the three forest types given that all are important forest community ecosystems in Mexico, which provide copious natural resources.

Cloud forest

The information obtained for this forest type indicates that it is a vulnerable system with diminutive changes in diversity and turnover on the last ~1400 years driven predominantly by climate change (Table 7.1). Epiphytes were important indicators of this forest type in the pollen record because the trees representative of cloud forest were either poor pollen producers or weak pollen dispersers. The cloud forest demonstrated the most irregular behaviour in terms of fire events with high erosion during the drier period. Its location in a deeper ravine probably sheltered it from significant disturbances such as fires and desiccation. Site-specific protection schemes for this forest type are therefore crucial for the future preservation of this forest. In summary cloud forest is a vulnerable community, distinctive in temporal taxa composition and unique in its physiographical location. Results from this study support the actual protection scheme for cloud forests in Manantlan where areas are kept in exclusion zones, namely the *core* areas of the Sierra de Manantlan Biosphere Reserve, in which timber extractions, grazing and agricultural activities are excluded. These are the best conservation strategies for the long-term maintenance of the cloud forest dynamics.

Transitional forest

The transitional forest was a good system to evaluate succession as it represented an intermediate development stage among pine, pine-oak and cloud forests where *Pinus* and/or *Quercus*, together with other broadleaved trees, were dominating this type. The significance in this site was to ascertain if it was a cloud forest in the past and how it developed into *Pinus-Carpinus-Quercus* forest. This study demonstrated that a cloud forest developed from 1230 to 1045 cal. yr BP associated with a wet environment. This stage was interrupted during ~400 years (during ~10-12th century A.D.) when a drier climate turned the forest into an open canopy landscape dominated by Asteraceae, Poaceae, *Plantago* and *Zea*. The cloud forest, following cyclical succession, returned from 655 cal yr BP with a highest diversity. Given the present-day progressing predictions of global warming, the goal in this forest is to avoid its conversion into an open-land dominated by cultural taxa similar to the one described for the 10-12th century A.D.

The second fundamental result from the transitional forest was that fire increased significantly on the last ~500 years. This event brought about the increase of human-related taxa such as *Pinus* and *Acacia* (Table 7.1). It is likely that logging of cloud forest taxa for timber purposes or land clearance for agriculture and grazing activities allow the proliferation of *Pinus*. The conversion of broadleaved trees and oaks into *Pinus* dominated communities following shifting cultivation is a process already documented in Mexico (Galindo-Jaimes et al., 2002; Garcia-Barrios and Gonzalez-Espinosa, 2003; Ramirez-Marcial et al., 2001). Subsequently, particular care should be put in the extraction of *Quercus* species and broadleaved trees, particularly those taxa characteristics of cloud forests.

The actual site of the transitional forest is already preserved and fenced as it is confined in the perimeter of *Las Joyas Scientific Station*, a protected spot since 1987 where grazing, agriculture and logging are not allowed. However other areas exist in the region with similar floristic and environmental characteristics. Here management strategies for the extraction of timber species should be carefully designed to allow the regeneration of cloud forest taxa limiting the advance of *Pinus*. Also of significance is the establishment of a defence scheme against frequent fires to arrest the development of prone-to-fire taxa.

Pine forest

The long history of the pine-dominated forest covered in this research (~4200 years) indicated a naturally occurring vegetation type increasing during drier periods (Table 7.1). In fact *Pinus* has been conceived as a taxa strongly associated to droughts (Garcia et al., 2007; Pederson et al., 2005). Accordingly the information acquired in this study should be incorporated into any climate-change conservation strategies for this region.

What also emerges from this study, however, is the evidence that people have been using these forests for at least the past 800 years with no apparent negative effect on its ecology. Thus the present-day conservation plans permitting timber production, small-scale agriculture and prescribed burning in some zones of the study area, namely the *buffer* areas of the Sierra de Manantlan Biosphere Reserve are consistent with the long-term dynamics of the pine-dominated forests. Finally, fire was determined as an essential natural component of the pine-dominated forest. Consequently conservation and management strategies should always regard fire as an important tool for its present and future perpetuation.

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9. APPENDICES

Appendix 1

Abbreviations for the taxa considered in Figures 6.7a, 6.7b and 6.7c

TAXA	ABBREVIATION
Trees and Shrubs	
By genus or species	
Acacia sp.	Acac
Acer skutchii	Acer
Alnus sp.	Alnu
Arbutus xalapensis	Arbu
Bouvardia sp.	Bouv
Carpinus tropicalis	Carp
Cestrum sp.	Cest
Cirsium sp.	Cirs
Clethra sp.	Clet
Cleyera sp.	Cley
Cornus sp.	Corn
Dendropanax arboreus	Dend
Eugenia culminicola	Euge
Fraxinus uhdei	Frax
Fuchsia sp.	Fuch
Garrya laurifolia	Garr
Hedyosmum mexicanum	Hedy
Ilex brandegeana	Ilex
Inga sp.	Inga
Ipomoea sp.	Ipom
Juglans sp.	Jugl
Lepechinia sp.	Lepe
Magnolia iltisiana	Magn
Meliosma dentata	Meli
Metaltesma sp.	Meta
Mimosa sp.	Mimo
Parathesis villlos	Para
Phyllanthus sp.	Phyl
Pinus sp.	Pinu
Piper amalago	Pipe
Prunus sp.	Prun
Quercus sp.	Quer
Rhamnus hintonii	Rham
Rondeletia sp.	Rond
Rubus sp.	Rubu
Ruellia jaliscana	Ruel
Salix microphylla	Sali
Sebastiana jalicensis	Seba
Tilia americana var. mexicana	Tili
Trichilia havanensis	Tric

Triumfetta sp.	Triu
Trophis racemosa	Trop
Vaccinium sp.	Vacc
Vernonia sp.	Vern
Viburnum hartwegii	Vibu
Xylosma flexuosum	Xylo

By family

CELASTRACEAE	Cela
LAURACEAE	Laur
MELASTOMATACEAE	Mela
MIMOSAE	Mimo

Herbs

By genus or species

Arisaema macrospathum	Aris
Begonia sp.	Bego
Crotalaria sp.	Crot
Dalea sp.	Dale
Desmodium sp.	Desm
Equisetum hyemale	Equi
Plantago australis	Plan
Zea sp.	Zeas

By family

ASTERACEAE	Aste
CARYOPHYLLACEAE	Cary
CHENOPODIACEAE	Chen
CYPERACEAE	Cype
JUNCACEAE	Junc
MALVACEAE	Malv
POACEAE	Poac
SOLANACEAE	Sola
UMBELLIFERAE	Umbe

Epiphytes

By genus or species

Adiantum sp.	Adia
Anograma leptophylla	Anog
Botrichium virginianum	Botr
Cheilanthes sp.	Chei
Pteridum aquilinum	Paqui
Pteris sp.	Pteri
Pytirogramma tartarea	Pyti

By family

ASPLENIACEAE	Aspl
HYMENOPHYLLACEAE	Hyme
POLYPODIACEAE	Poly

THELYPTERIDACEAE	Thel

Appendix 2

Abbreviations for the pollen taxa considered in Figure 3.6

TAXA	ABBREVIATION
Trees and Shrubs	
By genus	
Abies sp.	ArelP
Acacia sp.	AcacP
Alnus sp.	AjorP
Arbutus sp.	AxalP
Carpinus sp.	CtroP
Cleyera sp	CleP
Clethra sp.	CletP
Fraxinus sp.	FuhdP
Fuchsia sp.	FuchP
Hedyosmum sp.	HedyP
Ilex sp.	IbranP
Juglans sp.	JuglP
Magnolia sp.	MiltP
Parathesis sp.	PvilP
Phyllantus sp.	PhyP
Pinus sp.	PinusP
Quercus sp.	QuerP
Rondeletia sp.	RonP
Salix sp.	SaliP
Sebastiana sp.	SebaP
Tilia sp.	TmexP
Trophis sp.	TroP
Xylosma sp.	XfleP
Zinowiewia sp.	ZconP
By family	
LAURACEAE	LaurP
MELASTOMATACEAE	MelaP
Herbs	
By genus	
Crotalaria sp.	CrotP
Salvia sp.	SalvP
Plantago sp.	PlanP

Rubus sp.	RadeP
Zea sp.	ZeaP

By family

ASTERACEAE	AsteP
CARYOPHYLLACEAE	CaryP
CHENOPODIACEAE	ChenP
POACEAE	PoacP
UMBELLIFERAE	UmbeP

Epiphytes

By genus

Adiantum sp.	AdiaP
Pteridium sp.	PaquP

By family

POLYPODIACEAE	PolyP
HYMENOPHYLLACEAE	HymeP