5-2003

The paleoecological significance of stable carbon isotopes in lake sediments from the Chirripo Paramo of Costa Rica

Chad Steven Lane

Recommended Citation

Lane, Chad Steven, "The paleoecological significance of stable carbon isotopes in lake sediments from the Chirripo Paramo of Costa Rica. " Master's Thesis, University of Tennessee, 2003.
https://trace.tennessee.edu/utk_gradthes/5250

To the Graduate Council:

I am submitting herewith a thesis written by Chad Steven Lane entitled "The paleoecological significance of stable carbon isotopes in lake sediments from the Chirripo Paramo of Costa Rica." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geography.

Sally Hom, Claudia Mora, Major Professor

We have read this thesis and recommend its acceptance:

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

I am submitting herewith a thesis written by Chad Steven Lane entitled "The Paleoecological Significance of Stable Carbon Isotopes in Lake Sediments from the Chirripó Páramo of Costa Rica." I have examined the final paper copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geography.

Sally P. Horn
Dr. Sally P. Horn, Major Professor

Claudia I. Mora
Dr. Claudia I. Mora, Major Professor

I have read this thesis and
recommend its acceptance:

Dr. Kenneth H. Orvis

Acceptance for the Council:

Vice Provost and Dean of
Graduate Studies

THE PALEOECOLOGICAL SIGNFICANCE OF STABLE CARBON ISOTOPES IN LAKE SEDIMENTS FROM THE CHIRRIPO PARAMO OF COSTA RICA

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

Chad Steven Lane
May 2003

DEDICATION

This thesis is dedicated to my parents, Steven and Martha Lane,
for their amazing love and support that have made all paths
in life available and all goals readily achievable.

ACKNOWLEDGEMENTS

Numerous people deserve my deepest gratitude for their assistance and support during the research and writing of this thesis. First of all, I wish to thank my co-advisors, Dr. Sally Horn and Dr. Claudia Mora, for not only allowing me to use their facilities, but for their endless guidance and their ability to make research at the University of Tennessee truly enjoyable and rewarding. The collaboration of Dr. Horn and Dr. Mora made it possible for me to gain exposure to, and a better understanding of, both paleoecology and isotope geochemistry, thereby making me a more well rounded student with numerous tools for future research.

I also wish to thank Dr. Ken Orvis for his endless support in the laboratory, in the field, and also in the classroom. Dr. Orvis' wide ranging knowledge of issues covering all facets of paleoenvironmental research was essential in every stage of my thesis research and writing. Also, I feel incredibly lucky to have had the opportunity to work with Dr. Orvis on projects outside the scope of this thesis and am grateful for his interest in working with me. I am immensely grateful to have been lucky enough to work with all of these professors as they are not only outstanding scientists, but also fantastic people whose friendships I will hold as sacred as their bestowed knowledge in any future endeavors I may undertake.

I wish to also recognize the unending support and encouragement from the members of the Global Environmental Change Research Group at the University of Tennessee; Dr. Lee Cooper, Dr. Steven Driese, Dr. Jackie Grebmeier, Dr. Henri Grissino-Mayer, Dr. Carol Harden, Dr. Sally Horn, Dr. Claudia Mora, and Dr. Ken Orvis. Without the Global Environmental Research Group none of this research would have been possible. I am thankful not only for their funding support, but also for the exposure to the multiple disciplines and research interests of those involved in this research group. I consider myself incredibly lucky to have had the opportunity to work with such an incredible team of researchers during my graduate career.

I must also express my utmost appreciation to Dr. Zheng-Hua Li. As the research associate in charge of the stable isotope geochemistry laboratory, Dr. Li was the person most responsible for teaching me the laboratory techniques involved with isotopic analyses. Not only was his instruction in the methodology of these analyses essential to the writing of this thesis, but his assistance in the interpretation of my data was also very important and helpful. Dr. Li's amazing patience and incredible knowledge in the field of isotope geochemistry made laboratory work both enjoyable and rewarding.

I must also thank Dr. Lynn Clark for providing me with modern plant samples for my research; Dr. Rowan F. Sage for information regarding *Muhlenbergia* grasses; and Dr. Gerardo Umaña for his observations on the extent of *Bottryococcus braunii* in páramo lakes. I am grateful also to the Costa Rican Ministry of Environment and Energy and the La Amistad-Pacifico Conservation Area for allowing me to conduct research in Chirripó National Park.

I certainly must also express my appreciation of numerous graduate students at the University of Tennessee for their invaluable moral support and input into this project. Marty Arford, Duane Cozadd, Kevin Anchukaitis, Kimberly Crider, Dana Miller, Chris Fleming, and Jake Cseke were all outstanding in helping me in various aspects of my research. I would also like to especially acknowledge Daniel Lewis, who

was an incredible help during fieldwork and a great motivator when it came to getting me up and down a 3800 m mountain.

Finally, and most importantly, I must thank my parents, Steven and Martha, for 23 years of unwavering love, support, and encouragement, which has directly resulted in successes I have experienced and hope to continue to experience into the future. Without my parents, I know I would never have been capable of achieving all that I have to this day, and for that I am both infinitely grateful and forever in their debt.

This research was funded by the Global Environmental Change Research Group at the University of Tennessee as part of the President's Initiative for Teaching, Research, and Service. The recovery and initial radiocarbon, pollen, and charcoal analyses of the cores I examined were funded by a grant to Sally Horn from the National Geographic Society. Later analyses of magnetic susceptibility and macroscopic charcoal by Brandon League, on which my study also builds, were funded by an NSF Research Experience for Undergraduates Supplement to Carol Harden, Sally Horn, and Ken Orvis. Field observations and collections in the Chirripó páramo in January 2003 were made during an expedition funded in part by the Global Environmental Change Research Group and in part by a grant to Sally Horn from The A.W. Mellon Foundation.

ABSTRACT

The high elevation páramos of Costa Rica are dominated by C_3 grasses (primarily bamboo) and evergreen shrubs; however, the high altitude C_4 grass *Muhlenbergia flabellata* may dominate suitable microhabitats with coarse substrates, such as glacial till. To explore late Pleistocene and Holocene C_3–C_4 vegetation dynamics, I measured the stable carbon isotope compositions of total organic carbon ($\delta^{13}C_{TOC}$) in two parallel lake sediment cores (core 1: 6 m, core 2: 5.6 m) from Lago de las Morrenas 1 (3477 m) at the foot of Cerro Chirripó.

Both sediment records begin in late Pleistocene (~11,700 cal. yr. BP) glacial silt deposited as the ice last retreated from the Chirripó massif. Average $\delta^{13}C_{TOC}$ values are more positive in the basal glacial silts of both cores than in overlying organic-rich Holocene sediments, possibly suggesting the greater importance of C_4 plants during the late Pleistocene. An increase in the proportion of C_4 plants in the late Pleistocene may have been the result of decreased atmospheric pCO_2, increased aridity (perhaps seasonally), and/or well-drained soil conditions on newly exposed bedrock and glacial till that favored the C_4 grass *Muhlenbergia flabellata*.

The lake sediment $\delta^{13}C_{TOC}$ record shows a strong link to fire dynamics. Periods of increased macroscopic charcoal input to the lake sediments are characterized by more depleted $\delta^{13}C_{TOC}$ during the Holocene and more enriched $\delta^{13}C_{TOC}$ values during the late Pleistocene. Relatively enriched average $\delta^{13}C_{TOC}$ values of ~ –20‰ occur throughout the Holocene despite evidence for continued C_3 plant dominance. These enriched $\delta^{13}C_{TOC}$ values may reflect the utilization of HCO_3^- photosynthesis by aquatic plants and algae, such as *Bottryococcus braunii*, and/or trophic level fractionations imparted

by zooplankton within the lake. Future compound-specific isotopic analyses will assist in isolating the contribution of these various sources to the organic carbon pool.

TABLE OF CONTENTS

LIST OF TABLES

TABLE

LIST OF FIGURES

FIGURE

CHAPTER 1

INTRODUCTION

In early analyses of global climate change, the tropics were viewed as largely disconnected from the changes happening elsewhere in the world (CLIMAP 1981). While higher latitudes cooled during glacial times, climate in the earth's low latitudes was thought to have remained essentially stable. More recently, the idea of a stable tropical climate has been discarded in the face of studies showing significant temporal climatic changes in tropical localities (e.g. Hodell *et al.* 1991; Islebe *et al.* 1995; Leyden 1995; Thompson *et al.* 1995; Curtis *et al.* 1996; Thompson 2000). In fact, the tropical latitudes are quickly becoming regarded as one of the primary drivers in world climate and climatic change.

Much of the data suggesting significant climate changes in the tropics has been the result of studies based on fossil pollen preserved in lake sediments or peat as a proxy of vegetation change (e.g. Markgraf 1989; Bush and Colinvaux 1990; Hooghiemstra *et al.* 1992; Hooghiemstra and van der Hammen 1993; Burney *et al.* 1995; Islebe *et al.* 1996; Wille *et al.* 2001). Several limitations inherent to pollen studies, such as the similarity between pollen grains of different species, the unequal representation of particular pollen types, and human impacts on pollen spectra, may hinder the ability to make accurate and complete vegetation and climate reconstructions from these data alone. In addition, Huang *et al.* (1999) suggest that pollen may not have the rapid response or sensitivity required to act as a reliable proxy for some vegetation or climate changes.

The lack of sensitivity to climatic change is especially a problem for vegetation assemblages that do not typically yield an informative pollen signature, such as vegetation types dominated by grasses. Pollen of most members of the grass, or Poaceae, family is not identifiable to species, or even genus, and therefore provides very limited information on plant community compositions or environmental change (Livingstone and Clayton 1980). In addition, even when vegetation types have distinct pollen signatures, the dominant photosynthetic pathways used by that vegetation (Calvin-Benson cycle (C_3); the Hatch-Slack pathway (C_4); crassulacean acid metabolism (CAM)) are not typically discernable from pollen records.

For the reasons outlined above, many researchers have examined stable carbon isotopes in sediments, which can provide climate information by revealing the dominant photosynthetic pathways utilized by grasses and other plants. Numerous studies from around the world have used stable carbon isotopes from a variety of media, such as lake sediments, peat deposits, soils, herbivore teeth, fossilized dung, and even fossilized egg shells, as a proxy for the relative abundance of C_3 vs. C_4 vegetation at different times during the Quaternary (e.g. Street-Perrott *et al.* 1997; Boutton *et al.* 1998; Connin *et al.* 1998; Ficken *et al.* 1998; Gasse and Lin 1998; Pessenda *et al.* 1998; Street-Perrott *et al.* 1998; Johnson *et al.* 1999; Scott and Vogel 2000; Barker *et al.* 2001; Boom *et al.* 2001; Clark *et al.* 2001; Huang *et al.* 2001; Baker *et al.* 2002; Ficken *et al.* 2002; Mora and Pratt 2002; Scott 2002). The analysis of stable carbon isotopes has become the preferred method for assessing the relative abundance of C_3 and C_4 plants in modern ecosystems as well, despite the ability of researchers to make direct observations regarding the photosynthetic pathways presently being used (Tieszen and Archer 1990).

It is the ability of the stable carbon isotope record to provide this otherwise masked information that makes its use worthwhile in areas where pollen signals alone may not be enough to tell the whole ecological and climatic story.

As mentioned above, one of the major problems affecting pollen-based reconstructions of paleovegetation and paleoclimate in the tropics is that of human disturbance. Multiple studies have documented vegetation disturbance by humans extending into the mid-Holocene in the neotropics (e.g. Burney *et al.* 1994; Northrop and Horn 1996; Kennedy and Horn 1997; Goman and Byrne 1998; Bush *et al.* 2000; Clement and Horn 2001; Rosenmeier *et al.* 2002). This anthropogenic disturbance of vegetation may swamp or mask any vegetation change occurring solely due to climatic changes, thereby making climate reconstructions in these situations nearly impossible. For this reason, when trying to reconstruct climatic change using vegetation proxies it is ideal to have a study site unaffected by human activity.

The site chosen for this study, Lago de las Morrenas 1, is remote from areas of prehistoric or historic human settlement in Costa Rica (Stone, 1977). Lago de las Morrenas 1 is located near the highest peak of the Cordillera de Talamanca of Costa Rica, Cerro Chirripó (3820 m). The treeless, tropical alpine vegetation that surrounds the lake is known as páramo. The páramo vegetation of the Chirripó massif is dominated by bamboo and other grasses (Horn 1989; Horn 1993), which produce pollen that is difficult or impossible to separate to genus or species. As a whole, the Poaceae family contains the greatest number of species utilizing the C_4 photosynthetic pathway (Deines 1980; Sage *et al.* 1999a; Boom *et al.* 2001), which means that stable carbon isotopic analyses, in combination with pollen records, have the potential to provide more information on vegetation change in a grass dominated community than pollen records alone. Currently, the only known C_4 plant species in the Chirripó páramo are grasses in the genus *Muhlenbergia.* As an ecosystem dominated by grasses and containing a modern day C_4 plant component, the Costa Rican páramo is an ecosystem in which data on the changing carbon isotopic composition of plant matter, in combination with various other proxy analyses, may provide a more detailed record of late Quaternary vegetation and climate change.

The C_4 photosynthetic pathway is most advantageous under warm, dry, high light intensity conditions, due to its high water use efficiency. The C_4 photosynthetic pathway has also been found to be highly advantageous during periods of decreased partial pressures of atmospheric CO_2 (pCO_2), due to its ability to actively concentrate atmospheric CO_2 during photosynthesis (Ehleringer and Monson 1993; Ehleringer *et al.* 1997; Collatz *et al.* 1998; Sage *et al.* 1999b).

The C_3 photosynthetic pathway begins with the fixation of carbon dioxide catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Rubisco is also capable of catalyzing the fixation of oxygen during the initial stages of photosynthesis, a process termed photorespiration. Photorespiration greatly hinders the efficiency of photosynthesis as it has no useful function for the plant. Plants using the C_4 photosynthetic pathway have evolved to eliminate the inefficient process of photorespiration by using phosphoenolpyruvate (PEP) as the initial catalyst to carbon fixation. C_4 plants still use the C_3 photosynthetic pathway, except it is isolated within bundle sheath cells surrounded by mesophyll. PEP has both a higher affinity for CO_2 and a greater maximum velocity than does Rubisco. PEP is located in the mesophyll surrounding the bundle sheath cells and acts to actively concentrate CO_2 into the bundle sheath cells by diffusing it through the mesophyll during carbon fixation like a pump. This greatly increases the concentration of CO_2 in the bundle sheath cell as compared to the outside of the plant and greatly reduces the rates of photorespiration. The ability to "pump" CO_2 into the bundle sheath cells during photosynthesis gives C_4 plants a distinct advantage over C_3 plants during periods of decreased atmospheric levels of CO_2. The ability to concentrate CO_2 also allows C_4 plants to keep their stomata closed for longer periods of time, thereby reducing transpiration. This provides C_4 plants with a distinct advantage over C_3 plants under conditions of high light intensity, high temperature, and increased aridity. CAM plants are also capable of both photosynthetic pathways, only they separate the steps temporally instead of spatially, using the C_4 photosynthetic pathway at night with open stomata, and then using the C_3 photosynthetic pathway during the day with stomata closed to limit transpiration (Ehleringer and Monson 1993).

The different methods of carbon fixation in these photosynthetic pathways cause these respective pathways to discriminate differently against ^{13}C during photosynthesis resulting in the formation of plant tissues with distinct $\delta^{13}C$ values (Farquhar *et al.* 1989). These distinct carbon isotope ratios exist in living plants and plant detritus and can be incorporated into sediments. The C_4 pathway discriminates less against ^{13}C and produces a $\delta^{13}C$ value in bulk organic carbon of the plant tissue ranging from –14‰ to –10‰ (PDB), while C_3 species are more discriminating against ^{13}C and produce a $\delta^{13}C$ value ranging from –35‰ to –20‰ (Bender 1971; O'Leary 1981; Cerling 1999). Plants utilizing CAM photosynthesis typically produce $\delta^{13}C$ values falling between these two ranges. These distinct carbon isotope ratios allow estimation in sediment records of the abundance of C_3 vs. C_4 plants in the watershed of a particular lake or bog as long as those plants contribute to the organic matter contained in the sediments. Changing isotope ratios could signal a possible vegetation shift that would not necessarily be evident in pollen records (Huang *et al.* 1999).

The determination of dominant photosynthetic pathways in previous studies of vegetation change has been used primarily to evaluate paleoclimate, in which the dominance of C_4 vegetation is interpreted to indicate either aridity or decreased atmospheric pCO_2 (e.g. Hillaire-Marcel *et al.* 1989; Aucour *et al.* 1993; Boom *et al.* 2001). Multiple studies (Jolly and Haxeltine 1997; Street-Perrott *et al.* 1997; Barker *et al.* 2001; Boom *et al.* 2001; Mora and Pratt 2001) have argued for increased C_4 plant dominance during glacial periods, despite cooler temperatures, due to decreased atmospheric pCO_2. Modeling studies of plant dominance (Figure 1.1) based on known biological characteristics of quantum yields (i.e. the efficiency productivity) under varying temperature and pCO_2 conditions show a crossover from C_3 dominance to increased C_4 plant dominance at lowered atmospheric pCO_2, even with 10°C depressions in temperature (Ehleringer *et al.* 1997; Collatz *et al.* 1998). With pCO_2 levels dropping to 180 to 200 ppmv (20 Pa) during the last glacial maximum (LGM; Barnola *et al.* 1987; Neftel *et al.* 1988; Leuenberger *et al.* 1992), it is quite possible that C_4 plants became much more dominant worldwide than they are today (Jolly and Haxeltine 1997; Collatz *et al.* 1998). Boom *et al.* (2001) have suggested that the C_4-dominated microhabitats they have studied in the northern Andes may in fact be relicts

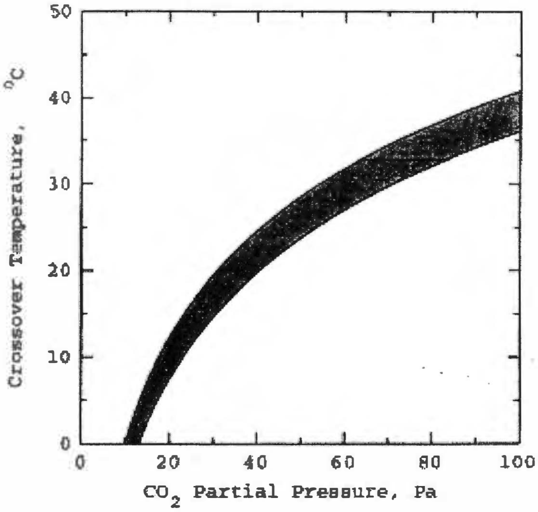

Figure 1.1. Crossover temperatures for C_3 vs. C_4 plant dominance with changes in atmospheric pCO_2 (Collatz *et al.* 1998).

from the Pleistocene, when low atmospheric pCO_2 allowed for a much greater dominance of C_4 plants in the highland ecosystems.

It is important to emphasize that lowered pCO_2 is not the only factor potentially contributing to C_4 plant expansion. C_4 plants also tend to dominate under conditions of high daytime growing temperatures, high light intensities, or predominantly warm-season precipitation (Sage *et al.* 1999b; Huang *et al.* 2001). Multiple studies have also explained increased C_4 plant dominance in tropical regions as a consequence of increased aridity in the past (Quade *et al.* 1989; Talbot and Johannesen 1992; Sukumar *et al.* 1993; Aucour and Hillaire-Marcel 1994; Giresse *et al.* 1994; Huang *et al.* 2001).

The purpose of this study is to examine the stable carbon isotope composition of organic matter in lake sediments from Lago de las Morrenas 1, one of ~30 lakes of glacial origin in the Chirripó páramo of Costa Rica. This study constitutes the first paleoecological study in Costa Rica, and one of very few in Central America as a whole, utilizing stable carbon isotopes from lake sediments. Simply trying to interpret a carbon isotope signal as it stands alone can prove to be both difficult and inaccurate. In order to limit possible misinterpretation of isotope data and maximize interpretation of environmental change, I chose to carry out this study using sediment cores from Lago de las Morrenas 1 in which sediment, pollen, microscopic charcoal, macroscopic charcoal, and diatoms have already been examined (Horn 1993; Haberyan and Horn 1999; League and Horn 2000).

Using stable carbon isotopes and other proxies of vegetation change extracted from sediments of Lago de las Morrenas 1, I address the following questions: Were C_4 plants more dominant in the Chirripó páramo during the late Pleistocene when atmospheric pCO_2 levels were much lower than today? Is it possible that existing C_4 dominated microhabitats in the Chirripó páramo are relicts from the Pleistocene as suggested by Boom *et al.* (2001) for the northern Andes? Do shifts in the isotopic composition of Lago de las Morrenas 1 lake sediments throughout the Holocene signal shifts in C_4 plant dominance in response to climatic change?

Further context for these questions is provided in Chapter 2, in which I describe the environmental setting and environmental history of the Chirripó páramo. Chapter 3 explains the laboratory and field methods employed to try to answer these questions. I present the results of this study in Chapter 4 and discuss their significance in Chapter 5. Finally, in Chapter 6, I conclude and summarize my findings.

CHAPTER 2

ENVIRONMENTAL SETTING AND LATE QUATERNARY VEGETATION AND CLIMATE HISTORY

A. Valle de las Morrenas

The highest peaks of the Cordillera de Talamanca in southern Costa Rica support treeless páramo vegetation. The largest of these Costa Rican páramos, covering approximately 5000 ha, is the Chirripó páramo surrounding Cerro Chirripó (3819 m, 9°29'27" N, 83°29'27" W), the country's highest peak. The Chirripó páramo and some 50,000 ha of surrounding montane vegetation is protected within Chirripó National Park, established in 1975 (Horn 1998).

Some thirty glacial lakes and ponds occur within the Chirripó páramo (Horn *et al.* 1999). The Valle de las Morrenas or "Valley of the Moraines," located on the northern side of Cerro Chirripó, contains the greatest number of these lakes (Figures 2.1 and 2.2). The multiple lake basins in the Valle de las Morrenas were formed by two primary geomorphic processes (Horn *et al.* 1999; Orvis and Horn 2000). First, the intrusive igneous bedrock is strongly jointed, causing spatially variable susceptibility to glacial erosion within the valley by alpine glaciers in the past. Second, the uneven bedrock valley floor is itself covered by an uneven blanket of meltout till and scattered moraines deposited during glacial advances and retreats. These till deposits dam several of the ponds and lakes in the valley; others are bedrock tarns. S. Horn and K. Orvis have numbered the main chain of lakes Lago de las Morrenas 0 through Lago de las Morrenas 4 (or in abbreviated form, Lago or Lake 1, 2, etc.). Smaller lakes that feed

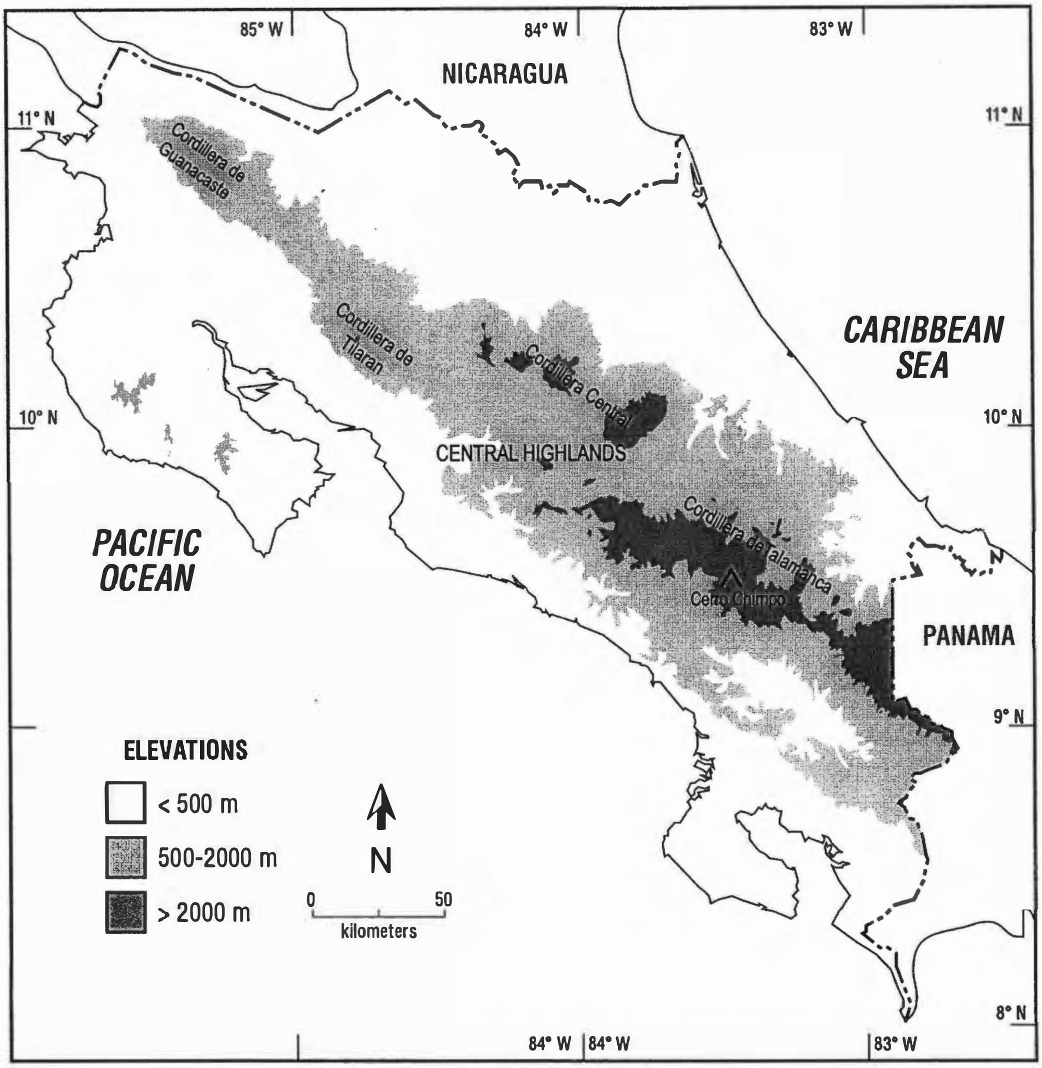

Figure 2.1. Map of Costa Rica showing the location of Cerro Chirripó (Adapted from Clement and Horn 2001).

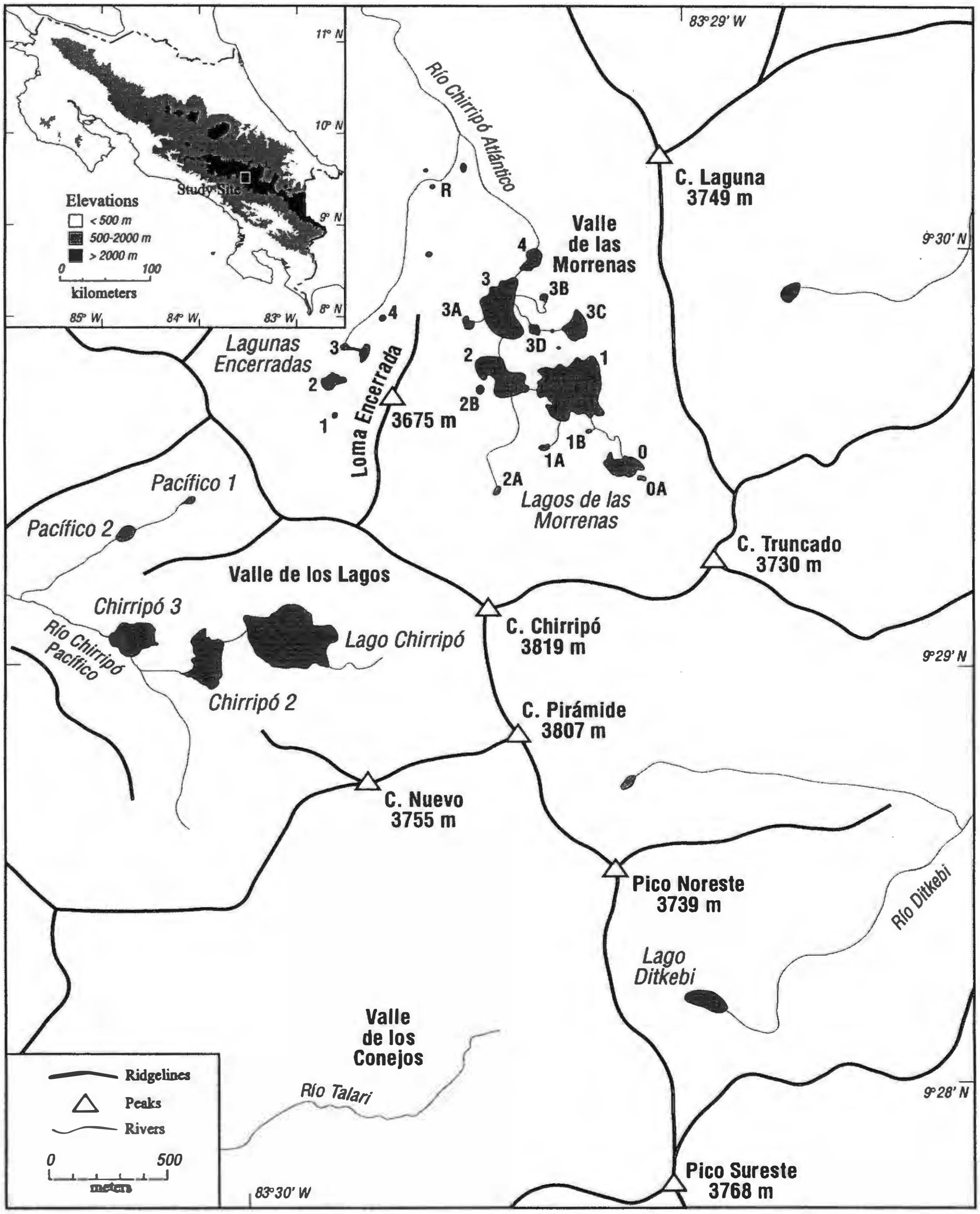

Figure 2.2. Valle de las Morrenas and the surrounding region. Note the numbering system used for the Morrenas lakes (Adapted from Horn *et al.* forthcoming).

into larger lakes are identified with the number of the lake drained into, plus a letter (i.e. Lago 0A drains into Lago 0,Lago 2A drains into Lago 2; Figure 2.2; Horn *et al.* forthcoming).

B. Lago de las Morrenas 1

Lago de las Morrenas 1 (3477 m, 9°29'40" N, 83°29'14" W) is the largest lake in the Valle de las Morrenas (Horn *et al.* 1999; Figure 2.2). Several intermittent streams feed into the lake, the largest of which enters from the south. There is also an intermittent outlet located on the western edge of the lake. Lago de las Morrenas 1 has a surface area of 5.6 ha (Horn *et al.* 1999) and a maximum water depth of 8.3 m was measured by Horn in 1989 (Horn 1993).

C. Climate

Few site-specific meteorological data are available for the Chirripó páramo. However, the Cerro Páramo meteorological station (3466 m, 9°33'41"N, 83°45'18"W; K. Orvis, personal communication 2003) located in the Buenavista páramo on Cerro Buenavista (Figure 2.3; also known as Cerro de la Muerte) likely provides representative meteorological data. The Cerro Páramo station recorded a mean annual temperature of 8.5°C and mean annual precipitation of 2581 mm between 1971 and 2000 (K. Orvis, personal communication 2003). Orvis and Horn (2000) made the important observation that the Valle de las Morrenas is subject to more cold air drainage than is the meteorological station on Cerro Buenavista, as the meteorological station is located on a mountain top. This likely makes mean annual temperatures in the Valle

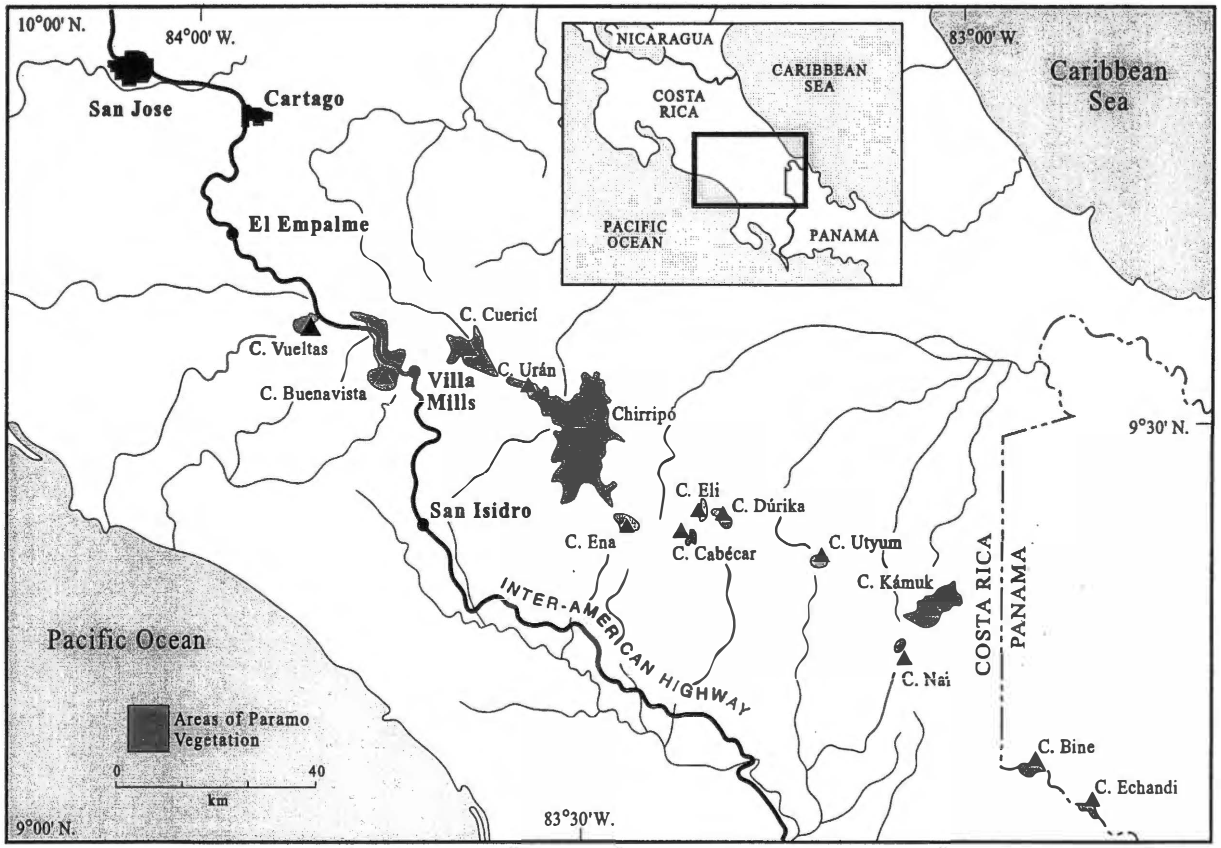

Figure 2.3. Map showing the highest peaks of the Cordillera and the extent of páramo vegetation in Costa Rica. Cerro Buenavista is the location of the closest meterological station to Cerro Chirripó (Modified from Horn *et al.* forthcoming).

de las Morrenas slightly lower than those reported at the Cerro Páramo station. Precipitation records from Cerro Buenavista show a distinct wet and dry season, with the majority of precipitation, ~2286 mm, falling between May and November and only ~295 mm falling during the dry season from December to April (K. Orvis, personal communication 2003). No reliable records of snowfall exist for the páramos of Costa Rica (Coen, 1983), but morning frosts are common.

D. Vegetation

Páramo vegetation in Chirripó National Park extends from about 3300 to 3819 m (Horn 1993). The lower limit of páramo vegetation varies depending on atmospheric moisture delivery. On the more humid Atlantic slopes of the Cordillera the lower elevational limit of páramo vegetation may be as high as 3400 m (Hooghiemstra *et al.* 1992). The dwarf bamboo *Chusquea subtessellata* Hitchc. dominates the páramo and has been documented in vegetation surveys to reach as much as 60% cover (Horn 1989; Horn 1993), but this figure is likely higher in other locations not surveyed in these studies (S. Horn, personal communication 2003). No other woody plant species in the páramo has been documented as exceeding 10% cover (Horn 1989; Horn 1993). However, certain microhabitats do support more extensive shrub cover, for example talus slopes.

In total, about 48 vascular plant families are present in the páramo with the majority of species belonging to the Asteraceae, Cyperaceae, Ericaceae, Hypericaceae, Poaceae, and Rosaceae families (Horn 1989; Cleef and Chaverri 1992; Hooghiemstra *et al.* 1992). Some of the most prominent shrub species in the Chirripó páramo include

Hypericum strictum Kunth, *H. irazuense* Kuntze, *Pernettya prostrata* (Cav.) DC., *Pentacalia firmipes* (Greenm.) Cuatrec., *Vaccinium consanguineum* Klotzsch, *Escallonia myrtilloides* var. *patens* (Ruiz and Pav.) Sleumer, and *Myrsine dependens* (Ruiz and Pav.) Spreng. (Kappelle 1991; League and Horn 2000; Horn forthcoming). Several herbaceous species, especially in the Poaceae family, are also present in the Chirripó páramo and are capable of dominating particular habitats.

Of particular interest to this study is the presence of grasses in the genus *Muhlenbergia* in the páramos of Costa Rica. In the genus *Muhlenbergia*, there are 160 species that use the C_4 photosynthetic pathway (Sage *et al.* 1999a). Based on the available literature this means the vast majority, if not all, of the Muhlenbergia species utilize the C_4 photosynthetic pathway. Three *Muhlenbergia* species have been documented in the páramos of Costa Rica; *M. calcicola* Swallen., *M. flabellata* Mez., and *M. nigra* Hitchc. (Pohl 1980). *Muhlenbergia flabellata*, which is a C_4 grass (Herrera-Arrieta and Grant 1994; Peterson and Herrera-Arrieta 2001), seems to particularly flourish in microhabitats near Lago de las Morrenas 1 (Horn 1989). The ability of the C_4 photosynthetic pathway to exist in this environment today suggests the possibility of past establishments and changes in the dominance of plants utilizing this photosynthetic pathway, evidence of which may be preserved in the stable carbon isotope signature of lake sediments.

Species in the genus *Muhlenbergia* are some of the most cold tolerant C_4 plants in existence today, and are therefore one of the few species of C_4 plants that is able to succeed at high altitudes and high latitudes (Sage *et al.* 1999b). *Muhlenbergia* species can be found as far north as the boreal forests of Canada (Schwarz and Redmann 1988), and as high as 4000 m elevation in the Rocky Mountains (Sage 1999b; R. Sage, personal communication 2001). This extreme cold tolerance makes species in the *Muhlenbergia* genus especially capable of expanding under the low pCO_2 conditions during the Pleistocene when temperatures were lower (see Vegetation and Climate History below). In the Chirripó páramo, *M. flabellata* presently seems to be restricted to microhabitats with a coarse substrate and relatively low moisture availability, such as glacial till (see further discussion in Chapter 5). No other plant genera in the Chirripó páramo have been documented as using the C_4 photosynthetic pathway.

Also of interest in this study are the aquatic plants and algae of Lago de las Morrenas 1. These provide an autochthonous source of carbon that can significantly influence the isotopic dynamics within the lake and sediments. The primary aquatic macrophyte in Lago de las Morrenas 1 is *Isoetes storkii* T.C. Palmer (Horn 1993). Interestingly, the genus *Isoetes* contains several species that utilize the crassulacean acid metabolism (CAM) photosynthetic pathway, which is typically only utilized by plants growing under conditions of water stress, such as epiphytes or desert succulents. As water is certainly not a limiting resource to aquatic plants, it is thought that the use of CAM photosynthesis by aquatic plants is an adaptation to low dissolved CO_2 levels in some water bodies (Keeley 1981, 1989; Sternberg *et al.* 1984; Sandquist and Keeley 1990; Keeley and Sandquist 1991).

Also thought to currently exist in Lago de las Morrenas 1, but still unverified, is the alga *Botryococcus braunii* Kützing. *Botryococcus braunii* has been reported in Lago Chirripó, which is less than 0.5 km away on the southern flank of Cerro Chirripó, and is at a similar elevation to Lago de las Morrenas 1 (Figure 2.2; Jones *et al.* 1993;

Haberyan *et al.* 1995). The close proximity and similar environmental conditions of Lago Chirripó and Lago de las Morrenas 1 make it likely that the alga is present in Lago de las Morrenas 1 as well (G. Umaña, personal communication with S. Horn 2002). Jones *et al.* (1993) do not report the presence of *B. braunii* in Lago de las Morrenas 1, however I identified what are most likely fossil remains of *B. braunii* at all sediment levels analyzed for pollen analysis by Horn (1993) from Lago de las Morrenas 1 (Chapter 5). The presence of *B. braunii* is of interest in this study as it is known to be capable of HCO_3^- photosynthesis under conditions of low dissolved CO_2 (Huang *et al.* 1999). Photosynthesis using HCO_3^- photosynthesis leads to an isotopic enrichment in ^{13}C in the plant, as bicarbonate is 7–12‰ more enriched in ^{13}C than CO_2, and can have significant effects on the bulk organic sedimentary $\delta^{13}C$ values in a lake (Mook *et al.* 1974).

E. Vegetation and Climate History

Several paleovegetation and paleoclimatic studies have been published concerning the Chirripó páramo (Horn 1993; Haberyan and Horn 1999; League and Horn 2000; Orvis and Horn 2000). Fossil pollen in the Lago de las Morrenas 1 sediments indicates that páramo vegetation has existed around the lake since deglaciation at about 10,000 ^{14}C yr. B.P., and suggests no major changes in vegetation since that time (Horn 1993). Microscopic (Horn 1993) and macroscopic (League and Horn 2000) charcoal records indicate that the vegetation surrounding Lago de las Morrenas 1 has burned many times throughout the last 10,000 years. Variations in charcoal influx have been thought to possibly reflect changes in precipitation, with low charcoal influxes indicating increased fire intervals possibly in response to wetter conditions and high charcoal influxes possibly indicating drier conditions and decreased fire intervals (League and Horn 2000). Conspicuously low charcoal influx between 6800 – 4200 ^{14}C yr. B.P. may signal one of the wetter periods for the area since deglaciation (League and Horn 2000).

There is little or no evidence for significant limnological changes in Lago de las Morrenas 1 in the past. A diatom study of Lago de las Morrenas 1 carried out by Haberyan and Horn (1999) shows an overwhelming dominance by the cosmopolitan diatom genus *Aulacoseira* throughout the history of the lake. However, the possible lack of sensitivity of this cosmopolitan diatom to changes in water chemistry may also explain its persistence throughout the 10,000 ^{14}C yr. sediment record.

Few published studies exist of climate and vegetation history prior to the formation of Lago de las Morrenas 1. Geomorphic and sedimentary evidence (Horn 1993; Orvis and Horn 2000; Lachniet and Seltzer 2002) confirm glaciation of the Valle de las Morrenas prior to the formation of Lago de las Morrenas 1 at the time of last ice retreat. Equilibrium line altitude (ELA) estimates made from geomorphic reconstructions of glacial extent and thickness in the Valle de las Morrenas suggest mean annual temperature depressions of as much as 8–9° C during the coldest periods of the Pleistocene (Orvis and Horn 2000).

Two sedimentary pollen records extending beyond 10,000 ^{14}C yr. B.P. have been analyzed in Costa Rica, both from the vicinity of El Empalme (Figure 2.3) at the northwestern end of the Cordillera de Talamanca (Martin 1964; Islebe and Hooghiemstra 1997). Martin (1964) was one of the first researchers to suggest significant climate changes in the tropics, based on a coarse resolution pollen study from the Parque Vicente Lachner bog, which showed evidence of significant cooling during the Pleistocene for the region. In a more detailed pollen study, Hooghiemstra *et al.* (1992) report similar depressions in temperature during the Pleistocene around La Chonta bog (2 km southeast of the Vicente Lachner bog). La Chonta bog is a mid-elevation (2310 m) bog hypothesized to be as much as 80,000 years old (Hooghiemstra *et al.* 1992; Islebe and Hooghiemstra 1997). Fossil pollen analyses from La Chonta bog suggest numerous changes in the vegetation composition around the bog throughout its history. The most significant changes in vegetation composition are reported to have occurred in the late Pleistocene (~50,000–13,000 yr. B.P.). La Chonta bog pollen assemblages suggest a drop in treeline to an elevation of ~2000 m, at which time the bog was surrounded by páramo vegetation. This ~1300 m drop in treeline is attributed to temperatures at that time being some 8°C lower than today (Hooghiemstra *et al.* 1992; Islebe *et al.* 1996; Islebe and Hooghiemstra 1997). The La Chonta pollen record also indicates a drop in treeline elevation during what is considered to be the Younger Dryas Chron. This drop in treeline is suggested to represent a ~2–2.5°C decline in mean annual temperature as compared to today from 11,000 to 10,400 yr. B.P. for Costa Rica. Following this hypothesized temperature depression, modern treelines, and presumably modern temperatures, were established by 10,400 yr. B.P. (Hooghiemstra *et al.* 1992; Islebe *et al.* 1996; Islebe and Hooghiemstra 1997).

CHAPTER 3

METHODOLOGY

A. Sediment Coring

Two parallel sediment cores were retrieved from Lago de las Morrenas 1 in January 1989 by S. Horn. The cores were raised from an anchored platform using a square rod piston corer (Wright *et al.* 1984) at water depths of 5.4 m (core 1A: 6.0 m long) and 7.5 m (core 2A: 5.6 m long). In addition to these cores, one parallel core section intended to recover the transition from the organic rich lake sediment to the glacial sediments was taken for core 1A (1B), and three parallel core sections of this transition were taken for core 2A (2B, 2C and 2D). Near-surface sediments (0–1 m) were collected using a PVC pipe fitted with a rubber piston. The PVC pipe allowed for the relatively undisturbed recovery of the unconsolidated uppermost sediments. Core segments acquired using the square rod piston corer were extruded in the field, wrapped in plastic and foil, and then sealed in plastic tubes. Sediments retrieved using the PVC pipe were sampled in the field at 2 cm intervals and stored in plastic bags. All sediments were stored at 6° C upon their return to the University of Tennessee.

B. Dissolved CO_2 Measurements

In January of 2003 I measured dissolved CO_2 in Lago de las Morrenas 1, Lago de las Morrenas 3C, and Lago Ditkebi. I took three water samples at different locations around each lake from the shoreline and measured their dissolved CO_2 content immediately after collection using a LaMotte field CO_2 test kit.

C. Radiocarbon Dating

Horn (1993) obtained six radiocarbon dates on bulk sediment from Lago de las Morrenas 1 core 2A. Radiocarbon determinations were carried out by Beta Analytic Laboratory, Inc., in Miami, Florida. These samples were not corrected for differential fractionation effects with ^{13}C measurements. Radiocarbon dates were calibrated using version 4.3 of the CALIB radiocarbon age calibration program (Stuiver and Reimer 1993) and the dataset of Stuiver *et al.* (1998). In addition, to assist in correlating Lago de las Morrenas core 1A and core 2A I have submitted six sediment samples from core 1A to the University of Arizona for bulk AMS radiocarbon determinations.

D. Modern Reference Pollen

As a possible additional means of detecting changes in C_4 plant populations from evidence in the Lago de las Morrenas 1 sediment profiles, I prepared and examined reference pollen slides of *Chusquea subtessellata* and *Muhlenbergia flabellata*. Martin Arford and I isolated pollen grains from their anthers using a modified version of standard palynological techniques (Berglund, 1986; Appendix A) and mounted them in silicone oil. The objective of my analysis was to determine if pollen gains from *Chusquea subtessellata* and *Muhlenbergia flabellata* could be distinguished by grain diameter, annulus diameter, pore diameter, or a combination of these measurements as a ratio. Vouchered *C. subtessellata* plant specimens and anthers were provided by S. Horn. Vouchered *M. flabellata* anthers were provided by Lynn Clark from the Ada Hayden Herbarium at Iowa State University.

I measured modern *C. subtessellata* and *M. flabellata* pollen grains at 400x magnification. I converted the eyepiece reticule measurement scale units into micrometers using a Reichert-Jung micrometer calibration slide. I made measurements of grain diameter, annulus diameter, and pore diameter at the widest dimension on fifty grains per individual. I measured pollen grains from two individuals of each of the two species analyzed, yielding a total of 100 measurements per grass species.

E. Identification of *Bottryococcus braunii* Fossil Remains

I scanned slides prepared for pollen analysis by Horn (1993) for the presence of *Bottryococcus braunii* fossil remains. Slides were prepared by S. Horn according to standard palynological techniques (HCl, HF, KOH, acetolysis; Berglund 1986). I identified *B. braunii* remains at 400x magnification based on the descriptions of *B. braunii* made by Prescott (1969). I made no attempt to quantify the number of *B. braunii* fossil remains, I only noted their presence or absence.

F. Bulk Stable Carbon Isotope Analysis

I took sediment sub-samples from Lago de las Morrenas 1 core 1, core 1B, core 2, core 2B, and core 2D for stable carbon isotopic analysis on sediment total organic carbon ($\delta^{13}C_{TOC}$). I took samples consisting of approximately 1g of wet sediment. I collected sediment sub-samples from the center of the sediment core to avoid contamination that may affect the outermost portion of the core slug. I decalcified these samples for one hour in 10% HCl, and then rinsed and neutralized them with distilled water. Once neutralized to a pH of ~7, I dried these samples at 50°C overnight, crushed them in a mortar and pestle, and mixed them with 500 mg Cu, 500 mg CuO, and a small platinum wire in quartz tubes. I then sealed the quartz tubes under vacuum and combusted the organic matter at 800°C for three hours. Following combustion, I cryogenically cleaned and trapped all extracted CO_2 in collection vessels using a vacuum extraction line. I analyzed the isotopic composition of the evolved CO_2 using the dual-inlet Finnigan MAT Delta-plus mass spectrometer at the University of Tennessee, Knoxville. I report all isotopic compositions in standard δ-per mil notation relative to the Vienna-Pee Dee belemnite (VPDB) marine-carbonate standard, where:

$$\delta^{13}C \text{ (per mil)} = 1000\ [(R_{sample}/R_{standard}) - 1],$$

$$\text{where } R = {}^{13}C/{}^{12}C.$$

The USGS graphite standard used in this study (USGS24) is reported to have an isotopic composition of –15.99 +/– .10‰ V-PDB. An isotopic composition of –15.95 +/– .11‰ V-PDB (n=15) was measured during this study for USGS 24.

Due to the numerous other analyses carried out on sediments from Lago de las Morrenas core 2A, many sections of the core had inadequate material remaining for $\delta^{13}C_{TOC}$ analysis. For example, there was inadequate material for $\delta^{13}C_{TOC}$ analysis from the uppermost sediments of core 2A down to 246 cm. Inadequate sample material remained for numerous other sample intervals below 246 cm, including those used for bulk radiocarbon dates.

Where possible, I sampled remaining sediments below 246 cm from core 2A with at least a 360 year, but typically much finer, resolution. I sampled sediments from core 1A at a coarser interval. Based on the correlation of cores 1A and 2A using magnetic susceptibility (see discussion below), samples used for $\delta^{13}C$ analysis from core 1A provide, on average, a resolution of about 350 years between samples, but this value likely varies due to uncertainties in core correlation. These sample intervals also vary due to the occurrence of a 48 cm section of poorly consolidated sediments from 94–142 cm in core 1A that were transferred to plastic bags during field extrusion of the core. These segments were therefore mixed, not allowing for sedimentation rate estimates as no date could reliably be applied to such a large sediment interval.

G. Modern Plant $\delta^{13}C$ Measurements

I measured the $\delta^{13}C$ of modern plant specimens from the Chirripó páramo that are members of genera documented to contain species using C_4 photosynthesis. I cleaned modern plant samples ultrasonically in distilled water and dried them overnight at 50°C. I then froze each sample using liquid nitrogen and ground it using a mortar and pestle before combusting the sample, collecting the extracted CO_2, and isotopically analyzing the sample using the same procedure outlined above for bulk sediments. Samples analyzed for $\delta^{13}C$ consisted primarily of leaf tissue from multiple individuals. Although it is preferable to use whole plant matter when measuring the $\delta^{13}C$ signature of plants, I primarily used leaf tissues in this study as whole plant matter is not essential in determining the photosynthetic pathway used by the plant.

H. Temporal Correlation of the Sediment Cores using Magnetic Susceptibility

I correlated the multiple sediment cores used in this study using magnetic susceptibility and changes in sediment stratigraphy. High resolution (typically 1 cm interval) magnetic susceptibility measurements were carried out by Brandon League on Lago de las Morrenas core 2A using a Bartington MS2B magnetic susceptibility meter (League 1998). This high resolution record included several distinct peaks in magnetic susceptibility. In this study I compared the distinct magnetic susceptibility peaks in the Lago de las Morrenas 1 core 2A sediment profile to peaks in magnetic susceptibility that I detected in Lago de las Morrenas 1 core 1A using a Bartington MS2C magnetic susceptibility meter. The Bartington MS2B magnetic susceptibility meter measures samples packed into 10 cm^3 sampling pots, while the MS2C magnetic susceptibility meter is designed so that entire core segments can be passed through a sensing loop. All measurements were taken at low frequency settings and are reported in SI units.

CHAPTER 4

RESULTS

A. Sediments and Stratigraphy[1]

Lago de las Morrenas 1 cores 1A and 2A exhibit very similar sediment stratigraphies (Table 4.1, 4.2, and Figure 4.1a, 4.1b). The uppermost sediments in both cores (core 1A: 0–541 cm; core 2A: 0–527 cm) consist of organic rich gÿttja (Munsell 10YR 2/1 – 10YR 2/2) containing an abundance of zooplankton fecal pellets and have organic contents, as determined by loss on ignition, ranging from 16% to 49% (Horn 1993, League 1998). Transitional sediments (Munsell 5Y 2.5/2 – 2.5Y 4/2 – 5Y 3/1) between the organic rich gÿttja and underlying mineral glacial flour at the base of the core are present in both cores (core 1A: 541–582 cm; core 2A: 527–545 cm). Both cores end in mineral rich glacial flour (Munsell 5Y 4/1) deposited during the deglaciation of the valley (core 1A: 582–602 cm; core 2A: 545–564 cm).

Shorter parallel sediment slugs intended to retrieve the organic gÿttja to glacial flour transition (cores 1B, 2B, and 2D) were collected by moving the raft from the positions at which cores 1A and 2A were collected. Due to variations in sediment deposition and lake basin shape, the depth stratigraphy of the shorter sediment slugs collected from Lago de las Morrenas 1 at these locations do not exactly match those of cores 1A and 2A (Figure 4.1). Core 1B is a short sediment slug recovered from 512–

---

[1] All depths reported in this section are depths below the sediment-water interface and are not reported in "core 2 correlated depths" (see Magnetic Susceptibility Stratigraphy and Core Correlation in this chapter).

Table 4.1. Sediment Stratigraphy of Lago de las Morrenas 1 Core 1A.

Depth (cm)	Sediment Description	Munsell Color and Description
0–541	Organic rich, gelatinous gÿttja dominated by zooplankton fecal pellets	10YR 2/1 and 10YR 2/2 Black grading to very dark brown
541–582	Transitional sediments, combination of softer overlying organic sediments and more mineral rich sediments	5Y 2.5/2, 2.5Y 4/2, and 5Y 3/1 Black to dark grayish brown, grading into very dark gray
582–602	Glacial flour	5Y 4/1 Dark gray

Reported depths are the depth below the sediment-water interface and are not "core 2A equivalent depths" as reported elsewhere in this study. Information is taken from unpublished core logs compiled by S. Horn.

Table 4.2. Sediment Stratigraphy of Lago de las Morrenas 1 Core 2A.

Depth (cm)	Sediment Description	Munsell Color and Description
0–527	Organic rich, gelatinous, gÿttja dominated by zooplankton fecal pellets	10YR 2/1 and 10YR 2/2 Black grading to very dark brown
527–545	Transitional sediments, combination of softer overlying organic sediments and more mineral rich sediments	5Y 3/2 and 2.5Y 4/2 Dark olive gray to dark grayish brown
545–564	Glacial flour	5Y 4/1 Dark gray

Reported depths are the depth below the sediment-water interface. Information taken from Horn (1993) and unpublished core logs.

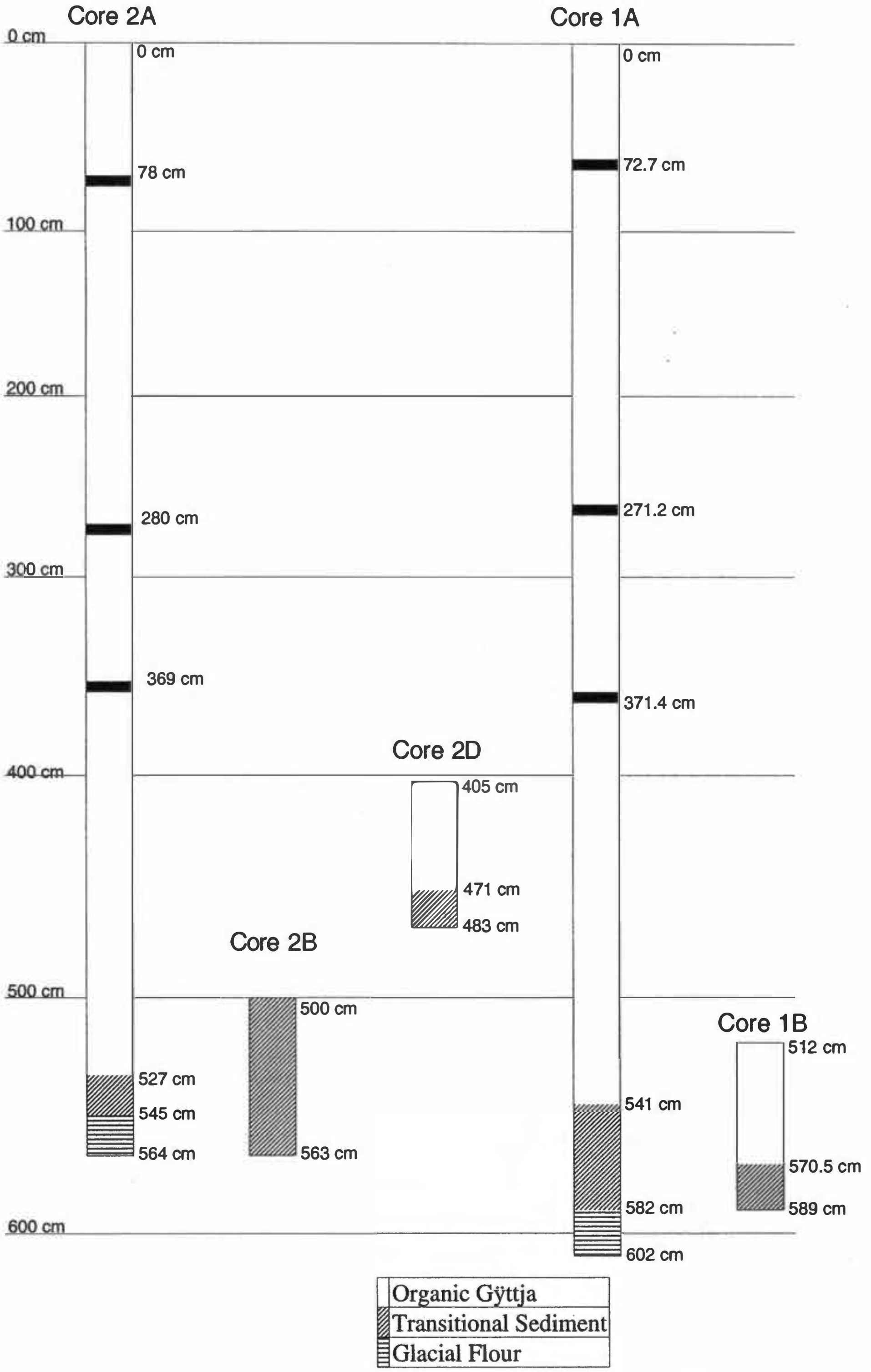

Figure 4.1a. Sediment stratigraphy and magnetic susceptibility spike stratigraphy for Lago de las Morrenas 1 cores 1A, 1B, 2A, 2B, and 2D. Information taken from Horn (1990; 1993) and unpublished core logs. Black bars indicate magnetic susceptibility spikes.

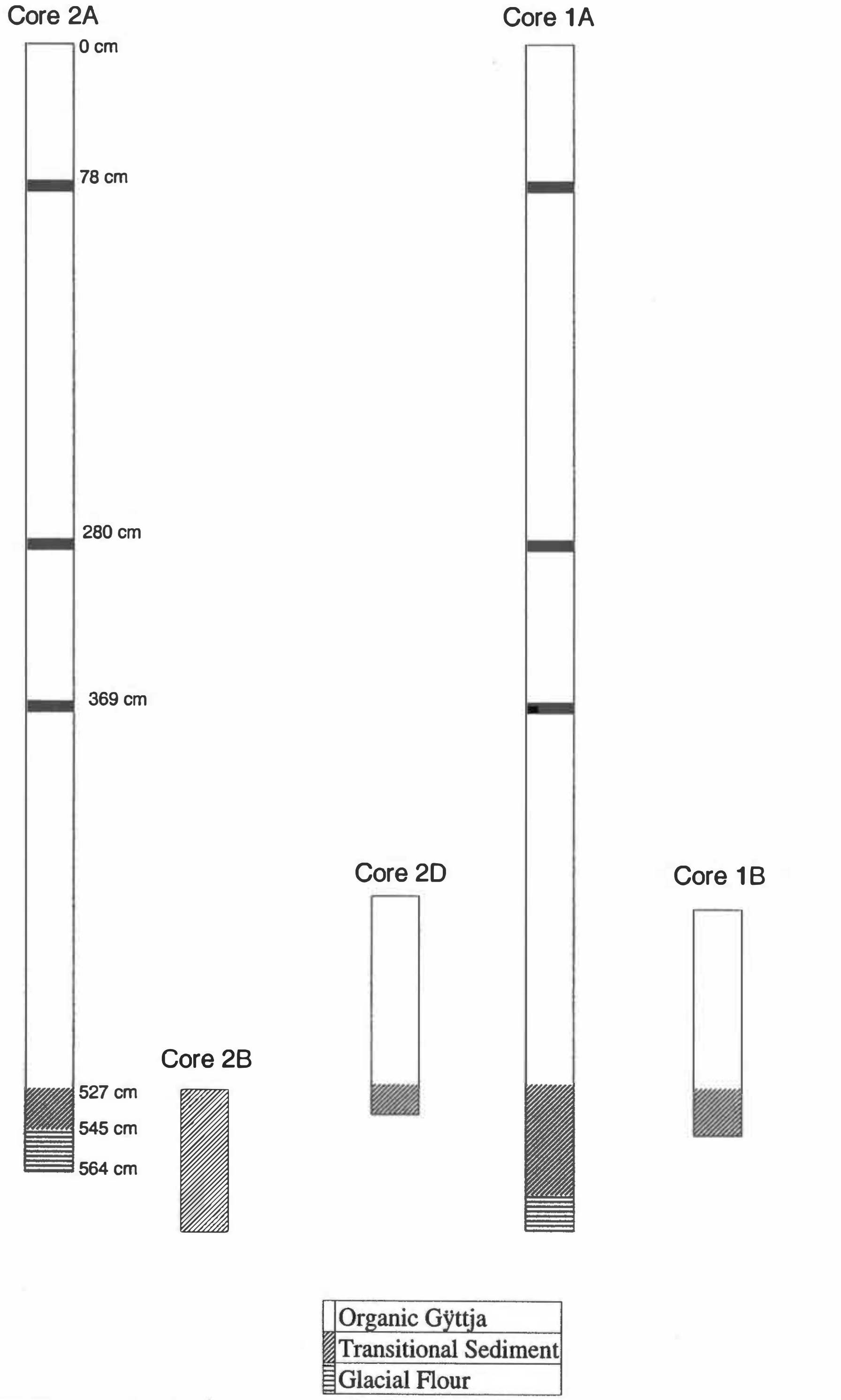

Figure 4.1b. Sediment stratigraphy and magnetic susceptibility spike stratigraphy for Lago de las Morrenas 1 cores 1A, 1B, 2A, 2B, and 2D after correlation to core 2A. Black bars indicate magnetic susceptibility spikes.

589 cm in the Lago de las Morrenas 1 sediment profile and includes the interface between the organic gÿttja and transitional sediments (Figure 4.1a, 4.1b). Organic rich sediments (Munsell 10 YR 2/1) are present from 512–570.5 cm. Transitional sediments (Munsell 5Y 3/2 – 2.5Y 3/2) make up the lowermost sediments in this short sediment slug.

Cores 2B and 2D are similar sediment slugs collected with the idea that they would span the glacial flour to organic rich gÿttja transition (Figure 4.1). Core 2B (500–563 cm) consists entirely of transitional sediments (Munsell 5YR 4/2). Core 2D (405–483 cm) consists of organic gÿttja from 405 cm to 471 cm (Munsell 5Y 2.5/1 – 5Y 2.5/2), which is underlain by transitional sediments from 471 to 483 cm (Munsell 5Y 3/2).

B. Magnetic Susceptibility Stratigraphy and Core Correlation

I found stratigraphic peaks in the magnetic susceptibility of Lago de las Morrenas 1 core 1A by slowly passing the core sections through the Bartington MS2C meter while resting on carriers that I made by slicing clear plastic tubes lengthwise. I noted stratigraphic depths registering increased magnetic susceptibility measurements and then compared those to peaks in magnetic susceptibility previously recorded in core 2A by League (1998; Figure 4.1a, 4.1b). I assumed that the corresponding peaks in magnetic susceptibility from the cores represented the same periods in time, and therefore allow for the correction of differing sedimentation rates at the sites of cores 1A and 2A. I calculated differences in sedimentation rates assuming linear sedimentation rates between magnetic susceptibility peaks. I then determined a correction factor to produce an equivalent depth for core 1A measurements compared to core 2A. The "core 2A correlated depth" reported for any sediment interval is the calculated depth at which equivalent core 1A sediment was being deposited. For example, a depth of 435 cm in core 1A has a "core 2A correlated depth" of 430.6 cm. This means that sediment was deposited at a depth of 435 cm at the position of core 1A at the same time as sediments were being deposited at the position of core 2A at a depth of 430.6 cm.

In addition to magnetic susceptibility peaks, I also assumed the change in sediment type from the transitional sediments to the homogeneous organic gÿttja must have occurred at about the same time in all of the cores (Figure 4.1a, 4.1b). This added yet another point that I could correlate temporally between the sediment cores. This was the only means available for correlating the shorter sediment transition slugs (1B, 2B, and 2D) and is also the method I used for the base of core 1A. I then applied a simple linear correction factor to the cores such that the sediment transition in all "core 2A correlated depths" occurred at the same time as in core 2A. Unfortunately, there was no organic gÿttja present in core 2B so I assumed that the top of core 2B was the transition point from the gÿttja to the transitional sediments for correlation purposes. Furthermore, it appears that these shorter sediment slugs do not contain the transitional sediment to glacial flour interface present in cores 1A and 2A. The absence of this stratigraphic marker disallowed the chronological correlation of the base of the short sediment slugs (1B, 2B, and 2D) to core 2A. Therefore, the correlation of cores 1B, 2B, and 2D to core 2A are based on the organic gÿttja to transitional sediment interface only (Figure 4.1b).

C. Radiocarbon Dates

The six radiocarbon analyses carried out by Beta Analytic Laboratory on bulk sediment samples from Lago de las Morrenas 1 core 2A show a normal stratigraphic sequence with no age reversals or anomalies (Table 4.3 and Figure 4.2). The lowermost radiocarbon date (527–542.5 cm, 12,360–11,230 cal. yr. BP) is located at the position where sediment types shift from transitional sediments to glacial flour and verifies that this sedimentary record spans the late Pleistocene and the entire Holocene. The calibrated radiocarbon dates suggest variable sedimentation rates, the slowest of which occurred in the late Pleistocene (0.08 mm/yr.) and early Holocene. A general increase in sedimentation rates can be seen throughout the Holocene with maximum rates occurring during the late Holocene and present times (0.79 mm/yr.; Figure 4.2). These sedimentation rate calculations are also influenced by the compaction of sediments at depth. Thus, the calculated sedimentation rates are likely underestimated in the lowermost sediments in the core.

D. Poaceae Pollen Separation by Size

Summary statistics for *C. subtessellata* and *M. flabellata* pollen grain diameters, annulus diameter, pore diameter, and all possible ratios of these individual measurements are shown in Table 4.4. I used an F-test (two sample for variances, α=.05) to analyze variances between samples and then applied the appropriate (equal or unequal variance) two-sample means test (two-tailed, α=.05) to each of the diameter

Table 4.3. Radiocarbon Determinations on Sediments from Lago de las Morrenas 1 Core 2A (from Horn and League forthcoming).

Lab Number	Sediment Interval	Uncalibrated ^{14}C Age (^{14}C yr. BP)	Calibrated Age Range (cal. yr. BP ± 2σ)
β-30431	81–111 cm	1230 ± 170	1510–790
β-30432	215–236 cm	3100 ± 90	3470–3080
β-30433	315–335 cm	4250 ± 90	5040–4530
β-30434	415–435 cm	6830 ± 120	7930–7440
β-30435	515–527 cm	8900 ± 100	10,240–9600
β-31787	527–542.5 cm	10,140 ± 120	12,360–11,230

All radiocarbon determinations were made on bulk sediment by Beta Analytic Laboratory. Radiocarbon ages were calibrated using version 4.3 of the CALIB radiocarbon age calibration program (Stuiver and Reimer 1993) and are based on the dataset of Stuiver *et al.* (1998).

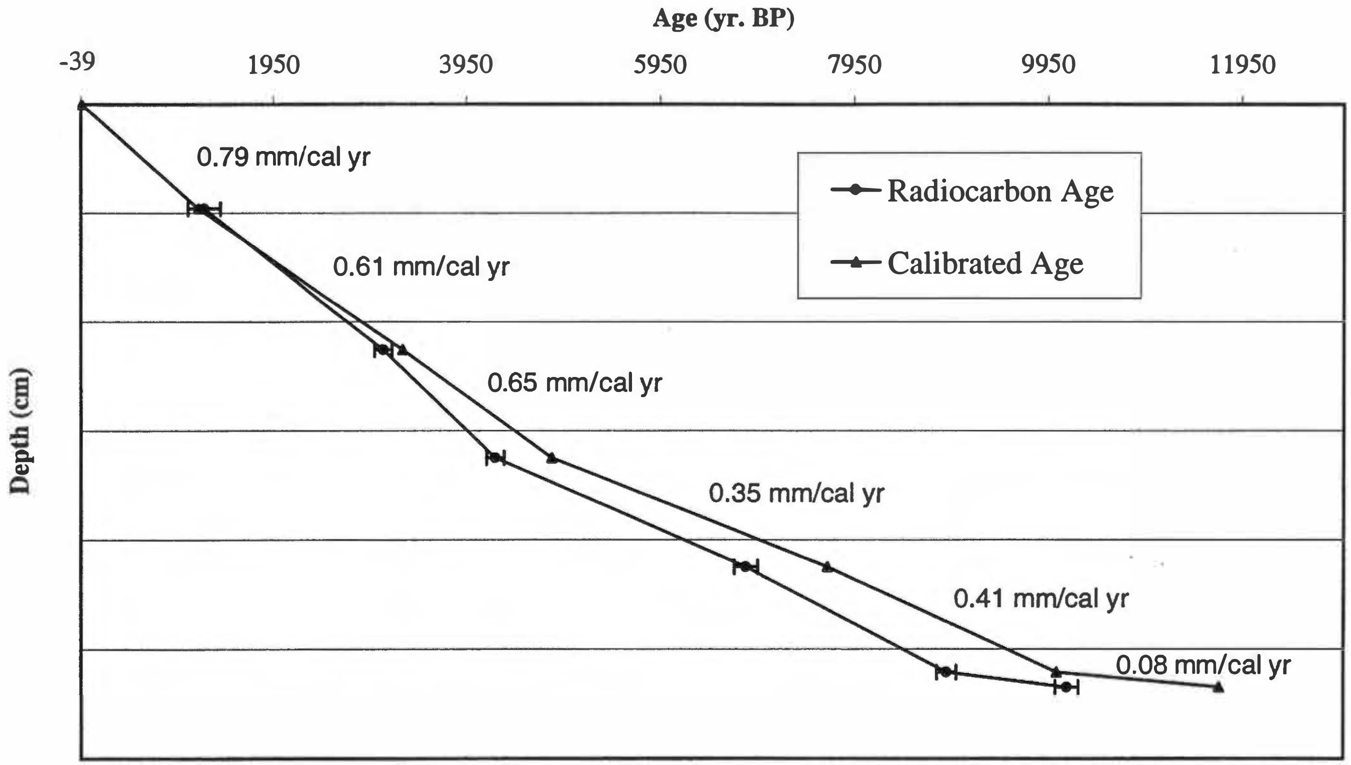

Figure 4.2. Age-depth diagram for Lago de las Morrenas 1 core 2A, showing both radiocarbon and calibrated ages. I calculated sedimentation rates using the calibrated ages. Depth positions are the mean of the depth interval sampled. Error bars on ^{14}C dates are 2 standard deviations. For the radiocarbon dates calibrating to more than one calendar year, I used the average of the youngest and oldest calendar ages.

Table 4.4. Individual and Combined Mean Pollen Diameters for Specimens of *Chusquea subtessellata* and *Muhlenbergia flabellata*.

Individual Diameter Means

	Chusquea subtessellata		*Muhlenbergia flabellata*	
	CR Horn 11	CR Horn 67	ISC Ocampos 1489	ISC Burger and Gomez 8309
Grain Diameter	43.73	41.11	36.31	41.53
Annulus Diameter	7.58	7.32	6.12	8.37
Pore Diameter	3.14	2.92	2.95	3.97
Grain/Annulus Diameter Ratio	5.89	5.68	6.12	5.07
Grain/Pore Diameter Ratio	14.58	14.57	12.79	11.04
Annulus/Pore Diameter Ratio	2.48	2.58	2.19	2.18

Species Diameter Means

	Chusquea subtessellata	*Muhlenbergia flabellata*
Grain Diameter	42.42	38.92
Annulus Diameter	7.45	7.25
Pore Diameter	3.04	3.46
Grain/Annulus Diameter Ratio	5.79	5.60
Grain/Pore Diameter Ratio	14.58	11.91
Annulus/Pore Diameter Ratio	2.53	2.18

All measurements are in micrometers.

measurements and the various ratios of diameter measurements for each of the grass species (Table 4.5). A significant difference in grain diameter (ts=6.641, df=198, $P<.05$), pore diameter (ts=3.622, df=179, $P<.05$), grain diameter to pore diameter ratio (ts=6.459, df=198, $P<.05$), and annulus to pore diameter ratio (ts=4.831, df=198, $P<.05$) exists for the combined measurements of the two species of grass I analyzed. A significant difference in annulus diameter (ts=1.067, df=169, $P<.05$) and the grain diameter to annulus diameter ratio (ts=1.349, df=187, $P<.05$) does not exist for the combined diameter measurements of the two specimens of *C. subtessellata* or for the combined measurements of the two specimens of *M. flabellata*.

E. Lacustrine Dissolved CO_2 Measurements

I measured very low concentrations of dissolved CO_2 in water samples from Lago de las Morrenas 1 and surrounding lakes. The average dissolved CO_2 concentration for Lago de las Morrenas 1 was 3.5 mg/L (Table 4.6). Average dissolved CO_2 concentrations for nearby Lago Ditkebi and Lago de las Morrenas 3C (Figure 2.2) were even lower (Table 4.6).

F. Identification of *Bottryococcus braunii* Fossil Remains

Using light microscopy, I identified *Bottryococcus braunii* fossil remains at every level analyzed for fossil pollen by Horn (1993; Table 4.7). These remains were sparse and generally quite degraded, but could be identified on at least one microscope slide from each level.

Table 4.5. F-Test and t-Test Results for the Combined Mean Pollen Diameters

	F-Test Statistic	F-Test Critical Value*[!]	t-Test Statistic (Equal Variances)	t-Test Statistic (Unequal Variances)	t-Test Degrees of Freedom	t-Test Critical Value (Two-Tailed)*	H_o Accepted?**
Grain Diameter	1.066	1.394	6.641	▨	198	1.972	No
Annulus Diameter	2.407	1.394	▨	1.067	169	1.974	Yes
Pore Diameter	1.983	1.394	▨	3.622	179	1.973	No
Grain/Annulus Diameter	1.621	1.394	▨	1.349	187	1.973	Yes
Grain/Pore Diameter	0.779	1.394	6.459	▨	198	1.972	No
Annulus/Pore Diameter	1.236	1.394	4.831	▨	198	1.972	No

*a = .05 for all statistical analyses

**H_o = The mean values for the two species are not significantly different.

[!] df = 99, 99 for all F-test critical values

Table 4.6. Dissolved CO_2 Concentrations in Selected Lakes of the Chirripó Páramo.

	Sample 1	Sample 2	Sample 3	Average
Lago de las Morrenas 1	4.5 mg/L	3.0 mg/L	3.0 mg/L	3.5 mg/L
Lago de las Morrenas 3C	1.5 mg/L	1.0 mg/L	1.0 mg/L	1.2 mg/L
Lago Ditkebi	3.0 mg/L	3.0 mg/L	2.5 mg/L	2.8 mg/L

Measurements were made in the field with a LaMotte CO_2 test kit.

Table 4.7. Results of Scans for the Presence of *Bottryococcus braunii* Fossil Remains.

Pollen Sample ID	Sediment Depth	*Bottryococcus* Present (Y/N)
0-2 cm	0 cm	Y
10-12 cm	15 cm	Y
20-22 cm	30 cm	Y
30-32 cm	45 cm	Y
40-42 cm	60 cm	Y
50-52 cm	75 cm	Y
60-62 cm	90 cm	Y
70-72 cm	105 cm	Y
80-82 cm	120 cm	Y
90-92 cm	135 cm	Y
100-102 cm	150 cm	Y
905 cm	155 cm	Y
925 cm	175 cm	Y
945 cm	195 cm	Y
965 cm	215 cm	Y
985 cm	235 cm	Y
1005 cm	255 cm	Y
1025 cm	275 cm	Y
1045 cm	295 cm	Y
1065 cm	315 cm	Y
1085 cm	335 cm	Y
1105 cm	355 cm	Y
1125 cm	375 cm	Y
1145 cm	395 cm	Y
1165 cm	415 cm	Y
1185 cm	435 cm	Y
1205 cm	455 cm	Y
1225 cm	475 cm	Y
1245 cm	495 cm	Y
1265 cm	515 cm	Y
1285 cm	535 cm	Y
1305 cm	555 cm	Y

I made scans on pollen slides prepared by Horn (1993). I identified *B. braunii* remains at 400x magnification based upon the description of Prescott (1969). Pollen sample identification numbers represent two different systems of uncorrected depth reporting.

G. Stable Carbon Isotope Analyses of Modern Plants

Table 4.8 presents the $\delta^{13}C$ values of leaf tissues from selected Chirripó páramo plant specimens. The only plant found to possess $\delta^{13}C$ values that suggest the utilization of the C_4 photosynthetic pathway was *Muhlenbergia flabellata* (–11.8‰). All other plants I analyzed possessed $\delta^{13}C$ values typical of C_3 plants (–22.8‰ to –27.6‰). Both submerged and emergent *Isoetes storkii* samples produced $\delta^{13}C$ values (–26.8‰ and –25.8‰) falling well within the range of C_3 plants despite the documented use of the CAM photosynthetic pathway by all species that have been analyzed in this genus (Keeley 1981, 1989; Sternberg *et al.* 1984; Sandquist and Keeley 1990; Keeley and Sandquist 1991).

H. Stable Carbon Isotope Ratios of Total Organic Carbon ($\delta^{13}C_{TOC}$)[2]

Lago de las Morrenas 1 Core 1A

The stratigraphic $\delta^{13}C_{TOC}$ values for Lago de las Morrenas 1 core 1A (Figure 4.3) vary stratigraphically, showing a general trend from more positive $\delta^{13}C_{TOC}$ values in the basal mineral rich sediments (mean = –16.2‰) to more negative $\delta^{13}C_{TOC}$ values throughout the uppermost organic rich sediments (mean = –19.6‰). The average $\delta^{13}C_{TOC}$ value for the core as a whole is –18.9‰. The $\delta^{13}C_{TOC}$ values show considerable variation in the core with a maximum $\delta^{13}C_{TOC}$ value of –13.8‰ and a minimum $\delta^{13}C_{TOC}$ value of –21.6‰.

---

[2] All depths reported in this section and the respective figures are depths below the sediment-water interface and are reported in their "core 2 correlated depths" (see Magnetic Susceptibility Stratigraphy and Core Correlation in this chapter).

Table 4.8. The Carbon Isotope Composition and Photosynthetic Pathway Used by Selected Plant Specimens from the Chirripó Páramo of Costa Rica.

Plant Species	δ^{13}C V-PDB	Photosynthetic Pathway
Calamagrostis sp.	–24.0‰	C_3
Carex donnell-smithii	–23.7‰	C_3
Carex sp.	–22.8‰	C_3
Carex sp.	–25.9‰	C_3
Chusquea subtessellata	–26.9‰	C_3
Chusquea tonduzii	–27.6‰	C_3
Cortaderia haplotricha	–25.2‰	C_3
Emergent *Isoetes storkii*	–26.8‰	CAM*
Submerged *Isoetes storkii*	–25.8‰	CAM*
Muhlenbergia flabellata	–11.8‰	C_4

The material analyzed was leaf tissue collected from multiple individuals. *The utilization of CAM photosynthesis by species in the genera *Isoetes* is documented by Keeley and Sandquist (1991).

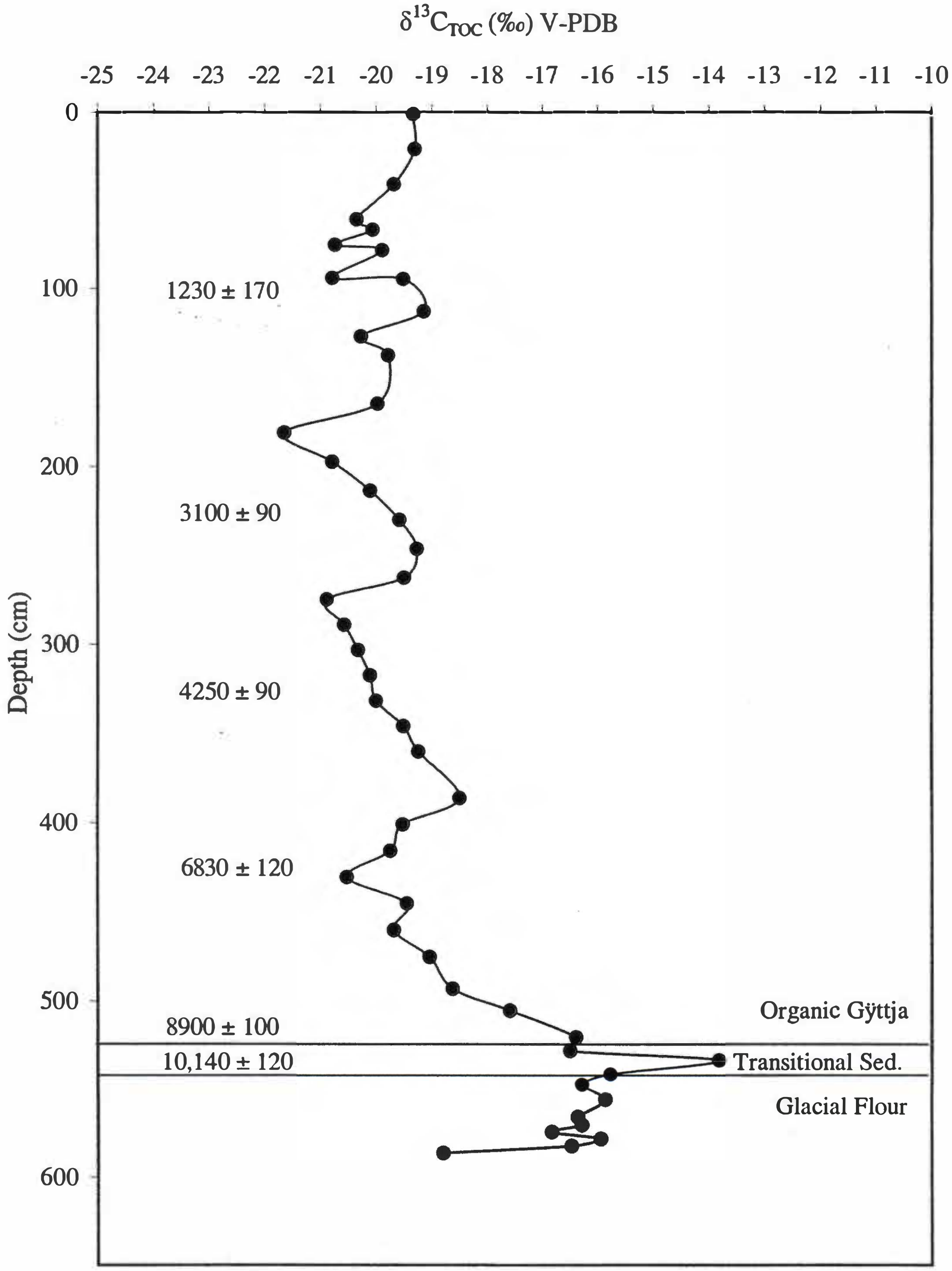

Figure 4.3. Lago de las Morrenas 1 core 1A sedimentary $\delta^{13}C_{TOC}$ values. Reported depths are core 2A equivalent depths. Radiocarbon dates are those determined for core 2A and are reported in radiocarbon years before present. Also marked is the transition in sediment types between glacial flour, transitional sediments, and organic gÿttja.

Lago de las Morrenas 1 Core 2A

On average, the Lago de las Morrenas 1 core 2A sediments have more negative $\delta^{13}C_{TOC}$ values (mean = –20.5‰) than the core 1A sediments (–18.9‰; Figure 4.4). Despite the difference in average $\delta^{13}C_{TOC}$ values between the cores, similar trends in $\delta^{13}C_{TOC}$ values can be seen. Like core 1A, core 2A shows more positive average $\delta^{13}C_{TOC}$ values in the basal mineral rich sediments (mean = –19.7‰) as compared to the overlying organic rich gÿttja (mean = –20.7‰). However, core 2A shows considerably more variability between samples in the mineral rich glacial flour, with values ranging from –22.5‰ to –15.1‰, than does core 1A.

Lago de las Morrenas 1 Cores 1B, 2B, and 2D

Depth-correlated $\delta^{13}C_{TOC}$ values for cores 1B, 2B, and 2D are shown in Figure 4.5. Figure 4.6 shows the $\delta^{13}C_{TOC}$ values for all cores: 1A, 1B, 2A, 2B, and 2D. The shorter parallel slugs of transitional sediment collected in cores 1B, 2B, and 2D display similar trends in $\delta^{13}C_{TOC}$ values as those seen in cores 1A and 2A, with the most positive $\delta^{13}C_{TOC}$ values occurring in the basal mineral rich sediments and more negative values in the overlying organic rich sediments. Similarly to core 2A, core 2B shows considerable variability in $\delta^{13}C_{TOC}$ values with a minimum $\delta^{13}c_{TOC}$ value of –24.9‰ and a maximum $\delta^{13}C_{TOC}$ value of –10.8‰, both occurring in the transitional sediments.

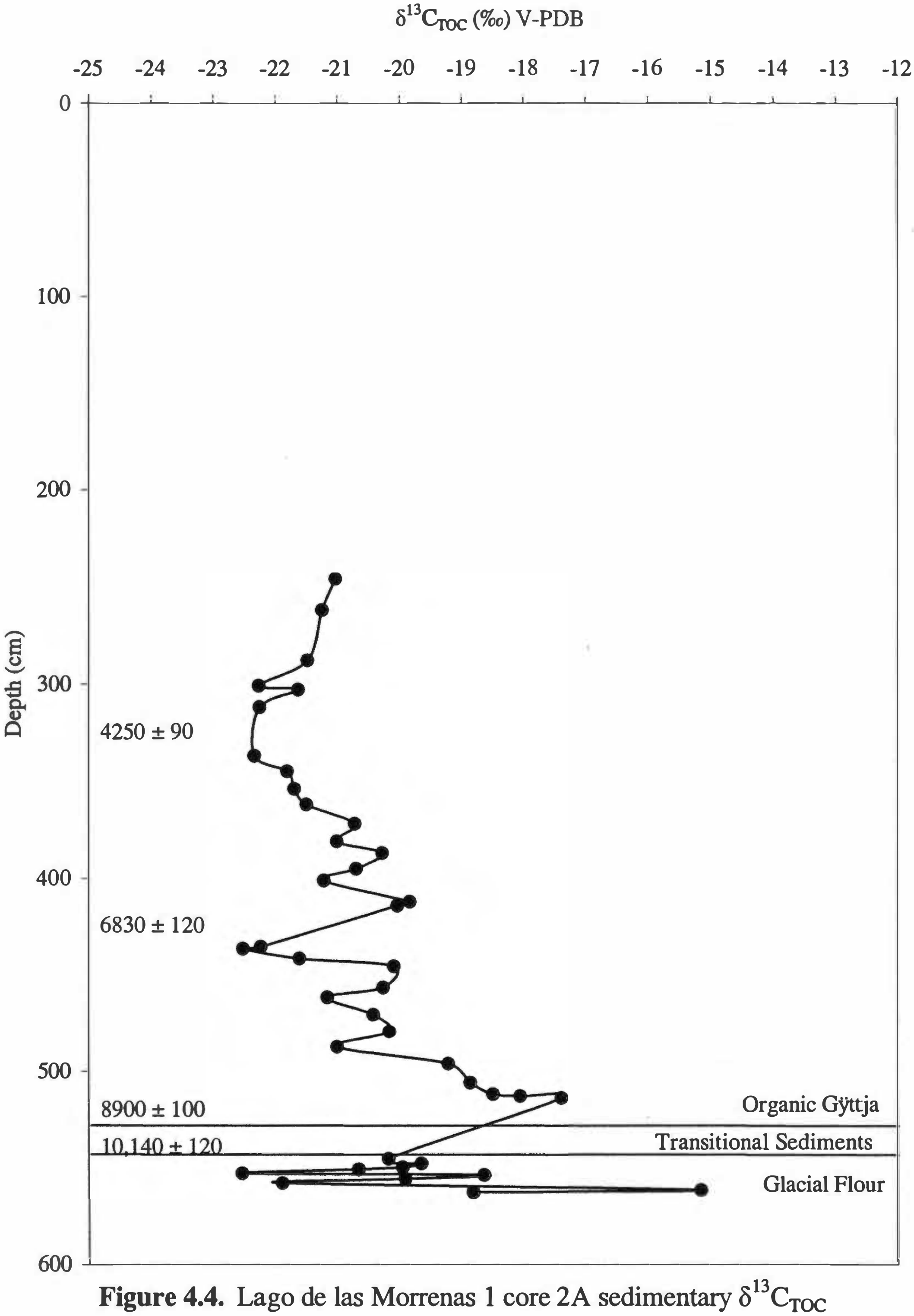

Figure 4.4. Lago de las Morrenas 1 core 2A sedimentary $\delta^{13}C_{TOC}$ values. Radiocarbon determentations on bulk sediments and the transition in sediment types between glacial flour, transitional sediments, and organic gÿttja are also marked.

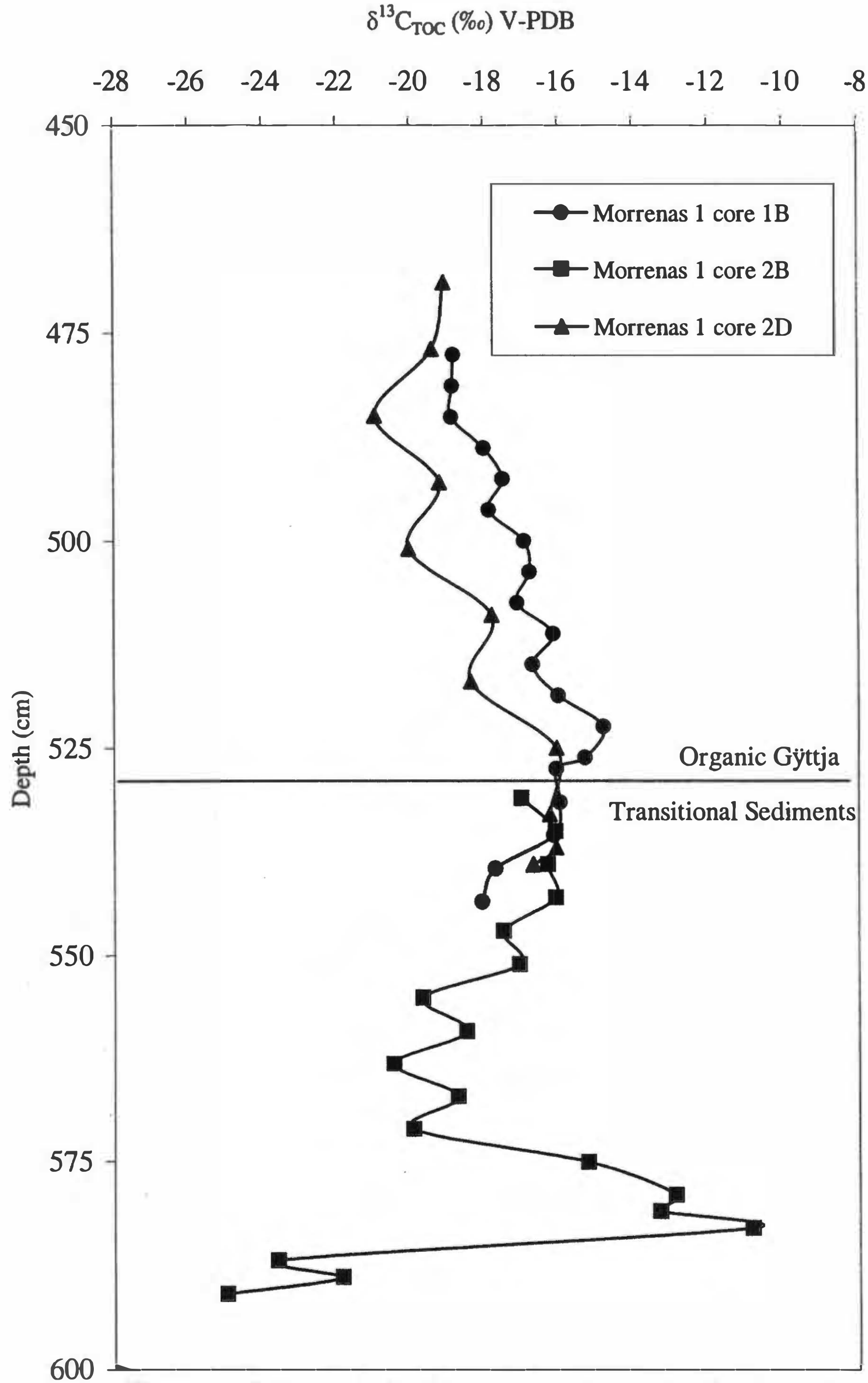

Figure 4.5. Lago de las Morrenas 1 core 1B, 2B, and 2D sedimentary $\delta^{13}C_{TOC}$ values. Reported depths are core 2A equivalent depths. Also marked is the change in sediment types between glacial flour and transitional sediments. Note the depth scale change.

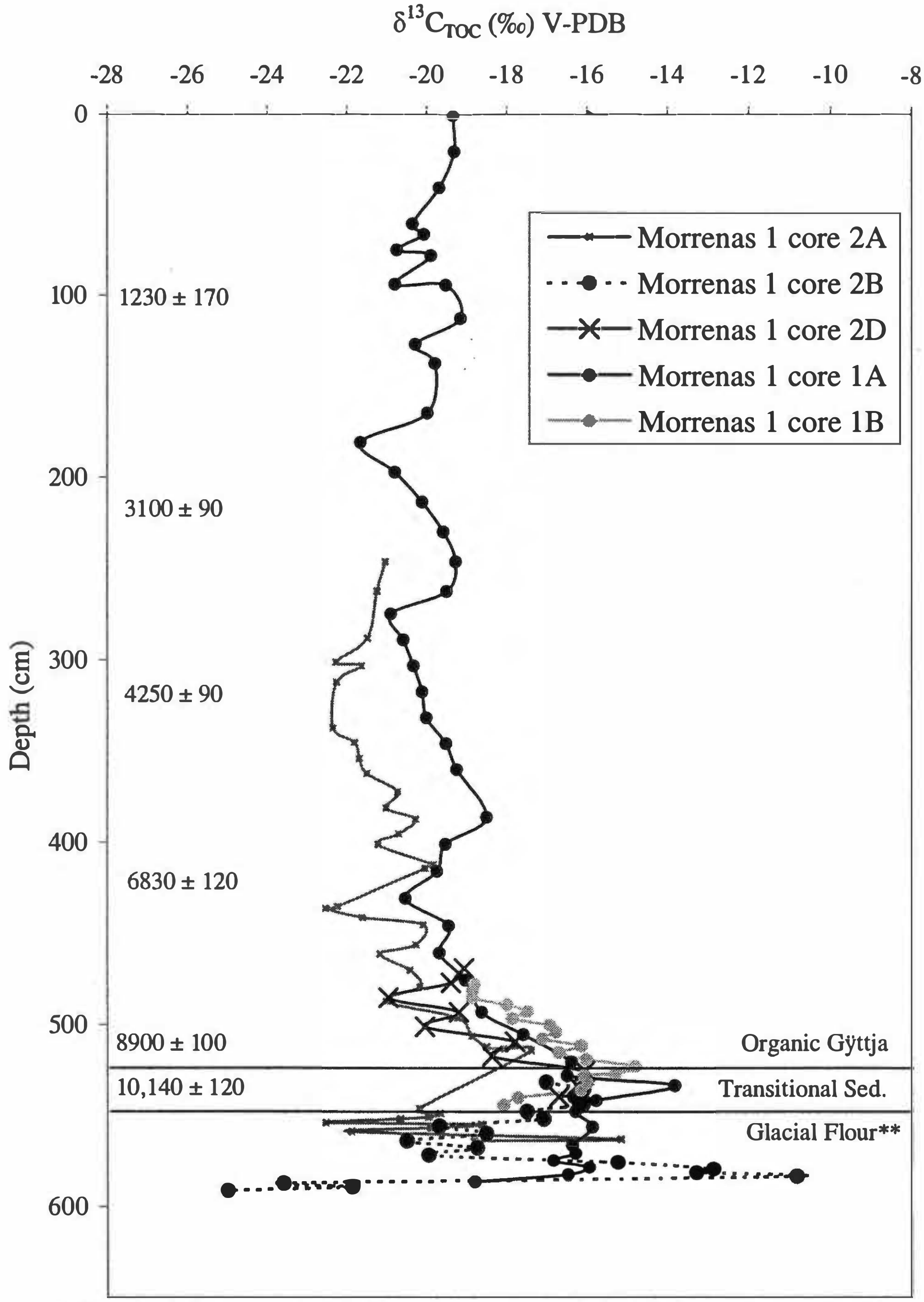

Figure 4.6. Lago de las Morrenas 1 core 1A, 1B, 2A, 2B, and 2D sedimentary $\delta^{13}C_{TOC}$ values. Reported depths are core 2A equivalent depths. Radiocarbon dates are those determined for core 2A and are reported in radiocarbon years before present. Also marked is the transition in sediment types between glacial flour, transitional sediments, and organic gÿttja. ** The glacial flour sediments are only present in cores 1A and 2A. These are transitional sediments in cores 2B, 2D, and 1B.

CHAPTER 5

DISCUSSION

A. Poaceae Pollen Identification and Separation by Size

As a possible additional proxy for temporal shifts in the dominance of C_3 and C_4 plants in the Chirripó páramo, I explored possibilities for differentiating pollen grains of *Chusquea subtessellata* and *Muhlenbergia flabellata* based on size. Numerous grass species are present in the Chirripó páramo, but the overwhelming dominance of *C. subtessellata* and the utilization of the C_4 photosynthetic pathway by *M. flabellata* make them the logical starting point for exploring the possible differentiation of grass pollen grains by size from this location. The work of Salgado-Labouriau (1984) suggests *C. subtessellata* grains should be relatively large (>40 µm) similarly to pollen grains of many other páramo bamboo species. No prior measurements of *M. flabellata* pollen grains are reported in the literature, but Salgado-Labouriau (1984) reports pollen grains from other species in the genus *Muhlenbergia* are smaller diameter (<35 µm) than bamboo species in the Venezuelan Andes. Based on this information, I hypothesized that *M. flabellata* grains should be smaller, on average, than *C. subtessellata* grains in the Chirripó páramo.

The t-test results indicate that differentiation between *C. subtessellata* and *M. flabellata* pollen grains based on measurements of the annulus diameter and the grain diameter to annulus diameter ratio are not reliable (Table 4.5). Conversely, the t-test results indicate that differences in the mean values for the grain diameter, the pore diameter, the grain diameter to pore diameter ratio, and the annulus to pore diameter ratio are significantly different (Table 4.5). These results suggest that differentiation between pollen of these two species, using these measurements, is possible. However, when plotted on a scatter plot, the data indicate that any such differentiation is hazardous as individual pollen grain measurements from the specimens in each of these size categories overlap considerably (Figures 5.1–5.6). These conflicting data suggest a type I error may be occurring in these statistical analyses (Sokal and Rohlf, 1995).

To test for the possibility of a type I error in these statistical analyses I applied the same t-test statistic on an individual specimen basis, as opposed to the species, or combined individual basis (Table 5.1). When I calculated the t-test statistic for the individual specimens, the only measurement that showed a significant difference between the two species was the annulus to pore diameter ratio (ts=2.70 and 4.24, df=98, P<.05) and the grain to pore diameter ratio (ts=3.08 and 6.25, df=98, P<.05). Despite the significant difference in these ratios, discerning between pollen types using either of these ratios would be extremely difficult due to the fact that each reticule unit is approximately 2.44 μm. This creates very coarse and inaccurate measurements for such small pore diameters, which averaged 3.03 μm for *C. subtessellata* and 3.46 μm for *M. flabellata* (Table 4.4), and probably creates a considerable amount of error in individual measurements or measurement ratios. The coarse nature of these measurements can be seen in the clumping of measurements around integers of the reticule measurements factor on the y-axis of the scatter plots for the annulus diameter, the pore diameter, and the annulus to pore diameter ratio (Figures 5.2, 5.3, and 5.6). This clumping is an artifact of reticular measurements being to the nearest 0.5 reticule units, as more accurate measurements are virtually impossible at 400x magnification

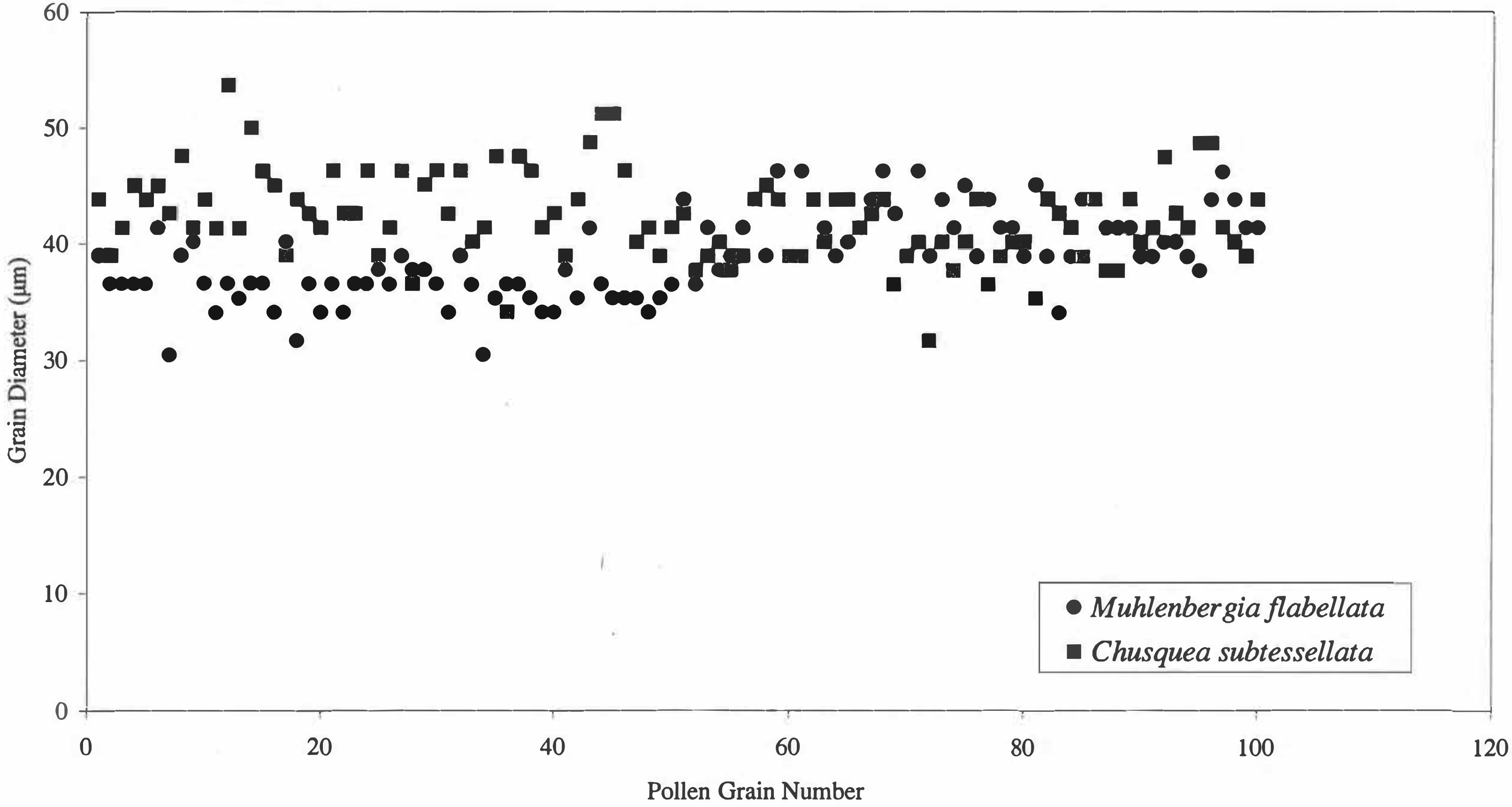

Figure 5.1. Pollen grain diameters of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

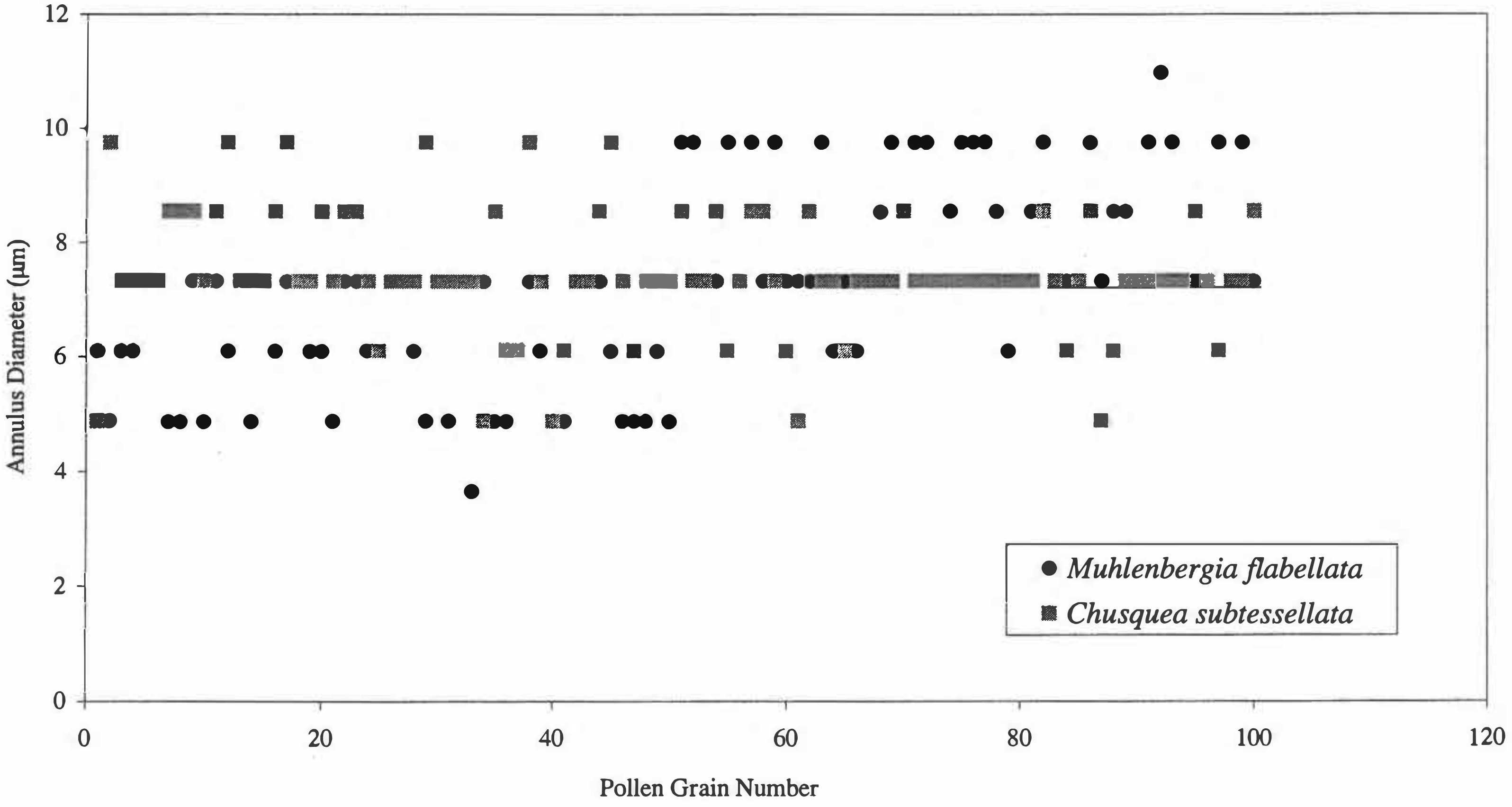

Figure 5.2. Pollen annulus diameters of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

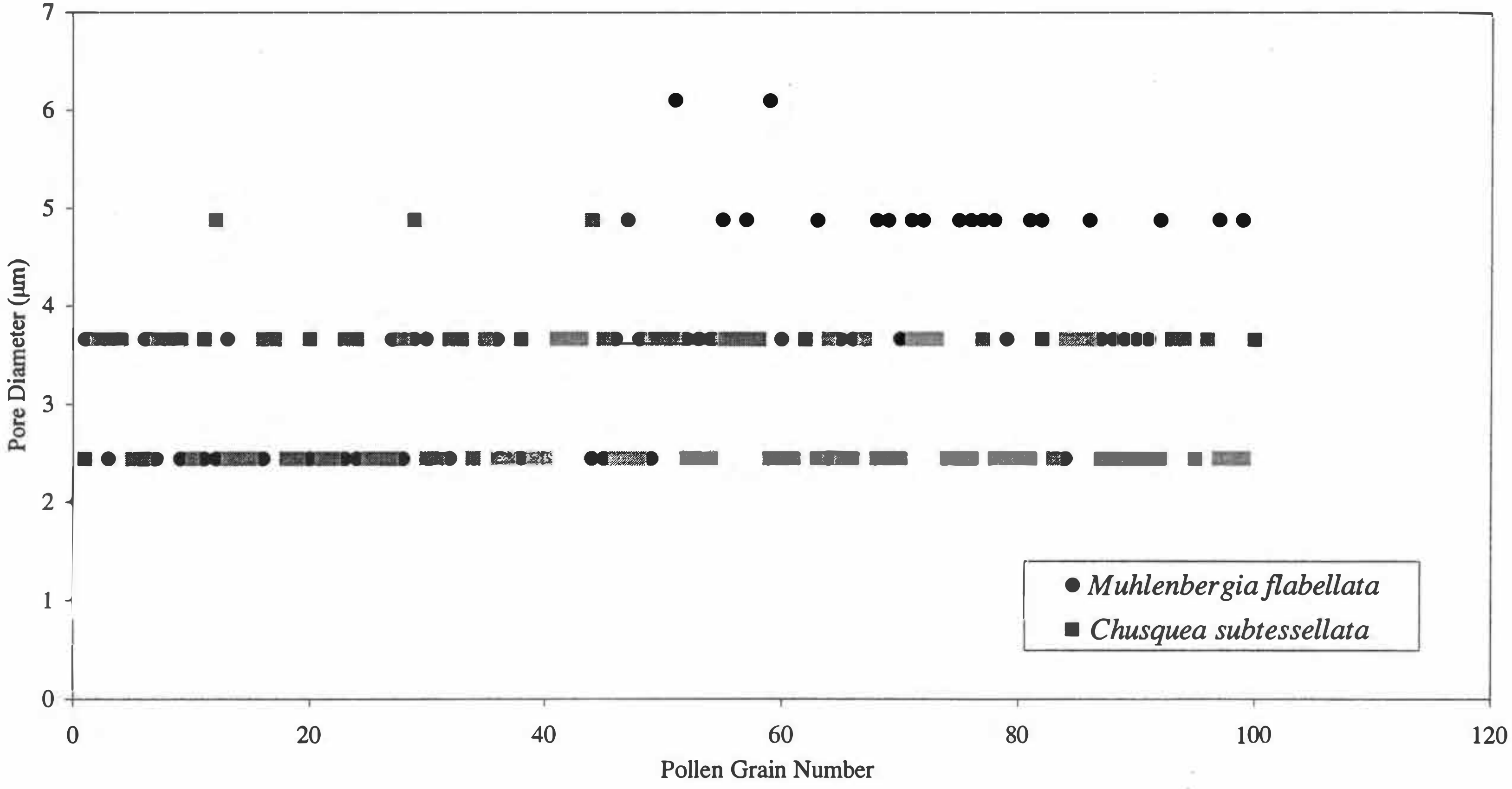

Figure 5.3. Pollen pore diameters of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

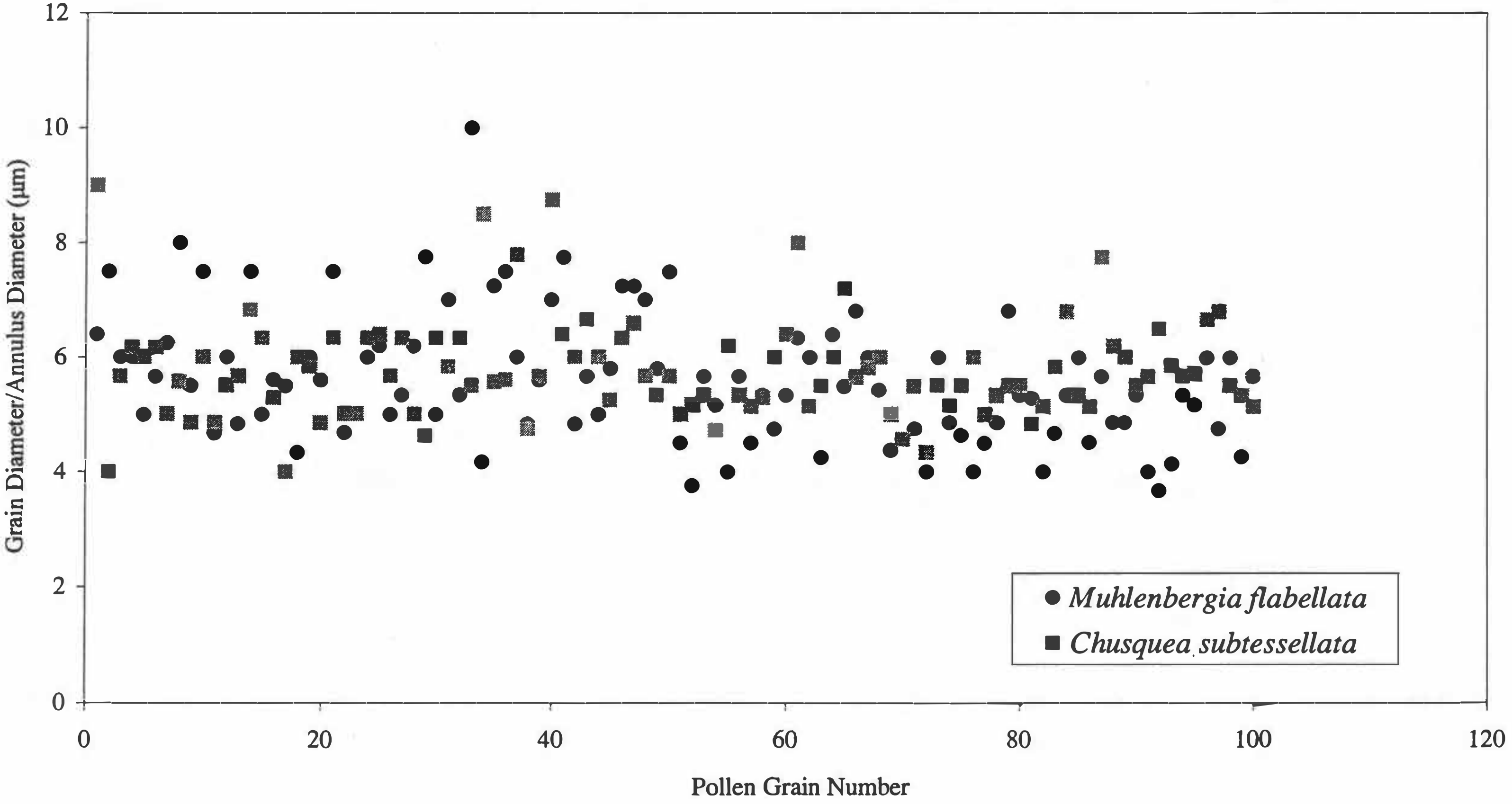

Figure 5.4. Pollen grain diameter to annulus diameter ratio of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

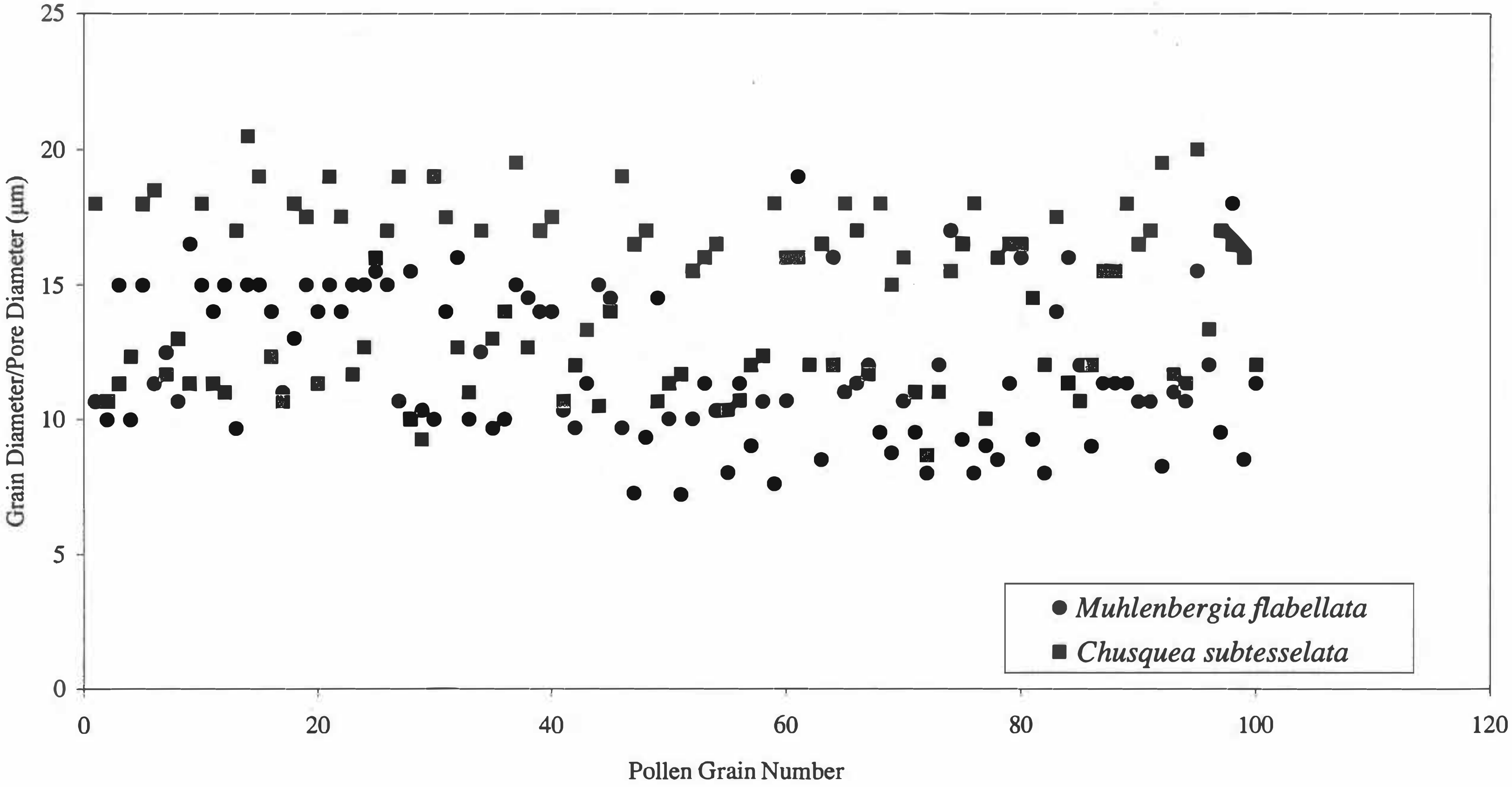

Figure 5.5. Pollen grain diameter to pore diameter ratio of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

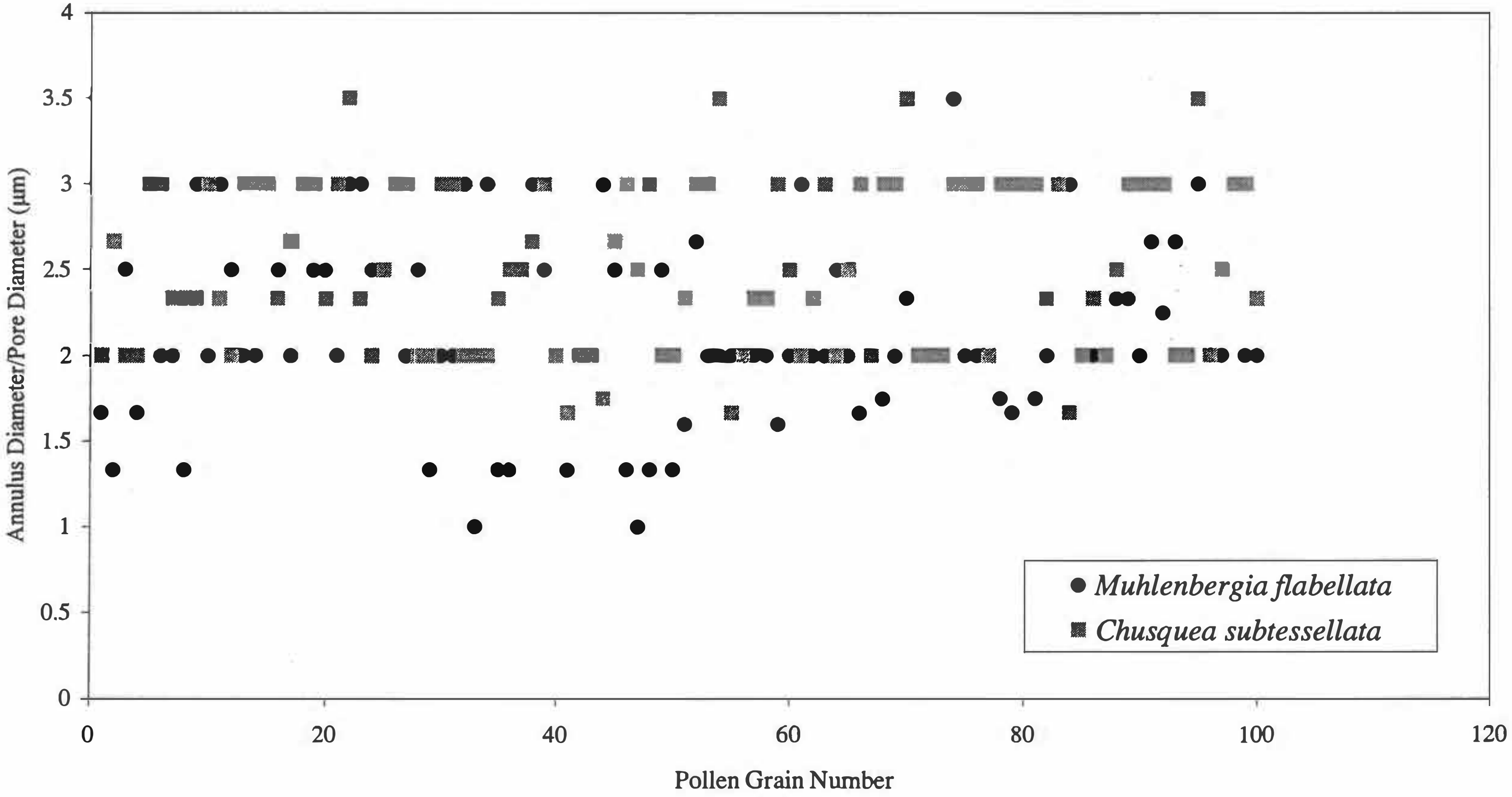

Figure 5.6. Pollen annulus diameter to pore diameter ratio of two *Chusquea subtessellata* and two *Muhlenbergia flabellata* specimens.

Table 5.1. t-Test Statistical Analyses of Pollen Grain Diameters from Specimens of *Chusquea subtessellata and Muhlenbergia flabellata.*

First Pair of Individuals

	t-Test Statistic (Equal Variances)[1]	t-Test Statistic (Unequal Variances)[1]	t-Test Degrees of Freedom	t-Test Critical Value (Two-Tailed)*	H_o Accepted?**
Grain Diameter	11.751		98	1.984	No
Annulus Diameter		6.348	97	1.985	No
Pore Diameter		1.392	97	1.985	Yes
Grain/Annulus Diameter		1.013	96	1.985	Yes
Grain/Pore Diameter	3.089		98	1.984	No
Annulus/Pore Diameter	2.705		98	1.984	No

Second Pair of Individuals

	t-Test Statistic (Equal Variances)[1]	t-Test Statistic (Unequal Variances)[1]	t-Test Degrees of Freedom	t-Test Critical Value (Two-Tailed)*	H_o Accepted?**
Grain Diameter	0.676		98	1.984	Yes
Annulus Diameter		4.819	85	1.988	No
Pore Diameter		6.598	83	1.989	No
Grain/Annulus Diameter		3.982	97	1.985	No
Grain/Pore Diameter	6.260		98	1.984	No
Annulus/Pore Diameter	4.243		98	1.984	No

[1] Assumption of equal or unequal variances is based on F-Test results for combined individual measurements.

*a = .05 for all statistical analyses

**H_o = The mean values for the two species are not significantly different.

with the reticule I used. When this measurement is multiplied by the conversion factor to convert the reticular units into micrometers it causes the observed clumping of diameter and diameter ratio measurements.

B. Lake Sediment $\delta^{13}C_{TOC}$ Values

Before studying the carbon isotopic composition of lacustrine sediments or peat, it is essential to understand the possible sources of carbon isotopes entering a lake or bog. Stuiver (1975) suggests three sources of organic carbon that can be incorporated into lake sediments: terrestrial plants, aquatic organisms, and pondweeds or other emergent plants. Terrestrial ecosystems are the dominant source of C_4 plant species in most situations; therefore their contribution of allochthonous organic matter to the sediment record is key in indicating shifts in C_4 plant dominance.

Bicarbonate Photosynthesis by Aquatic Plants

Autochthonous sedimentary carbon sources, such as aquatic macrophytes and plankton, can have a significant effect on the isotopic composition of lake sediments (Talbot and Johannessen 1992). The vast majority of aquatic plants use the C_3 photosynthetic pathway, but under highly alkaline or saline conditions, some aquatic plants will begin to utilize HCO^{-}_{3} - based metabolism (Smith and Walker 1980; Lucas 1983). Photosynthesis using this metabolism can produce organic matter that is enriched in ^{13}C (Mook *et al.* 1974; Smith and Walker 1980). These more positive values of $\delta^{13}C_{TOC}$ could be misinterpreted as an environmental or climate proxy and result in an overestimation of C_4 plant dominance. In fact, multiple studies using compound-specific isotopic analyses, which are capable of separating the isotopic contributions of terrestrial and aquatic vegetation, have found discrepancies between sediment $\delta^{13}C_{TOC}$ values, which reflect a combination of allochthonous and autochthonous carbon sources, and compound-specific $\delta^{13}C$ values that can be specifically attributed to the terrestrial plants around the lake (Ostrom *et al.* 1998; Huang *et al.* 1999; Brincat *et al.* 2000). When the terrestrial isotopic contributions to a sediment matrix are the data of interest, it is essential to try to isolate all of the isotopic contributions to that matrix so that the likelihood of misinterpretations is minimized. The presence of the CAM aquatic macrophyte *Isoetes storkii* and the likely presence of the HCO_3^- utilizing alga *Bottryococcus braunii* in Lago de las Morrenas 1, in particular, necessitate a cautious interpretation of the $\delta^{13}C_{TOC}$ values from the lake sediment profiles (Figure 5.7).

Post-Depositional Influences on the Isotopic Composition of Organic Matter

Post-depositional processes, such as diagenesis and methanogenesis, can also affect $\delta^{13}C$ ratios of bulk organic matter. Diagenesis in lake sediments or peat is most likely the result of the biological reworking of sediments. Diagenesis often results in consistent, monotonic decreases in the carbon isotopic ratio of sediments throughout the depth of the core (Talbot and Johannessen, 1992). No such trends are apparent in the Lago de las Morrenas 1 isotopic records (Figures 4.3–4.6).

Methanogenesis can result from reduction by methane producing bacteria (Nissenbaum *et al.,* 1972) or by fermentation (Rosenfeld and Silverman, 1959). Methanogenesis is relatively easy to infer as it drastically changes carbon isotopic

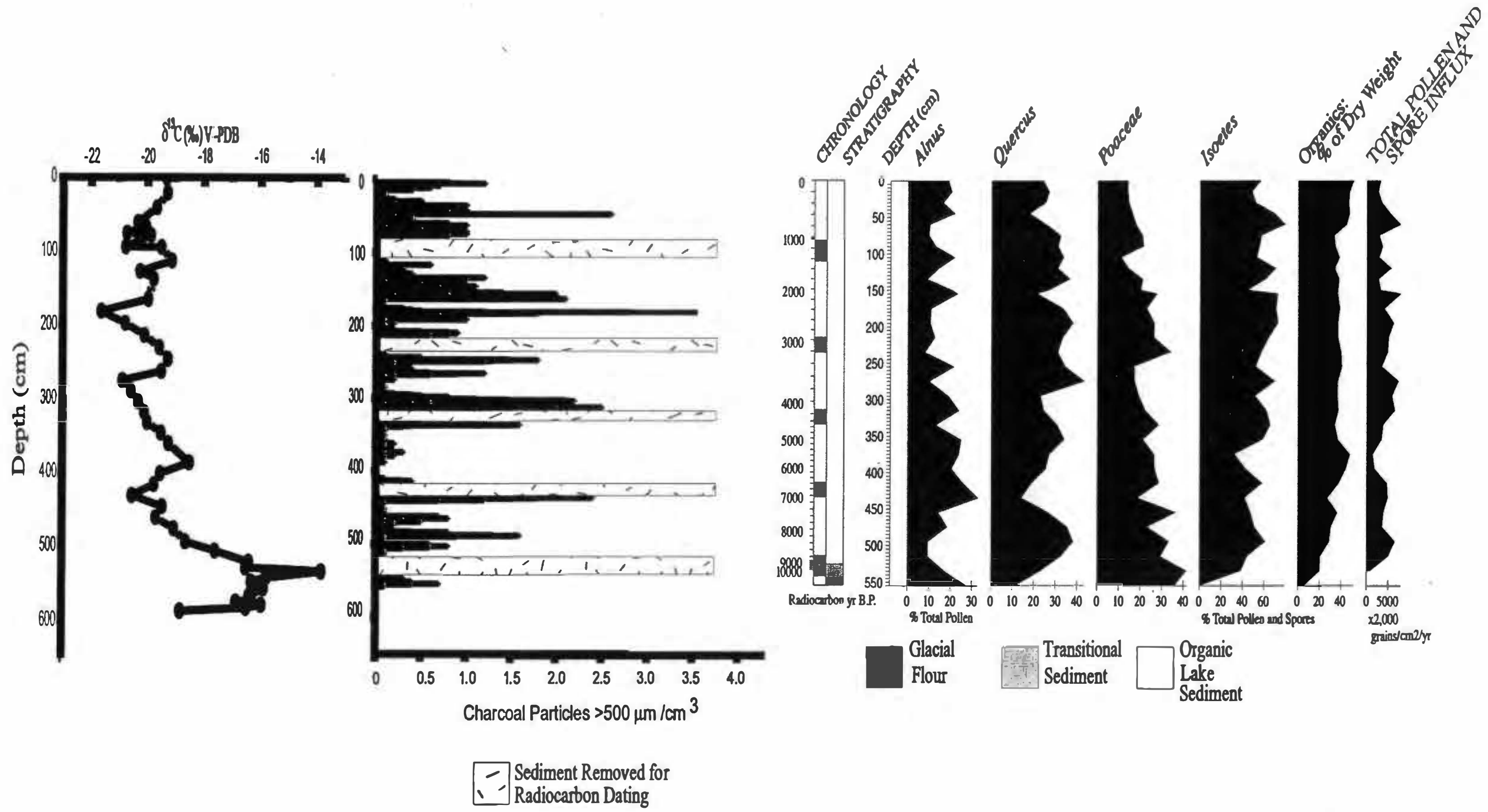

Figure 5.7. Comparison of stable carbon isotope, macroscopic charcoal concentration, and selected pollen data from Lago de las Morrenas 1. Macroscopic charcoal concentrations are from the dataset of League and Horn (2000) and fossil pollen data are from the dataset of Horn (1993).

signals. Methanogenesis by fermentation or bacterial production greatly discriminates against ^{13}C, yielding gas $\delta^{13}C$ ratios around –100‰ (Deines 1980) and leaving the remaining organic matter greatly enriched in ^{13}C. The relatively light isotopic signature of the Lago de las Morrenas 1 sediments (~–21‰) suggests that the production of enriched cogenetic organic matter during methanogenesis did not occur or is very limited in extent. This is further supported by the relatively high dissolved oxygen content of Lago de las Morrenas 1 water (6.6 mg/L) and the fact that Lago de las Morrenas 1 is currently polymictic (Horn *et al.* 1999), which would likely prevent the anoxic conditions necessary for methanogenesis as lake stratification would be minimized.

C. An Overview of the $\delta^{13}C_{TOC}$ Values Measured in Lago de las Morrenas 1

The most striking aspect of the $\delta^{13}C_{TOC}$ values measured in sediments from Lago de las Morrenas 1 is their relatively enriched isotopic compositions (Figures 4.3–4.6). The average $\delta^{13}C_{TOC}$ value for sediments from cores 1A and 2A was –19.6‰. In addition, surface sediments collected from the plastic tube core section of core 1A produced a $\delta^{13}C_{TOC}$ value of –19.3‰. Such enriched ^{13}C values for both average sediments at depth and surface sediments are not expected for a lake currently surrounded by vegetation dominated by C_3 components, and which are hypothesized to have been surrounded by the same vegetation since ~10,000 yr. B.P. (Horn 1993). Isotopic analysis of plant matter from *Chusquea subtessellata*, by far the dominant plant in the Chirripó páramo, show that the plant possesses a $\delta^{13}C$ signature of around –27‰ (Table 4.8). If *C. subtessellata* were the primary contributor to the organic carbon pool in Lago de las Morrenas 1, the $\delta^{13}C_{TOC}$ value of Lago de las Morrenas 1 sediments would be expected to be closer to this value.

In January 2003, I collected a charcoal sample from a charcoal deposit on the edge of the Lago de las Morrenas 0A basin. This charcoal was produced during the last fire in the valley (March 1976) and was subsequently transported to the basin by streams and wind. I hypothesized that this charcoal would be representative of allochthonous carbon sources presently entering the various lakes of the Valle de las Morrenas. As such, it should be well mixed, originating from multiple plant species in the valley, and transported to the lake in a manner similar to terrestrial plant detritus. This charcoal produced a relatively low $\delta^{13}C$ value of –26.5‰, consistent with the current dominance of C_3 plants in the valley. This low $\delta^{13}C$ value measured on a mixture of allochthonous carbon sources suggests the enriched carbon isotope values in the lake sediments originate from an autochthonous source of carbon.

D. Possible Sources of $^{13}C_{TOC}$ Enrichment in Lago de las Morrenas 1

The Possible Enrichment in Sediment $^{13}C_{TOC}$ due to CAM Photosynthesis

One possible autochthonous source for more enriched carbon isotope values is *Isoetes storkii*, which utilizes a CAM photosynthetic pathway. CAM plants are capable of switching their mode of carbon fixation between a mode similar to C_3 plants and a mode similar to C_4 plants, which can produce a wide range of $\delta^{13}C$ values that can overlap the $\delta^{13}C$ values produced by both C_3 and C_4 plants. Samples of *I. storkii* I analyzed in this study yielded $\delta^{13}C$ values of –25.8‰ and –26.8‰. The negative $\delta^{13}C$ values suggest these individuals relied mostly on fixation via the C_3 pathway. This $\delta^{13}C$

value could hypothetically become more positive if dissolved CO_2 levels were low enough to force the plant into a mode of carbon fixation more like that of C_4 plants. However, dissolved CO_2 measurements taken near the site of the *I. storkii* samples, and collected within the same week of plant sample collection, showed dissolved CO_2 levels are already quite low (~3 mg/L; Table 4.6). This suggests that *I. storkii* is most likely not changing its mode of carbon fixation in response to low dissolved CO_2 levels and probably did not do so previously. This makes *I. storkii* an unlikely source of the relatively enriched carbon isotope values measured in the sediments of Lago de las Morrenas 1.

The Possible Enrichment in Sediment $^{13}C_{TOC}$ *due to the Alga* Bottryococcus braunii

Another possible explanation for the relatively positive $\delta^{13}C_{TOC}$ values of sediments collected from Lago de las Morrenas 1 is the presence of the alga *Bottryococcus braunii.* Although the presence of *B. braunii* in Lago de las Morrenas 1 has not been verified, I was able to identify what appear to be fossil remains of the alga at all levels of the Lago de las Morrenas core 2A sediment analyzed for pollen by Horn (1993; Table 4.7). Huang *et al.* (1999) point out the danger in interpreting $\delta^{13}C_{TOC}$ values in the presence of *B. braunii* as it is known to assimilate ^{13}C-enriched HCO_3^- during photosynthesis. Cultured *B. braunii* specimens produced $\delta^{13}C$ values of –16.9‰, (Huang *et al.*, 1999). In addition, isoprenoid alkenes isolated from lake sediments and known to originate from *B. braunii* have been found to possess $\delta^{13}C$ values as high as –5.1‰ during the Pleistocene (Huang *et al.* 1999). Such enriched isotopic compositions could be responsible for the relatively positive $\delta^{13}C_{TOC}$ values observed for the sedimentary total organic carbon in Lago de las Morrenas 1.

The Possible Enrichment in Sediment $^{13}C_{TOC}$ due to Trophic Level Fractionations by Zooplankton

The sediments of Lago de las Morrenas 1 consist largely of zooplankton (copepod) fecal pellets (Horn 1993). If *B. braunii* and other algae are the primary food source for these zooplankton, and *B. braunii* is enriched in ^{13}C as compared to other planktonic and allochthonous carbon sources, the mixture of carbon sources could produce the observed average $\delta^{13}C_{TOC}$ value of –19‰ in Lago de las Morrenas 1 sediments. Zooplankton have been shown to induce no more than a 2‰ tropic level fractionation (Yoshioka *et al.* 1994; del Giorgio and France 1996), which is typical of most dietary fractionations observed in nature (DeNiro and Epstein 1978; Fry *et al.* 1984). Thus, the consumption of ^{13}C-enriched food sources, such as *B. braunii*, would give the zooplankton and its fecal pellets a similarly enriched isotopic value. A large contribution of relatively enriched carbon to the sediments of Lago de las Morrenas 1 from zooplankton fecal pellets could combine with relatively depleted allochthonous carbon sources to produce the $\delta^{13}C_{TOC}$ values of –19‰ measured here in the bulk sediment.

The Possible Enrichment in Sediment $^{13}C_{TOC}$ due to C_4 Vegetation

It is unlikely that the relatively positive $\delta^{13}C_{TOC}$ values measured in sediments from Lago de las Morrenas 1 are simply signaling the current and past mixture of C_3

vegetation, primarily *Chusquea subtessellata*, and C_4 vegetation, primarily *Muhlenbergia flabellata*, around Lago de las Morrenas 1. *Chusquea subtessellata* dominates the páramo vegetation surrounding Lago de las Morrenas 1 (Horn 1993), with vastly greater biomass and ground cover than *M. flabellata* (personal observation). While *M. flabellata* is capable of dominating some microhabitats, such as glacial till, it likely does not possess either the necessary dominance or biomass in the watershed to create the measured increase in $\delta^{13}C_{TOC}$ values without some other carbon source with a more positive $\delta^{13}C$ signature also contributing to the lake sediments of Lago de las Morrenas 1.

To test the possibility that *Muhlenbergia flabellata* could be causing the observed enrichment in $^{13}C_{TOC}$, I employed the mixing model developed by Phillips and Gregg (2001) with $\delta^{13}C$ end-members of –12.0‰ and –27.0‰, which are approximately the $\delta^{13}C$ compositions of plant matter from *Muhlenbergia flabellata* and *Chusquea subtessellata* respectively (Table 4.8). The mixing model results suggest a $\delta^{13}C_{TOC}$ value of –19‰ in the Lago de las Morrenas sediments would require 56% of the carbon entering the lake to originate from *Muhlenbergia flabellata* and only 46% of the carbon entering the lake to originate from *Chusquea subtessellata.* Any such partitioning of carbon contributions to Lago de las Morrenas 1 sediments is extremely unlikely considering *M. flabellata* does not exceed about 5% ground cover in the valley as a whole and constitutes an even smaller component of the total biomass (personal observation). Thus, it is extremely unlikely that *M. flabellata* alone can be responsible for the observed modern-day enrichment in ^{13}C in Lago de las Morrenas 1 sediments or that observed throughout the Holocene portion of the record.

E. The Paleoecological Significance of Lago de las Morrenas 1 Sedimentary $\delta^{13}C_{TOC}$ Values during the Late Pleistocene

The ecological interpretations I present here will focus primarily on $\delta^{13}C_{TOC}$ values of Lago de las Morrenas 1 Core 1A as it was the only core with the necessary material for a full stratigraphic $\delta^{13}C_{TOC}$ profile.

The Lago de las Morrenas 1 core 1A and core 2A sediments, as well as the supplemental core sections spanning the basal transition zone, all show more positive $\delta^{13}C_{TOC}$ values in the glacial flour and transitional sediments as compared to the overlying organic rich sediments (Figures 4.3–4.6). Average $\delta^{13}C_{TOC}$ values for the organic rich sediments from core 1A (mean $\delta^{13}C_{TOC} = -19.6‰$) are approximately 3.4‰ more depleted in ^{13}C than the underlying mineral rich sediments (mean $\delta^{13}C_{TOC} = -16.2‰$). Radiocarbon dates indicate the transition in sediment type and shift in average $\delta^{13}C_{TOC}$ values occur near the Pleistocene-Holocene transition (10,140 ^{14}C yr. B.P.). The more positive mean $\delta^{13}C_{TOC}$ values suggest a possible increased C_4 plant component in the Chirripó páramo during the late Pleistocene. In addition to the relatively positive mean carbon isotopic values occurring during the late Pleistocene, individual $\delta^{13}C_{TOC}$ measurements also suggest an expanded C_4 plant component around Lago de las Morrenas 1 during the Pleistocene. The most positive single $\delta^{13}C_{TOC}$ measurement (–13.8‰) is located within the transitional sediments of core 1A. A likely explanation for such a positive individual $\delta^{13}C_{TOC}$ value would be a significant contribution of allochthonous carbon by C_4 plants to the carbon pool of Lago de las Morrenas 1.

It is possible that the relatively positive carbon isotope compositions in the Pleistocene sediments of Lago de las Morrenas 1 are not signaling an expansion of C_4 plant dominance, but are instead the result of an increased utilization of HCO_3^- photosynthesis by aquatic plants and algae in response to low levels of dissolved CO_2 in the lake. Street-Perrott *et al.* (1997) and Huang *et al.* (1999) have documented a switch to HCO_3^- photosynthesis by *Bottryococcus braunii* during the late Pleistocene in sedimentary records from Mt. Kenya, which is hypothesized to have occurred in response to lower levels of dissolved CO_2 in the lakes as a result of decreased atmospheric pCO_2 levels.

According to Henry's Law, this would be expected in these high elevation lakes during the Pleistocene (Ficken *et al.* 1998). The low partial pressures of atmospheric CO_2 during the Pleistocene, combined with decreases in total air pressure at elevation, may lead to decreased diffusion of CO_2 across the water surface, and thus very low dissolved CO_2 levels in high elevation lakes. It is conceivable that a similar switch to HCO_3^- photosynthesis by aquatic plants in Lago de las Morrenas 1 may have occurred during the Pleistocene and could explain the increase in $\delta^{13}C_{TOC}$ values observed in these Pleistocene sediments.

Present conditions in Lago de las Morrenas appear conducive for HCO_3^--based photosynthesis, with very low modern levels of dissolved CO_2 (3.5 mg/L; Table 4.6) and the widespread availability of HCO_3^- anions (~81% of total anions in Lago de las Morrenas; Jones *et al.* 1993). Yet, despite the apparent ubiquity of *Bottryococcus braunii* and *Isoetes storkii* in the lake, the $\delta^{13}C$ of modern sediments are still more negative than Pleistocene sediments. It seems unlikely that dissolved CO_2 levels could have been much lower, such that HCO_3^--based photosynthesis would be so strongly preferred. It also seems unlikely that dissolved CO_2 levels could have been much lower during the Pleistocene compared to today and have still supported plant communities within the lake. Emergent aquatic plants, such as *Isoetes storkii*, may still be viable under conditions of low dissolved CO_2, but *I. storkii* spores reach their lowest levels during the late Pleistocene (Figure 5.7), suggesting that emergent aquatic plants may not have been as large a component of the late Pleistocene carbon pool as they are presently. Finally, influxes of granitic minerals in the form of glacial flour during the Pleistocene should have made Lago de las Morrenas 1 more acidic than today. This suggests that late Pleistocene lake conditions were possibly lower in $[HCO_3^-]$, not higher, and further suggests that a predominance of HCO_3^--based photosynthesis during the late Pleistocene was unlikely (Burkhardt *et al.* 1999).

Diatom assemblages for Lago de las Morrenas 1 show little or no variability throughout the ~10,000 ^{14}C yr. sedimentary record, suggesting no major changes in water chemistry occurred during the late Pleistocene or throughout the Holocene (Haberyan and Horn 1999). The combination of modern-day low dissolved-CO_2 levels, high concentrations of HCO_3^- anions, a possible decrease in pH levels during the Pleistocene, and similar diatom assemblages during the Pleistocene and today, suggest that HCO_3^- photosynthesis is just as likely, or more likely, to occur today as during the late Pleistocene. Thus, a C_4 plant expansion during the Pleistocene in the Chirripó páramo is a more likely explanation than increased utilization of HCO_3^- photosynthesis alone for the relative increase in $\delta^{13}C_{TOC}$ values observed for Lago de las Morrenas 1 Pleistocene sediments relative to the overlying Holocene sediments.

This interpretation assumes a consistent allochthonous carbon influx. It is entirely possible, however, that biomass surrounding the lake was considerably less following late Pleistocene deglaciation (see discussion below). If biomass were lower and HCO_3^- photosynthesis was being utilized by aquatic organisms such as *Bottryococcus braunii*, then a simple decrease in allochthonous carbon influx could conceivably produce the enriched carbon isotopic values seen in Lago de las Morrenas 1 Pleistocene sediments. In other words, by decreasing the amount of allochthonous carbon available for delivery to the lake, the autochthonous carbon sources would by default contribute a higher percentage of carbon to the total carbon pool of the lake. Organic carbon contents for the glacial flour are exceedingly low (~5%) when compared to those of the overlying organic gÿttja deposited throughout the Holocene (~35%; Figure 5.7). The low organic carbon content of the late Pleistocene sediments could be the result of either large mineral influxes or decreased allochthonous carbon influxes, or both. A decrease in allochthonous carbon influx leaves autochthonous carbon sources, such as *Bottryococcus braunii*, as the primary contributors to the carbon pool, and could have caused the observed increase in $\delta^{13}C_{TOC}$ values.

Finally, it is also possible that both a switch to HCO_3^- photosynthesis by aquatic plants and an increased C_4 plant component contributed to the enriched carbon isotope composition of the Pleistocene sediments of Lago de las Morrenas 1. In fact, using compound-specific isotopic analyses, both Street-Perrott *et al.* (1997) and Huang *et al.* (1999) provide overwhelming evidence for both increased C_4 plant components and an increase in HCO_3^- photosynthesis by aquatic algae for two high elevation lakes in equatorial Africa. There is no reason such a simultaneous C_4 plant expansion and switch to more HCO_3^- photosynthesis by aquatic plants and algae could not also have occurred at Lago de las Morrenas 1 during the Pleistocene.

F. Possible Causes for an Expansion in C_4 Plant Dominance during the Late Pleistocene

Decreased Atmospheric Levels of CO_2

Based on the known characteristics of C_4 plants, an increase in C_4 plant dominance over the now dominant C_3 plants in the Chirripó páramo may have been the result of one or a mixture of different forcings. Because of their ability to actively concentrate CO_2 during photosynthesis, C_4 plants are hypothesized to have been more competitive during the late Pleistocene (Ehleringer *et al.* 1997; Collatz *et al.* 1998), when atmospheric CO_2 concentrations were only half of the modern values (Barnola *et al.* 1987; Neftel *et al.* 1988; Leuenberger *et al.* 1992). Street-Perrott *et al.* (1997) present very convincing evidence that low atmospheric pCO_2 was likely the principal reason for an increase in C_4 plant dominance in high-altitude tropical vegetation in Kenya during the Pleistocene. Boom *et al.* (2001) and Mora and Pratt (2001) also hypothesize that low atmospheric pCO_2 had significant effects on C_4 plant dominance in high-altitude tropical vegetation in Colombia. Thus, it is very likely that the decreased atmospheric pCO_2 of the Pleistocene could have significantly influenced the C_4 plant component of high-altitude tropical vegetation around Lago de las Morrenas 1.

Possible Causes for an Expansion in C_4 Plant Dominance during the Late Pleistocene: Increased Aridity

Numerous studies have also suggested increases in C_4 plant dominance as a result of changes in precipitation regimes, with drier conditions and predominantly warm-season precipitation favoring C_4 plants over C_3 plants and vice versa (Quade *et al.* 1989; Talbot and Johannesen 1992; Sukumar *et al.* 1993; Aucour and Hillaire-Marcel 1994; Giresse *et al.* 1994; Huang *et al.* 2001). With ~2286 mm of precipitation falling between May and November, and only ~295 mm falling during the dry season from December to April, the present-day precipitation regime of Lago de las Morrenas 1 is quite seasonal and would tend to favor C_4 plants, but C_3 plants still dominate the watershed. Of course, modern pCO_2 levels are more favorable to C_3 plants than the lower pCO_2 levels of the Pleistocene. During the Pleistocene, the combination of precipitation seasonality and low atmospheric pCO_2 may have been responsible for the hypothesized C_4 plant expansions; however, there is no solid data regarding precipitation seasonality around Lago de las Morrenas during the Pleistocene.

A C_4 plant expansion around Lago de las Morrenas 1 during the late Pleistocene may also have resulted from of decreases in mean annual precipitation as increased aridity favors plants utilizing the C_4 photosynthetic pathway. Precipitation reconstructions for the Cordillera de Talamanca of Costa Rica during the Pleistocene are scarce. Fossil pollen studies from La Chonta bog (see Chapter 2, Environmental Setting and Late Quaternary Vegetation and Climate History) tend to focus more on temperature reconstructions during the Pleistocene as opposed to precipitation estimates. Hooghiemstra *et al.* (1992) and Islebe and Hooghiemstra (1997) do suggest wetter conditions around La Chonta bog during the early Holocene compared to the Pleistocene, but the magnitude of this change in precipitation is unclear. Nevertheless, a drier climate of any magnitude during the Pleistocene would have favored C_4 plants especially with decreased atmospheric pCO_2 levels.

What is perhaps the best precipitation reconstruction available for inferring precipitation in the Valle de las Morrenas during the formation of Lago de las Morrenas 1 does not even come from Costa Rica. Haug *et al.* (2001) present a high-resolution record of titanium and iron concentrations from sediments collected in the Cariaco Basin north of Venezuela, which may be responding to climate forcings that also affected Cerro Chirripó. The Cariaco Basin titanium and iron records are thought to be a proxy of Orinoco River discharge, and thus precipitation. The close correspondence between the inferred Orinoco River discharge and the record of macroscopic charcoal influx in Lago de las Morrenas 1 (League and Horn 2000) suggests the proxies at the two sites may be responding to the same climatic forcings.

The highest hypothesized rates of Orinoco River discharge into the Cariaco Basin, which are thought to be the result of wetter conditions, occur between ~11,000 and 5,000 cal. yr. BP. This hypothesized peak in precipitation coincides very nicely with the lowest influxes of macroscopic charcoal into Lago de las Morrenas 1 suggesting few fires, perhaps in response to wetter conditions, between ~11,700 and 4800 cal. yr. BP (League and Horn 2000). An increase in macroscopic charcoal influxes into Lago de las Morrenas 1 from 4800 cal. yr. BP to the present also coincides with hypothesized decreases in precipitation from the Cariaco Basin from ~5,000 cal. yr. BP to the present, perhaps suggesting increased aridity causing more frequent fires in the Chirripó páramo of Costa Rica. These strong links in proxy records suggest that the Orinoco watershed and Lago de las Morrenas 1 are both subject to similar climate forcings through time. Thus, increased C_4 plant dominance hypothesized to have occurred around Lago de las Morrenas at the end of the Pleistocene could have been the result of lower precipitation amounts as hypothesized for the Orinoco watershed during the late Pleistocene.

Habitat Availability

Another possible explanation for increased C_4 plant dominance during the late Pleistocene that has not been previously explored in prior studies of secular C_3-C_4 plant dynamics is that of habitat availability. On a glacial moraine in the Upper Rio Talari Valley (Valle de los Conejos, Figure 2.2) Horn (1989) found that *Muhlenbergia flabellata* reached 32.5% ground cover. This is exceptional, considering the absence of this grass from the other sites studied by Horn (1989). No quantitative study of the distribution of *M. flabellat*a has been undertaken in the Valle de las Morrenas. However, the species currently seems to dominate many glacial till deposits throughout the valley (personal observation). This is especially true for the less consolidated or coarser-grained glacial till deposits such as lateral moraines, end moraines, or ablation till. The ability of *M. flabellat*a to dominate these glacial till deposits is most likely the result of the poor water retention typical of these coarse grained substrates. The high water use efficiency (WUE) of C_4 plants such as *M. flabellata* would give them a distinct advantage under conditions of low soil moisture, which may be expected in these well drained till deposits. This is further supported by the absence of *M.*

flabellata on many of the lodgement till deposits in the valley (K. Orvis, personal communication 2003) that are more consolidated than the till deposits mentioned above, possibly resulting in significantly better water retention in these deposits.

After the deglaciation of the Valle de las Morrenas at the end of the Pleistocene, the most favorable sites for plant colonization may have been glacial till as much of the rest of the once glaciated valley would probably have been exposed bedrock due to the erosional processes of the alpine glacier. As *M. flabellata* seems to be dominant on glacial till deposits today, it seems possible that *M. flabellata* was the dominant plant in the late Pleistocene simply because glacial till was the primary substrate available for plant colonization.

G. The Paleoecological Significance of an Expansion in C_4 Plant Dominance during the Late Pleistocene

Recently, numerous studies from around the world have used stable carbon isotopic evidence to suggest an increased C_4 plant component in ecosystems during the Pleistocene that would have been undetectable in pollen records (e.g. Sukumar *et al.* 1993; Cole and Monger 1994; Giresse *et al.* 1994; Street-Perrott *et al.* 1997; Ficken *et al.* 1998; Huang *et al.* 1999; Boom *et al.* 2001; Huang *et al.* 2001; Mora and Pratt 2001). The stable carbon isotope record presented here also suggests a possible C_4 plant expansion occurring on Cerro Chirripó and probably for other localities in the high elevations of the Cordillera de Talamanca of Costa Rica. Sedimentary records from Lago Quexil, Guatemala to the north of Costa Rica and the Bogotá Basin, Colombia to the south of Costa Rica also provide strong evidence for C_4 plant expansions in the neotropics during the Pleistocene (Boom *et al.* 2001; Huang *et al.* 2001).

Boom *et al.* (2001) suggest that C_4-dominated plant assemblages that presently occur within particular microhabitats in the Andean páramo of Colombia may be relicts from the Pleistocene, when such communities were much more widespread throughout the páramo as a result of decreased atmospheric pCO_2. *Muhlenbergia flabellata*, the most dominant and widespread C_4 plant in the Chirripó páramo, seems currently to be restricted to favorable microhabitats as well. These C_4 microhabitats are quite similar to those described by Boom *et al.* (2001) consisting of a dry, stony, seemingly well-drained substrate. *Muhlenbergia flabellata* seems to be especially dominant on coarser tills, which are likely more well-drained than the surrounding soils because of their larger grain sizes, giving *M. flabellata* an advantage with its C_4 photosynthetic pathway providing a higher WUE as compared to the competing C_3 vegetation. Perhaps, as suggested for the Colombian Andes, these *Muhlenbergia* communities are relicts from the Pleistocene when they may have been much more widespread due to lowered atmospheric pCO_2 and immature soil development. Following deglaciation and subsequent increases in atmospheric pCO_2, *Muhlenbergia* species may have been replaced in the majority of the Valle de las Morrenas by competition with C_3 plants and are now only capable of dominating drier microhabitats, such as those provided by the well-drained glacial till deposits where they are dominant today.

Mora and Pratt (2002) used altitudinal transects of paleosols in the Bogotá Basin to reconstruct the extent of hypothesized C_4 plant expansions during the Pleistocene. Their results produced a maximum altitude for C_4 plant expansion of ~2700 m coinciding with the hypothesized 6–7°C mean annual temperature isotherm during the glacial period. Restriction of C_4 plant expansion to elevations below 2700 m and to mean annual temperatures greater than 6–7°C is in very good agreement with the modeling studies of Ehleringer *et al.* (1997) and Collatz *et al.* (1998). However, if the enriched carbon isotope values presented here are indeed the result of increased C_4 plant dominance in the Valle de las Morrenas during the Pleistocene, it would suggest C_4 plants were capable of gaining dominance under mean annual temperatures lower than the hypothesized 6–7°C isotherm. Based on temperature reconstructions from glacial ELA estimates (Orvis and Horn 2000; Lachniet and Seltzer 2002) and pollen evidence of treeline shifts (Hooghiemstra *et al.* 1992; Islebe *et al.* 1996; Islebe and Hooghiemstra 1997), C_4 plant expansion in this area of the Cordillera de Talamanca occurred at mean annual temperatures as low as 0°C. The extreme cold tolerance of most *Muhlenbergia* species would presumably have been a factor that facilitated this C_4 plant expansion at such low mean annual temperatures (Schwarz and Redmann 1988; Sage *et al.* 1999b).

Because of its potentially widespread effects on vegetation around the world, the low levels of atmospheric pCO_2 during the Pleistocene have received increased attention in paleoecological studies. Of particular interest has been the possible effect of lowered atmospheric pCO_2 on alpine treeline elevations. Street-Perrott *et al.* (1997) have suggested a need to reassess paleotemperature reconstructions based on Pleistocene treeline altitudes, as lowered levels of atmospheric pCO_2 and the decreased pCO_2 with increasing altitude may have driven a lowering of treelines, unrelated to climatic factors. It has also been suggested that this lowering of treeline elevation in response to non-climatic factors could lead to a suppression in pollen contributions from C_3 plant communities (i.e. sub-alpine forests) and lead to overestimations in treeline shifts, and hence overestimation of temperature depressions (Boom *et al.* 2001). Although I have presented strong evidence for a paleoecological response to decreased levels of atmospheric pCO_2 in Lago de las Morrenas 1 and the Valle de las Morrenas, this suppression of tree-line seems an unlikely event for the Cordillera de Talamanca of Costa Rica. Paleotemperature estimates made for the region using both pollen records of tree-line fluctuation (Hooghiemstra *et al.* 1992; Islebe *et al.* 1996; Islebe and Hooghiemstra 1997) and geomorphic glacier ELA reconstructions (Orvis and Horn 2000; Lachniet and Seltzer 2002) are roughly the same. Since the ELA reconstructions are independent of any atmospheric pCO_2 effects, the matching paleotemperature estimates made using pollen analysis suggest no atmospheric pCO_2 effect on treeline in the Cordillera de Talamanca of Costa Rica.

H. The Paleoecological Significance of Lago de las Morrenas 1 Sediment $\delta^{13}C_{TOC}$ Values during the Holocene

Fluctuations in the stable carbon isotope values of Holocene (~10,000 ^{14}C yr. BP to present) sediments of Lago de las Morrenas 1 show strong similarities to the macroscopic charcoal record of League and Horn (2000; Figures 5.8 and 5.9). Periods of increased macroscopic charcoal influx into Lago de las Morrenas 1 (i.e. increased charcoal concentration) correspond with periods of relatively negative $\delta^{13}C_{TOC}$ values (Figure 5.9). Conversely, periods of decreased macroscopic charcoal concentration and influx into Lago de las Morrenas 1 coincide with more positive $\delta^{13}C_{TOC}$ values.

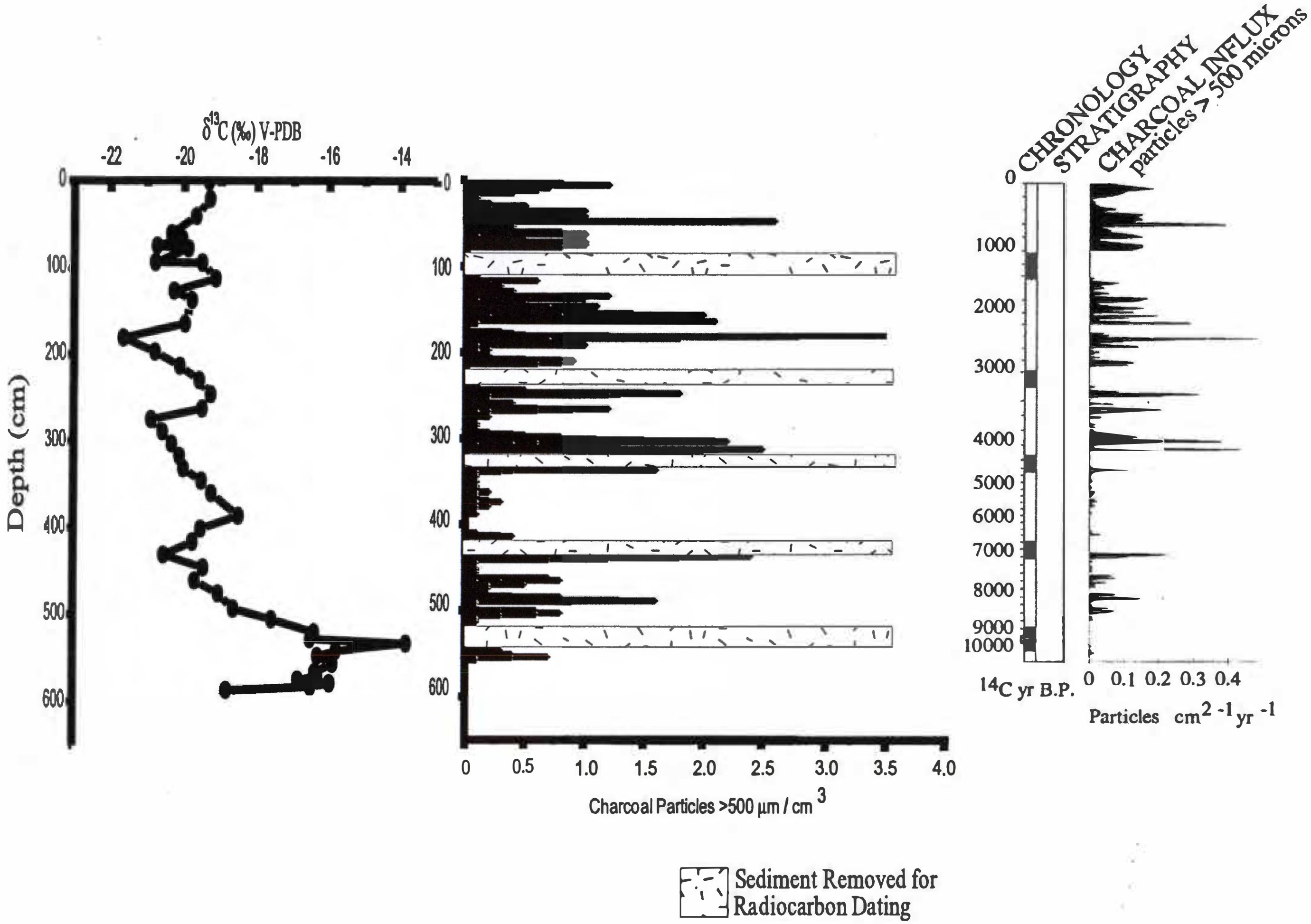

Figure 5.8. Comparison of stable carbon isotope, macroscopic charcoal concentration, and macroscopic charcoal influx data from Lago de las Morrenas 1. Macroscopic charcoal concentrations are from the dataset of League and Horn (2000) and the macroscopic charcoal influx diagram is adapted from League and Horn (2000).

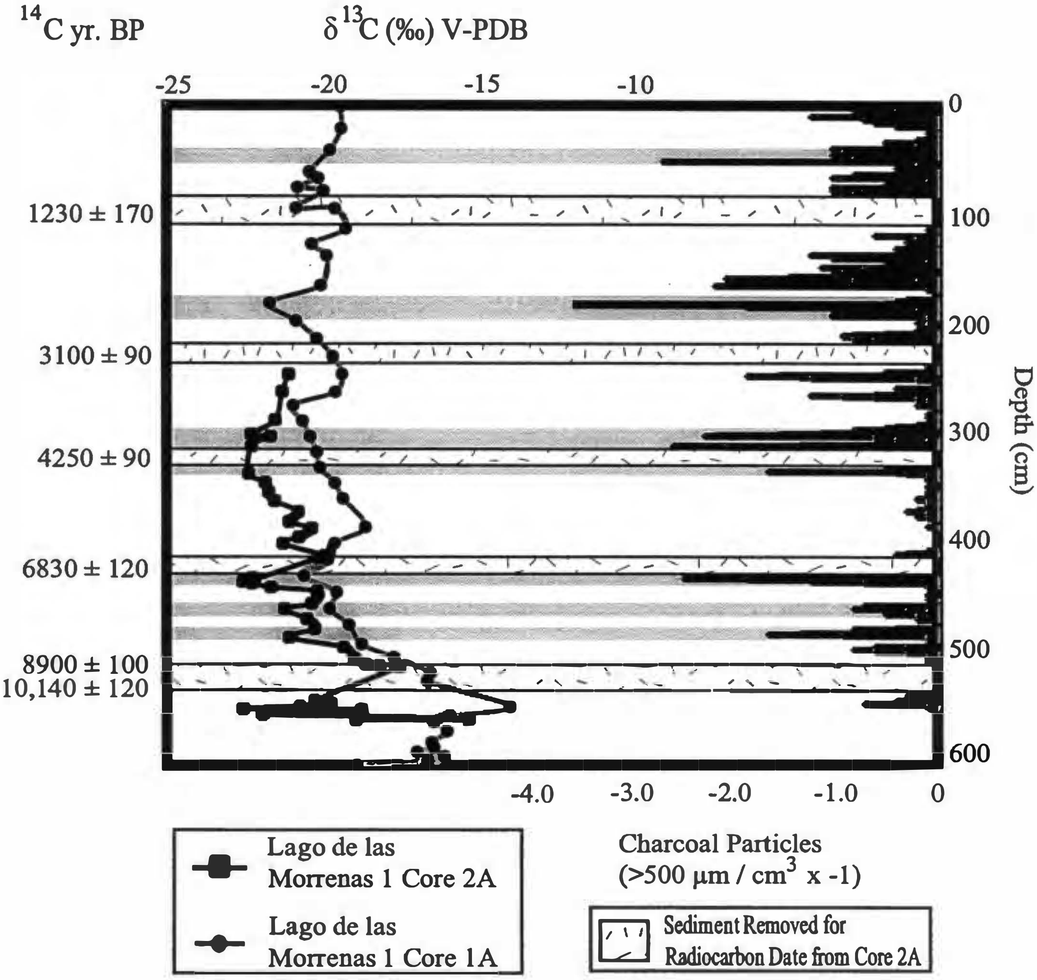

Figure 5.9. Comparison of macroscopic charcoal concentrations from Lago de las Morrenas 1 core 2A and stable carbon isotope values from Lago de las Morrenas cores 1A and 2A. Macroscopic charcoal concentrations have been multiplied by -1 for direct comparison to the isotope data.

Throughout the Holocene the $\delta^{13}C_{TOC}$ values never diverge too far from the average $\delta^{13}C_{TOC}$ value (~–19.6‰) of the Holocene sediments with a maximum $\delta^{13}C_{TOC}$ value of –18.5‰ and a minimum $\delta^{13}C_{TOC}$ value of –21.6‰.

If the primary carbon source for the sediments of Lago de las Morrenas 1 is autochthonous, as discussed previously, then the coincidence of decreased $\delta^{13}C_{TOC}$ values and increased macroscopic charcoal concentration and influx may signal increased allochthonous carbon delivery into Lago de las Morrenas 1. The total organic carbon constituent of sediments includes allochthonous charcoal. Although small in mass, charcoal can significantly influence the $\delta^{13}C_{TOC}$ value because it is such a concentrated form of carbon. With C_3 plants hypothetically dominating the vegetation around Lago de las Morrenas 1 since the beginning of the Holocene, it is likely that carbon entering the lake in the form of charcoal was considerably depleted in ^{13}C. I found charcoal produced by the 1976 fire in the Chirripó páramo to have considerably more positive $\delta^{13}C$ values (–26.5‰) than the total organic carbon of surface sediments (–19.3‰). Therefore, periodic influxes of terrestrial charcoal into Lago de las Morrenas 1 following fires in the Chirripó páramo are likely largely responsible for the coinciding decreases in sedimentary $\delta^{13}C_{TOC}$ values.

Furthermore, following these fires it is likely that erosion rates increased as there was decreased ground cover by vegetation. An increase in erosion rates in the Lago de las Morrenas 1 watershed would increase the delivery of terrestrial plant detritus dominated by C_3 plant material, thereby contributing to the lighter than average carbon isotope composition of TOC in the Lago de las Morrenas 1 sediments for some period following fire events. In other words, the Holocene $\delta^{13}C_{TOC}$ values are not indicating shifts in vegetation or climate, but are instead tracking shifts in the balance of allochthonous vs. autochthonous carbon delivery to Lago de las Morrenas 1. The close correlation between the Orinoco River discharge record from Cariaco Basin and the macroscopic charcoal record from Lago de las Morrenas 1 indicate that increases in allochthonous carbon influxes are the result of increased aridity and decreased fire intervals. Thus, the Holocene sediment $\delta^{13}C_{TOC}$ record may be signaling changes in precipitation around Lago de las Morrenas 1, but doing so indirectly.

CHAPTER 6

CONCLUSIONS

The importance of multi-proxy records in paleoecological studies is undeniable. No single proxy is capable of providing the information necessary to understand all aspects of ecosystem changes in the past. Fossil pollen is probably the single most important proxy of vegetation change, but like all proxies, it cannot signal all aspects of ecosystem dynamics. The stable carbon isotope record from Lago de las Morrenas 1 provides evidence of paleoecological changes not evident in fossil pollen, charcoal, or diatom records.

Relatively positive sediment $\delta^{13}C_{TOC}$ values in late Pleistocene sediments from Lago de las Morrenas 1 suggest an increased C_4 plant component in the Chirripó páramo, a switch to HCO_3^- photosynthesis by plankton, or both. The decreased atmospheric pCO_2 levels of the Pleistocene would have favored both situations.

Sediment $\delta^{13}C_{TOC}$ values in Holocene sediments from Lago de las Morrenas 1 show a strong link to macroscopic charcoal influxes. The ^{13}C depleted values of predominantly C_3 vegetation result in more negative sedimentary $\delta^{13}C_{TOC}$ values as terrestrial organic material was delivered more effectively to the sediments of Lago de las Morrenas 1 in the form of charcoal and increased surface runoff following fires. In this sense, the Holocene $\delta^{13}C_{TOC}$ values of Lago de las Morrenas 1 sediments are responding primarily to the balance of autochthonous vs. allochthonous carbon delivery.

The multitude of sources contributing to the carbon pool of Lago de las Morrenas 1 preclude definitive conclusions about C_3-C_4 plant dynamics based on isotope signatures in bulk organic matter. More confident interpretations of the paleoecological significance of stable carbon isotopic values preserved in the Lago de las Morrenas 1 sediments could result from using the relatively recently developed method of compound-specific isotopic analysis (Hayes *et al.* 1990). Compound-specific isotopic analyses are capable of separating the isotopic signature of terrestrial and aquatic carbon sources (e.g. Huang *et al.* 1999). This means that shifts in the dominant photosynthetic pathway being used by terrestrial plants can be detected regardless of shifts to the utilization of HCO_3^- during photosynthesis by aquatic organisms. The very recent installation of a mass spectrometer capable of compound-specific isotopic analyses at the University of Tennessee, Knoxville will make these analyses possible in the near future.

Despite problems in isolating the carbon sources contributing to Lago de las Morrenas 1 sedimentary $\delta^{13}C_{TOC}$ values, the $\delta^{13}C_{TOC}$ record from Lago de las Morrenas 1 suggests significant changes in carbon cycling during the late Pleistocene. With numerous studies elsewhere showing marked changes in ecosystem dynamics in response to the lower atmospheric pCO_2 levels during the Pleistocene, it appears most reasonable to attribute the shift in carbon cycling in Lago de las Morrenas 1 to decreased atmospheric pCO_2 levels.

The sensitivity of both aquatic and terrestrial communities in this locality to changes in atmospheric chemistry as well as climate should be taken into consideration in future paleoecological studies. The vast majority of paleoecological studies concentrate on vegetation dynamics in response to changing climate and fail to consider all possible forcings of vegetation change. In addition, with modern atmospheric pCO_2

levels climbing at an unprecedented rate, the apparent ecosystem sensitivity to past changes in atmospheric chemistry suggests the potential for rapid and significant responses in the future.

The inability of C_4 plants to effectively compete against C_3 plants under elevated levels of CO_2 could spell trouble for C_4 plants in an elevated CO_2 world (Collatz *et al.* 1998). In essence, with future increases in pCO_2, we could see a reversal of the hypothesized Pleistocene scenario of increased C_4 plant dominance. In fact, numerous researchers have already argued that observed treeline expansions across forest/grassland ecotones are the result of the anthropogenically increased CO_2 content of the atmosphere. As many grassland ecosystems are C_4-dominated, we may already be seeing a decrease in the ability of C_4 plants to compete against C_3 plants with increased atmospheric levels of CO_2. With many grazers, including livestock, dependent upon C_4 plants for subsistence this could prove harmful to grassland ecosystems and the food supply for much of the world. In addition, numerous important crops (e.g. corn, sugarcane, sorghum) utilize the C_4 photosynthetic pathway. It remains unclear whether or not the rapidly climbing atmospheric CO_2 levels will significantly affect C_4 crops in the future, as they are typically protected from competition by humans, but one could imagine increased virility in C_3 weeds causing increased competition with these C_4 crops under conditions of significantly higher atmospheric CO_2. By furthering our understanding of vegetation responses to past fluctuations in atmospheric CO_2 concentrations, we will be better prepared to predict any future changes in vegetation in response to the anthropogenic increases in atmospheric CO_2 in the future.

REFERENCES

REFERENCES

Aucour, A.M. and C. Hillaire-Marcel. 1994. Late Quaternary biomass changes from ^{13}C measurements in a highland peatbog from Equatorial Africa (Burundi). *Quaternary Research* 41: 225–233.

Aucour, A.M., C. Hillaire-Marcel, and R. Bonnefille. 1993. A 30,000 year record of ^{13}C and ^{18}O changes in organic matter from an equatorial peatbog. In *Climate Change in Continental Isotopic Records. Geophysical Monograph* 78: 343–351.

Baker, R.G., E.A. Bettis III, R.F. Denniston, L.A. Gonzalez, L.E. Strickland, and J.R. Krieg. 2002. Holocene paleoenvironments in southeastern Minnesota – chasing the prairie-forest ecotone. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 103–122.

Barker, P.A., R.A. Perrott, F.A. Street-Perrott, and Y. Huang. 2001. Evolution of the carbon cycle in Lake Kimilili, Mt. Elgon, Kenya, since 14000 cal. yr BP: a multiproxy study. *Palaeoecology of Africa* 27: 77–93.

Barnola, J.M., D. Raynaud, Y.S. Korotkevich, and C. Lorius. 1987. Vostok ice core provides 160,000-year record of atmospheric CO_2. *Nature* 329: 408–418.

Bender, M.M. 1971. Variations on the 13C ratios of plants in relation to the pathway of photosynthetic carbon dioxide fixation. *Phytochemistry* 10: 1239–1244.

Berglund, B.E. 1986. *Handbook of Holocene Paleoecology and Paleohydrology.* John Wiley and Sons, New York.

Boom, A., G. Mora, A.M. Cleef, and H. Hooghiemstra. 2001. High altitude C_4 grasslands in the northern Andes: relicts from glacial conditions? *Review of Palaeobotany and Palynology* 115: 147–160.

Boutton, T.W., L.C. Nordt, and D.D. Kuehn. 1998. Late Quaternary vegetation and climate change in the North American Great Plains: Evidence from $\delta^{13}C$ of palaeosol organic carbon. In *Isotope Techniques in the Study of Environmental Change.* International Atomic Energy Agency, Vienna. Pp. 653–662.

Brincat, D., K. Yamada, R. Ishiwatari, H. Uemura, and H. Naraoka. 2000. Molecular-isotopic stratigraphy of long-chain *n*-alkanes in Lake Baikal Holocene and glacial age sediments. *Organic Geochemistry* 31: 287–294.

Burkhardt, S., U. Riebesell, and I. Zondervan. 1999. Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO_2 availability. *Marine Ecology Progress Series* 184: 31–41.

Burney, D.A., L.P. Burney, and R.D.E. MacPhee. 1994. Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. *Journal of Archaeological Science* 21: 273–281.

Burney, D.A., R.V. DeCandido, L.P. Burney, F.N. Kostel-Hughes, T.R. Stafford, Jr., and H.F. James. 1995. A Holocene record of climate change, fire ecology, and human activity from montane Flat Top Bog, Maui. *Journal of Paleolimnology* 13: 209–217.

Bush, M.B. and P.A. Colinvaux. 1990. A pollen record of a complete glacial cycle from lowland Panama. *Journal of Vegetation Science* 17: 105–119.

Bush, M.B., M.C. Miller, P.E. Olivera, and P.A. Colinvaux. 2000. Two histories of environmental change and human disturbance in eastern lowland Amazonia. *The Holocene* 10: 543–553.

Cerling, T.E. 1999. Paleorecords of C_4 plants and ecosystems. *In* Sage, R.F. and R.K. Monson (*eds.*), *C_4 Plant Biology.* Academic Press, San Diego. Pp. 445–469.

Clark, J.S., E.C. Grimm, J. Lynch, and P.G. Mueller. 2001. Effects of Holocene climate change on the C_4 grassland/woodland boundary in the Northern Plains, USA. *Ecology* 82: 620–636.

Cleef, A.M., and A. Chaverri. 1992. Phytogeography of the Costa Rican páramo. *In* Balslev H. and J.L. Luteyn (*eds.*), *Páramo: An Andean Ecosystem Under Human Influence.* Academic Press, London. Pp. 45–60.

Clement, R.M., and S.P. Horn. 2001. Pre-Columbian land-use history in Costa Rica: a 3000-year record of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene* 11: 419–426.

CLIMAP Project Members. 1981. Seasonal reconstruction of the Earth's surface at the Last Glacial Maximum. *Map and Chart Series MC-36, Geological Society of America.*

Coen, E. 1983. Climate. *In* Janzen, D.J. (*ed.*), *Costa Rican Natural History.* University of Chicago Press, Chicago. Pp. 35–46.

Cole, D.R., and H.C. Monger. 1994. Influence of atmospheric CO_2 on the decline of C_4 plants during the last deglaciation. *Nature* 368: 533–536.

Collatz G.J., J.A. Berry, and J.S. Clark. 1998. Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. *Oecologia* 114: 441–454.

Connin, S.L., J. Betancourt, and J. Quade. 1998. Late Pleistocene C_4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. *Quaternary Research* 50: 179–193.

Curtis, J.H., D.A. Hodell, M. Brenner. 1996. Climate variability on the Yucatan peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. *Quaternary Research* 46: 37–47.

Deines, P., 1980. The isotopic composition of reduced organic carbon. *In* Fritz, P. and J.C. Fontes (*eds*.), *Handbook of Environmental Isotope Geochemistry* (volume 1). Elsevier Inc., New York.

del Giorgio, P.A., and R.L. France. 1996. Ecosystem-specific patterns in the relationship between zooplankton and POM or microplankton $\delta^{13}C$. *Limnology and Oceanography* 4: 359–365.

DeNiro, M.J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42: 495–506.

Ehleringer, J.R., T.E. Cerling, and B.R. Helliker. 1997. C_4 photosynthesis, atmospheric CO_2, and climate. *Oecologia* 112: 285–299.

Ehleringer, J.R., and R.K. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24: 411–439.

Farquhar, G.D., J.R. Ehleringer, and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* 40: 503–537.

Ficken, K.J., F.A. Street-Perrott, R.A. Perrott, D.L. Swain, D.O. Olago, and G. Eglinton. 1998. Glacial/interglacial variations in carbon cycling revealed by molecular and isotope stratigraphy of Lake Nkunga, Mt. Kenya, East Africa. *Organic Geochemistry* 29: 1701–1719.

Ficken, K.J., M.J. Wooller, D.L. Swain, F.A. Street-Perrott, G. Eglinton. 2002. Reconstruction of a subalpine grass-dominated ecosystem, Lake Rutundu, Mount Kenya: a novel multi-proxy approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 137–149.

Fry, B., R.K. Anderson, L. Entzeroth, J.L. Bird, and P.L. Parker. 1984. ^{13}C enrichment and oceanic food web structure in the northwestern Gulf of Mexico. *Contributions to Marine Science* 27: 49–63.

Gasse, F. and R. Lin. 1998. Lacustrine isotope archives of past climate and environmental changes in the tropics and subtropics. In *Isotope Techniques in the Study of Environmental Change*. International Atomic Energy Agency, Vienna. Pp. 519–531.

Giresse, P., J. Maley, and P. Brenac. 1994. Late Quaternary palaeoenvironments in the Lake Barombi Mbo (West Cameroon) deduced from pollen and carbon isotopes of organic matter. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 65–78.

Goman, M., and R. Byrne. 1998. A 5000-year record of agriculture and tropical forest clearance in the Tuxlas, Veracruz, Mexico. *The Holocene* 8: 83–89.

Haberyan, K.A., G. Umaña, C. Collado, and S.P. Horn. 1995. Observations on the plankton of some Costa Rican lakes. *Hydrobiologia* 312: 75–85.

Haberyan, K.A., and S.P. Horn. 1999. A 10,000 year diatom record from a glacial lake in Costa Rica. *Mountain Research and Development*: 19, 63–70.

Haug, G.H., K.A. Hughen, D.M. Sigman, L.C. Peterson, and U. Röhl. 2001. Southward migration of the Intertropical Convergence Zone through the Holocene. *Science* 293: 1304–1308.

Hayes, J.M., K.H. Freeman, B.N. Popp, and C.J. Hoham. 1990. Compound-specific isotopic analyses: A novel tool for reconstruction of ancient biogeochemical processes. *Organic Geochemistry* 16: 1115–1128.

Herrera-Arrieta, Y., and F. Grant. 1994. Anatomy of the *Muhlenbergia montana* complex (Poaceae). *American Journal of Botany* 81: 1038–1044.

Hillaire-Marcel, C., A.M. Aucour, R. Bonnefille, G.M. Riollet, A. Vincens, and D. Williamson. 1989. ^{13}C/palynological evidence of differential residence times of organic carbon prior to its sedimentation in East African rift lakes and peat bogs. *Quaternary Science Reviews* 8: 207–212.

Hodell, D.A., J.H. Curtis, G.A. Jones, A. Higuera-Gundy, M. Brenner, M.W. Binford, and K.T. Dorsey. 1991. Reconstruction of Caribbean climate change over the past 10,500 years. *Nature* 352: 790–793.

Hooghiemstra, H., A.M. Cleef, G.W. Noldus, and M. Kapelle. 1992. Upper Quaternary vegetation dynamics and palaeoclimatology of the La Chonta bog area (Cordillera de Talamanca, Costa Rica). *Journal of Quaternary Science* 7: 205–225.

Hooghiemstra, H., and T. van der Hammen. 1993. Late Quaternary vegetation history and paleoecology of Laguna Pedro Palo (subandean forest belt, Eastern Cordillera, Colombia). *Review of Palaeobotany and Palynology* 77: 235–262.

Horn, S.P. 1989. Postfire vegetation development in the Costa Rican páramos. *Madroño* 36: 93–114.

Horn, S.P. 1990. Timing of deglaciation in the Cordillera de Talamanca, Costa Rica. *Climate Research* 1, 81–83.

Horn, S.P. 1993. Postglacial vegetation and fire history in the Chirripo Paramo of Costa Rica. *Quaternary Research* 40: 107–116.

Horn, S.P. 1998. Fire management and natural landscapes in the Chirripó Páramo, Chirripó National Park, Costa Rica. *In* Zimmerer, K. and K. Young (*eds.*), *From Natures Geography: Biogeographical Landscapes and Conservation in Developing Countries.* University of Wisconsin Press, Madison, Wisconsin. Pp 125–146.

Horn, S.P. Forthcoming. Vegetation dynamics following recent fires in the Buenavista and Chirripó páramos of Costa Rica. *In* Kappelle, M., S. Horn, and Chaverri, A. (*eds.*), *Los Páramos de Costa Rica.* INBIO Press, Santo Domingo, Costa Rica.

Horn, S.P. and B.L. League. Forthcoming. Lake-sediment records of Holocene vegetation and fire history in the Chirripó Páramo of Costa Rica. *In* Kappelle, M., S. Horn, and Chaverri, A. (*eds.*), *Los Páramos de Costa Rica.* INBIO Press, Santo Domingo, Costa Rica.

Horn, S.P., K. Orvis, and K. Haberyan. 1999. Investigación limnológica y geomorfológica de lagos glaciares del Parque Nacional Chirripo, Costa Rica. *Revista Informe Semestral* 35: 95–106.

Horn, S.P., K.H. Orvis, and K.A. Haberyan. Forthcoming. Limnology of glacial lakes in the Chirripó Páramo of Costa Rica. *In* Kappelle, M., S. Horn, and Chaverri, A. (*eds.*), *Los Páramos de Costa Rica.* INBIO Press, Santo Domingo, Costa Rica.

Huang, Y., F.A. Street Perrott, S.E. Metcalfe, M. Brenner, M. Moreland, and K.H. Freeman. 2001. Climate change as the dominant control on glacial-interglacial variations in C_3 and C_4 plant abundance. *Science* 293: 1647–1651.

Huang, Y., F.A. Street-Perrott, R.A. Perrott, P. Metzger, and G. Eglinton. 1999. Glacial-interglacial environmental changes inferred from molecular and compound-specific $\delta^{13}C$ analyses of sediments from Sacred Lake, Mt. Kenya. *Geochimica et Cosmochimica Acta* 63: 1383–1404.

Islebe, G.A., and H. Hooghiemstra. 1997. Vegetation and climate history of montane Costa Rica since the last glacial. *Quaternary Science Reviews* 16: 589–604.

Islebe, G.A., H. Hooghiemstra, M. Brenner, J.H. Curtis, and D.A. Hodell. 1996. A Holocene vegetation history from lowland Guatemala. *The Holocene* 6: 265–271.

Islebe, G.A., H. Hooghiemstra, and K. van der Borg. 1995. A cooling event during the younger Dryas Chron in Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116: 73–80.

Islebe, G.A., H. Hooghiemstra, and R. van't Veer. 1996. Holocene vegetation and water level history in two bogs of the Cordillera de Talamanca, Costa Rica. *Vegetatio* 124: 155–171.

Johnson, B.J., G.H. Miller, M.L. Fogel, J.W. Magee, M.K. Gagan, and A.R. Chivas. 1999. 65,000 years of vegetation change in Central Australia and the Australian summer monsoon. *Science* 284: 1150–1152.

Jolly, D., and J. Haxeltine. 1997. Effect of low glacial atmospheric CO_2 on tropical African montane vegetation. *Science* 276: 786–787.

Jones, J.R., K. Lohman, and G. Umaña V. 1993. Water chemistry and trophic state of eight lakes in Costa Rica. *Verhandlungen, Internationale Verinigung für Theoretische und Angewandte Limnologie* 25: 899–905.

Kapelle, M. 1991. Distribucion altitudinal de la vegetacion del Parque Nacional Chirripo, Costa Rica. *Brenesia* 36: 1–14

Keeley, J.E. 1981. Isoetes howellii: A submerged aquatic cam plant? *American Journal of Botany* 68: 420–424.

Keeley, J.E. 1989. Stable carbon isotopes in vernal pool aquatics of differing photosynthetic pathways. *In* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy (*eds.*), *Stable Isotopes in Ecological Research.* Springer-Verlag, New York. Pp. 76–81.

Keeley, J.E., and D.R. Sandquist. 1991. Diurnal photosynthesis cycle in cam and non-cam seasonal-pool aquatic macrophytes. *Ecology* 72: 716–727.

Kennedy, L.M. and S.P. Horn. 1997. Prehistoric maize cultivation at the La Selva Biological Station, Costa Rica. *Biotropica* 29: 368–370.

Lachniet, M.S., and G.O. Seltzer. Late Quaternary glaciation of Costa Rica. *GSA Bulletin* 114: 547–558.

League, B.L. 1998. *Sedimentary Charcoal, Magnetic Susceptibility, and Páramo Fires in Chirripó National Park, Costa Rica.* Senior Honors Thesis, Department of Geography, University of Tennessee.

League, B.L., and S.P. Horn. 2000. A 10000 year record of Páramo fires in Costa Rica. *Journal of Tropical Ecology* 16: 747–752.

Leuenberger, M., U. Siegenthaler, and C.C. Langway. 1992. Carbon isotope composition of atmospheric CO_2 during the last ice age from an Antarctic ice core. *Nature* 357: 488–490.

Leyden, B. 1995. Evidence of the Younger Dryas in Central America. *Quaternary Science Reviews* 14: 833–839.

Livingstone, D.A., and W.D. Clayton. 1980. An altitudinal cline in tropical African grass floras and its paleoecological significance. *Quaternary Research* 13: 392–402.

Lucas, W.J. 1983. Photosynthetic assimilation of exogenous HCO^-_3 by aquatic plants. *Annual Review of Plant Physiology* 34: 71–104.

Markgraf, V. 1989. Paleoclimates in Central and South America since 18,000 BP based on pollen and lake-level records. *Quaternary Science Reviews* 8: 1–24.

Martin, P.S. 1964. Paleoclimatology and a tropical pollen profile. In *Report on the VI International Congress on the Quaternary, Warsaw, 1961*. Vol. 2: 319–323.

Mook, W.G., J.C. Bommerson, and W.J. Staberman. 1974. Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide. *Earth and Planetary Science Letters* 22: 169–176.

Mora G., and L.M. Pratt. 2001. Isotopic evidence for cooler and drier conditions in the tropical Andes during the last glacial stage. *Geology* 29: 519–522.

Mora, G., and L.M. Pratt. 2002. Carbon isotopic evidence from paleosols for mixed C_3/C_4 vegetation in the Bogota Basin, Columbia. *Quaternary Science Reviews* 21: 985–995.

Neftel, A., H. Oeschger, T. Saffelbach, and B. Stauffer. 1988. CO_2 record in the Byrd ice core 50,000–5,000 years BP. *Nature* 331: 609–611.

Nissenbaum, A., B.J. Presley, and I.R. Kaplan. 1972. Early diagenesis in a reducing fjord, Saanich Inlet, British Columbia, I. Chemical and isotopic changes in major components of interstitial water. *Geochimica et Cosmochimica Acta* 36: 1007–1027.

Northrop, L.A., and S.P. Horn. 1996. PreColumbian agriculture and forest disturbance in Costa Rica: Paleoecological evidence from two lowland rainforest lakes. *The Holocene* 6: 289–299.

O'Leary, M.H. 1981. Carbon isotope fractionation in plants. *Phytochemistry* 20: 553–567.

Orvis, K., and S.P. Horn. 2000. Quaternary glaciers and climate on Cerro Chirripo, Costa Rica. *Quaternary Research* 54: 24–37.

Ostrom, P.H., N.E. Ostrom, J. Henry, B.J. Eadie, P.A. Meyers, and J.A. Robbins. 1998. Changes in the trophic state of Lake Erie: discordance between molecular δ^{13}C and bulk δ^{13}C sedimentary records. *Chemical Geology* 152: 163–179.

Pessenda, L.C.R., S.E.M. Gouveia, B.M. Gomes, R. Aravena, R. Boulet, and A.S. Ribeiro. 1998. Studies of palaeovegeation changes in the central Amazon by carbon isotopes (^{12}C, ^{13}C, ^{14}C) of soil organic matter. In *Isotope Techniques in the Study of Environmental Change*. International Atomic Energy Agency, Vienna. Pp. 645–652.

Peterson, P.M., and Y. Herrera-Arrieta. 2001. A leaf blade anatomical survey of Muhlenbergia: (Poaceae: Muhlenberginae). *Sida* 19: 469–506.

Phillips, D.L., and Gregg, J.W. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171–179.

Pohl, R.W. 1980. Family #15, Graminieae. *In* Burger, W. (*ed.*), *Flora Costaricensis, Fieldiana: Botany* 4: 1–608. Field Museum of Natural History, United States.

Prescott, G.W. 1969. *How to Know the Freshwater Algae.* WM. C. Brown Company Publishers, Iowa.

Quade, J., T.E. Cerling, and J.R. Bowman. 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature* 342: 163–166.

Rosenfeld, W.D. and S.R. Silverman. 1959. Carbon isotope fractionation in bacterial production of methane. *Science* 130: 1658–1659.

Rosenmeier, M.F., D.A. Hodell, M. Brenner, J.H. Curtis, J.B. Martin, F.S. Anselmetti, D. Ariztegui, and T.P. Guilderson. Influence of vegetation change on watershed hydrology: implications for paleoclimatic interpretation of lacustrine $\delta^{18}O$ records. *Journal of Paleolimnology* 27: 117–131.

Sage, R.F., M. Li, and R.K. Monson. 1999a. The taxonomic distribution of C_4 photosynthesis. *In* R.F. Sage and R.K. Monson (*eds.*), *C_4 Plant Biology.* Academic Press, San Diego. Pp. 551–584.

Sage, R.F., D.A. Wedin, and M. Li. 1999b. The biogeography of C_4 photosynthesis. *In* R.F. Sage and R.K. Monson (*eds.*), *C_4 Plant Biology.* Academic Press, San Diego. Pp. 313–373.

Salgado-Labouriau, M.L. 1986. Late-Quaternary palynological studies in the Venezuelan Andes. *Erdwissenschaftliche Forschung* 18: 279–293.

Sandquist D.R., and J.E. Keeley. 1990. Carbon uptake characteristics in two high elevation populations of the aquatic cam plant Isoetes bolanderi (Isoetacae). *American Journal of Botany* 77: 682–688.

Schwarz, A.G., and R.E. Redmann. 1988. C_4 grasses from the boreal forest region of northwestern Canada. *Canadian Journal of Botany* 66: 2424–2430.

Scott, L. 2002. Grassland development under glacial and interglacial conditions in southern Africa: review of pollen, phytolith and isotope evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 47–57.

Scott, L., and J.C. Vogel. 2000. Evidence for environmental conditions during the last 20,000 years in Southern Africa from ^{13}C in fossil hyrax dung. *Global and Planetary Change* 26: 207–215.

Smith, F.A., and N.A. Walker. 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO^-_3 and to carbon isotopic discrimination. *New Phytology* 86: 245–259.

Sokal, R., and F.J. Rohlf. 1995. *Biometry.* W.H. Freeman and Company, New York.

Sternberg, L., M.J. Deniro, and J.E. Keeley. 1984. Hydrogen, oxygen, and carbon isotope ratios of cellulose from submerged aquatic crassulacean acid metabolism and non-crassulacean acid metabolism plants. *Plant Physiology* 76: 68–70.

Stone, D.Z. 1977. *Pre-Columbian Man in Costa Rica.* Peabody Museum Press, Cambridge, MA.

Street-Perrott, F.A., Y. Huang, R.A. Perrott, and G. Eglinton. 1998. Carbon isotopes in lake sediments and peats of last glacial age: implications for the global carbon cycle. In Griffiths, H. (*ed.*), *Stable Isotopes*. BIOS Scientific Publishers Ltd, Oxford. Pp. 381–396.

Street-Perrott, F.A., Y. Huang, R.A. Perrott, G. Eglinton, P. Barker, L.B. Khelifa, D.D. Harkness, and D.O. Olago. 1997. Impact of lower atmospheric carbon dioxide tropical mountain ecosystems. *Science* 278: 1422–1426.

Stuiver, M. 1975. Climate versus changes in ^{13}C content of the organic component of lake sediments during the late quaternary. *Quaternary Research* 5: 251–262

Stuiver, M., and P.J. Reimer. 1993. Extended C-14 database and revised Calib 3.0 C-14 age calibration program. *Radiocarbon* 35: 215–230.

Stuiver, M., P.J. Reimer, E. Bard, J.W. Beck, G.S. Burr, K.A. Hughen, B. Kromer, G. McCormac, J. van der Plicht, and M. Spurk. 1998. INTCAL98 radiocarbon age calibration, 24,000–0 BP. *Radiocarbon* 40: 1041–1083.

Sukumar, R., R. Ramesh, R.K. Pant, and G. Rajagopalan. 1993. A δ^{13}C record of late Quaternary climate change from tropical peats in southern India. *Nature* 364: 703–705.

Talbot, M. R., and T. Johannessen. 1992. A high resolution palaeoclimate record for the last 27,500 years in tropical West Africa from the carbon and nitrogen isotopic composition of organic matter. *Earth and Planetary Science Letters* 110: 23–37.

Thompson, L.G. 2000. Ice core evidence for climate change in the tropics: implications for our future. *Quaternary Science Reviews* 19: 19–35.

Thompson, L.G., E. Mosley-Thompson, M.E. Davis, P. -N. Lin, K.A. Henderson, J. Cole-Dai, J.F. Bolzan, and K. -b. Liu. 1995. Late glacial stage and Holocene tropical ice core records from Huascaran, Peru. *Science* 269: 46–50.

Tieszen, L.L., and S. Archer. 1990. Isotopic assessment of vegetation changes in grassland and woodland systems. In Osmond, C.B., L.F. Pitelka, and G.M. Hidy (*eds.*), *Plant Biology of the Basin and Range*. Springer-Verlag, Berlin. Pp. 293–321.

Wille, M., H. Hooghiemstra, H. Behling, K. van der Borg, A.J. Negret. 2001. Environmental change in the Colombian subandean forest belt from 8 pollen records: the last 50 kyr. *Vegetation History and Archaeobotany* 10: 61–77.

Wright, H. E., Jr., D.H. Mann, and P.H. Glaser. 1984. Piston corers for peat and lake sediments. *Ecology* 65: 657–659.

Yoshioka, T., E. Wada, and H. Hayashi. 1994. A stable isotope study on seasonal food web dynamics in a eutrophic lake. *Ecology* 75: 835–846.

APPENDIX

APPENDIX

PREPARATION OF MODERN POLLEN REFERENCE MATERIAL

This procedure is used to extract pollen grains from flowers or anthers from modern plant samples (living plants or herbarium specimens). Six samples are processed at a time in 15 ml polypropylene test tubes. All procedures should be done under the fume hood. We use an IEC tabletop centrifuge at ~2500 rpm. This procedure is done in a separate wet lab and all required beakers, test tubes, and sieves are used only for processing reference samples, to prevent contamination of fossil pollen samples.

PROCEDURE:

1. Start boiling water, turn off air filter, and label vials.

2. Place samples (flowers/anthers) in 15 ml polyethylene test tubes.

3. Add 10 ml 5% KOH, stir, and place in boiling bath for 3 minutes.

4. Remove from bath and sieve through 125 μm screens into labeled beakers. Rinse tube with distilled water and squirt distilled water through the screen. Use a stick to gently break up the flower parts and anthers to release the pollen.

5. Centrifuge down the beaker contents. Repeatedly fill the correct tube with the beaker contents, centrifuge, and discard the decant, until the beakers are empty.

6. Add 10 ml distilled water, stir, centrifuge, and decant.

7. Add 10 ml glacial acetic acid, stir, centrifuge, and decant.

8. Run acetolysis (add 1 part sulfuric acid to 9 parts acetic anhydride – for 6 tubes add sulfuric acid to 54 ml acetic anhydride to make 60 ml of solution). Add 10 ml of the acetolysis solution to each tube, stir, place tubes in boiling water bath for 3 minutes, centrifuge, and decant.

9. Ad 10 ml glacial acetic acid, stir, centrifuge, and decant.

10. Add 10 ml distilled water, stir, centrifuge, and decant for a total of TWO washes.

11. Add 1 drop Safranin stain, vortex stir for 10 seconds, then add 10 ml distilled water, stir, centrifuge, and decant.

12. Add 10 ml TBA, stir, centrifuge, and decant.

13. Vortex stir samples for 10 seconds, then transfer to corresponding vial. Add a couple drops of TBA to the tubes, vortex stir again, and transfer the remaining sample to the vial. Put corks on vials, centrifuge, and decant (remembering to put the capped glass bottles in the centrifuge below the sample vials).

14. Add two drops of silicone oil, stir sample with a toothpick, and leave container open overnight in the cabinet to allow the TBA to evaporate.

15. Clean lab, empty chemical waste bucket, and refill chemical squirt bottles.

VITA

Chad Steven Lane was born in Santa Maria, California on June 16th, 1979. He graduated from Eaglecrest High School in Aurora, Colorado in 1997. He then attended the University of Denver in Denver, Colorado where he graduated in 2001 *magna cum laude* with a Bachelor of Science degree in Environmental Sciences and with a minor in Physics. He became interested in paleoecology, paleoclimatology, and biogeography while conducting research at the University of Denver with his advisor Dr. Donald Sullivan. This research focused on lacustrine sedimentary records of climate and vegetation change over the last 20,000 years from western Colorado. Chad entered the graduate program in geography at the University of Tennessee in 2001 to study paleoecology and paleoclimatology in Costa Rica.

While at the University of Tennessee, Chad was a research assistant with the Global Environmental Change Research Group, which includes faculty from the departments of Geography, Geological Sciences, and Ecology and Evolutionary Biology. As a research assistant, Chad participated in several research projects in addition to the project described in this thesis. He analyzed the potential for using stable carbon isotopes in sediment records as a proxy for prehistoric agriculture and tropical forest clearance in the Costa Rican lowlands. He also helped to develop a method for the controlled laboratory production of reference charcoal. In addition to his laboratory work, Chad also assisted his advisor Dr. Sally Horn and committee member Dr. Kenneth Orvis with field work in the Dominican Republic in July 2002. Chad plans on continuing to pursue his interests in paleoecology, paleoclimatology, and biogeography into the future.