FOREST-USE HISTORY AND THE SOILS AND VEGETATION OF A LOWLAND FOREST IN BOLIVIA

By

CLEA LUCRECIA PAZ RIVERA

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To the memory of my grandfather Carlos Alfredo Rivera, whose love and inspiration have accompanied me through the years.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

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By

Clea Lucrecia Paz Rivera

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Land-use practices can dramatically affect soils and vegetation, even centuries after they cease. In Amazonia, soils enriched by nutrient and charcoal additions are indicators of ancient village sites and old agricultural plots. To ascertain whether past land-use practices also result in local enrichment with useful plants, I studied the anthropogenic soils and associated vegetation of a forestry concession in the Department of Santa Cruz, Bolivia. I compared the chemical properties of anthropogenic soils with surrounding soils and then compared the concentration of useful tree species on and off of anthropogenic soil areas.

Two types of anthropogenic soils were identified in the research area: *tierra negra* (TN) darkened with charcoal fragments and with abundant buried pottery shards; and *tierra morena* (MO), somewhat darkened but with little or no pottery. In an area of 216ha, nine TN soil patches (0.3 to 10 ha) and three MO soil patches were identified and compared with six nearby non-anthropogenic soils (inceptisols), which are referred to as

non-*tierra negra* (NTN). The abundance of seventeen useful tree species was measured in plots on the three soil types (TN, MO, and NTN).

Results of this study demonstrate that La Chonta's soils retain strong effects of past human activities that ceased 300 to 400 years ago, when the area was abandoned. The TN soils cover approximately 20% of La Chonta and are chemically different from the MO and NTN soils but all were circum neutral in pH, high in Ca content, and similar in total P. The TN soils had significantly higher contents of organic matter, extractable P, and extractable Ca than did NTN soils; and higher pH and extractable P than did MO soils. The MO soils had organic matter and Ca content similar to that of NTN soils and significantly less extractable K. Overall, TN soils had higher nutrient content than surrounding soils, both at the surface (0-10 cm) and deeper in the soil (40-50 cm).

Of the seventeen useful tree species studied, none were concentrated in TN areas. This unexpected result may be due to interactions between local dispersal agents and natural disturbances that masked historical patterns. Alternatively, past inhabitants of La Chonta may have managed or cultivated their useful tree species beyond anthropogenic soil areas. In any case, the influence of past land-use practices on plant species composition is not apparent in La Chonta.

CHAPTER 1
ANTHROPOGENIC SOILS OF A FORESTRY CONCESSION IN LOWLAND BOLIVIA

Introduction

Land-use history has played important roles in shaping modern landscapes and ecosystems. This study examines the history of the currently uninhabited timber concession of La Chonta, in the Guarayos Province of lowland Bolivia, and the effects of past land-use practices on its soil properties.

Humans are now recognized as having dramatically influenced Amazon Basin forests (Roosevelt et al. 1991, Denevan 1992b, Balée 1994, Smith 1999). Forests once considered pristine or virgin are increasingly viewed as resulting from regeneration after the cessation of human activities (Lentz 2000b). Human influences are to be expected, given that archeological studies reveal that humans were present in Amazonia at least 12,000 years ago (Roosevelt et al. 1991). Although hotly debated, estimates of pre-Columbian population density in Amazonia are all high. For example, Dobyns (1966) estimated 6 million for all of tropical South America, whereas Denevan (1992a) estimated a population of 8.6 million in lowland South America alone, a number that declined by 90% within 100 years after European contact. pre-Columbian societies in the Amazon have affected the region at all scales up to the landscape level, through constructing raised fields, earthen causeways, and hydraulic earthworks (Denevan 1966, 2001, Lippi 1988, Erickson 2000, Roosevelt 2000) as well as through use of more subtle forest-management practices (Posey 1985, Balée 1994, Denevan 1998, Peters 2000).

Past human disturbances may have influenced several attributes of present-day Neotropical landscapes (Balée 1994, Lentz 2000a). For example, Peters (2000) and Erickson (2000) working in Central American forests and Amazonian savannas respectively, showed that modern vegetation in their study sites was greatly altered by direct and indirect enrichment by pre-Columbian societies. Direct enrichment of useful plant species occurred through manipulations such as planting or thinning, while indirect enrichment was the creation or alteration of habitats such as those conducive to colonization by early successional species.

Despite the extent of landscape alterations by pre-Columbian societies, land-use history in dynamic tropical ecosystems can be difficult to unravel because ecological processes such as bioturbation, heavy rainfall, and rapid plant growth can obscure evidence of earlier human activities (Stahl 1995). Nevertheless, soils generally reflect human-induced alterations for long periods of time and therefore can serve as useful indicators of past land-use practices (Glaser 2002).

In Amazonia, dark anthropogenic soils (referred to as *tierra negra* in Bolivia, and *terra preta* and *terra preta do Indio* in Brazil) occur in patches from 0.5 to 300 ha, typically embedded in a matrix of infertile soils (mainly oxisols and ultisols). *Terra preta* are defined by a distinctive anthropogenic epipedon with intermixed potsherds and celts (Sombroek 1966, Smith 1980, Woods et al. 2000, Glaser et al. 2001). High organic matter and elevated nutrient contents (especially phosphorous, calcium, potassium, and sodium) distinguish the Amazonian anthropogenic soils from those in their surroundings (Smith 1980, Woods et al. 2000, Glaser et al. 2001, McCann et al. 2001).

Although the origin, distribution, and use of Amazonian anthropogenic soils are still unclear, it seems that fire was the most important factor in their formation (Woods et al. 2000). Apparently incorporation of charcoal (black carbon) and wood ash increases nutrient retention capacity, cation exchange capacity (CEC), and soil pH (Woods et al. 2000); ant it stabilizes soil organic matter (SOM) while reduces nutrient leaching from soils (Glaser et al. 2000 and 2001). Charcoal is also extremely resistant to weathering and can persist in soil for millennia (Rainho Texeira et al. 2002), thereby contributing to the maintenance of anthropogenic soil properties through time. The second factor related to the formation of these soils was the incorporation of household waste, such us food remains, shells, bones, feces, blood, and urine, all of which increased soil nutrient content (Smith 1980, McCann et al. 2001).

Initially, anthropogenic soils were reported on floodplains, especially on river bluffs along the main Amazon river (Sombroek 1966, Smith 1980). More recently, large areas of *terra preta* have been reported in *terra firme*, or upland forests (Heckenberger et al. 1999), and in floodplains along tributaries of the Amazon river (McCann et al. 2001). In any case, most of the reported occurrences of anthropogenic soils in South America to date are near permanent sources of water.

Two kinds of anthropogenic soils, *terra preta* and *terra mulata,* have been described as being clearly distinguishable in Brazil (Sombroek et al. 2002). *Terra preta* appears in former human settlements and, besides being enriched in nutrients and charcoal, is always associated with pottery and cultural debris (Smith 1980, Heckenberger et al. 1999). *Terra mulata* is thought to have developed in permanent agricultural fields, enriched by long-term soil-management practices such as mulching and infield burning (Denevan 1996, Woods et al. 2000, McCann et al. 2001). Despite some recent advances in our understanding, the nature and characteristics of pre Columbian agriculture that originated *terra mulata* still remain little known.

High nutrient levels of anthropogenic soils and the different ways vegetation was managed in and surrounding these areas are expected to influence the vegetation that either persists or colonizes the sites after their abandonment. In any event, it is obvious that the original vegetation in these areas was substantially modified by humans, and that certain species were either favored or introduced from other areas, perhaps permanently altering local species composition.

This study has two objectives. The first is to reconstruct the history of the Guarayos area through review of bibliographic sources. The second is to describe the anthropogenic soils of La Chonta and compare soil properties between anthropogenic and surrounding soils.

History of Study Area

Unraveling the history of human activities can help us understand the soils, vegetation, landscape, and successional patterns in modern ecosystems (Glenn 1999). Given that there are few published historical accounts of Guarayos, colonial archives and historical reports from nearby regions were used to reconstruct its probable land-use patterns and settlement history (Orbigny 1835, Cardús 1886).

Guarayos is a biological and cultural transitional region with influences from the humid forests of Amazonia to the north, the drier forests of Chiquitos (Chiquitania) and Chaco to the southeast, and the savannas of Mojos (Moxos) to the west (Figure 1-1). Both Mojos and Chiquitos were explored and settled by Europeans earlier than Guarayos and as a result there is relatively more historical information about them, but the histories of the three regions are intertwined.

Although the Swedish anthropologist Erland Nordenskiöld excavated in Guarayos in the early twentieth century (Nordenskiöld 1930), the secondary urn burials (urns containing fleshless bones) he unearthed have apparently not been dated. I am aware of no other pre-contact archeological data. Early reports from European explorers and missionaries provide the only descriptions of cultural and ecological conditions following European contact.

The Guarayos region is believed to have been inhabited by the Guarayo Indians, who likely migrated from Paraguay and inhabited the Guarayos region since at least 1400 (Orbigny 1835, Cardús 1886). The Guarayo language is of the Tupi-Guaraní family and is closely related to Guaraní (Cardús 1886), spoken by the Guaraní Indians who historically inhabited the Chaco region of southeastern Bolivia and northern Argentina and Paraguay. Despite their common language, the Guarayo and Guaraní have marked cultural and physical differences, suggesting that if the two groups were once more closely related, their separation took place long before European contact (Finot 1939).

Spaniards

The region now referred to as Guarayos and inhabited primarily by the Guarayo was probably first encountered by Europeans during a Spanish expedition that set out from Asunción, Paraguay in the 1540s. The objective of this and numerous similar explorations was to find the *tierra ricas* of indigenous legends that described the treasures and gold of *El Dorado*, *El Gran Paititi,* or *El Gran Mojos,* this last believed at one time to be located north of Chiquitos (Finot 1939).

Apparently the first expedition to pass through the Guarayos region was led by the Spanish captain Ñuflo de Chávez, who left Asunción in 1558 with 150 Spanish soldiers and 1500 Guaraní Indians. His mission was to establish a new town in the Xarayes marshes (located in Mato Grosso, Brazil, and southeastern Bolivia) but upon arrival, he found the area unsuitable for settlement and decided to continue the expedition, traveling west and northwest in search of *El Dorado*. Although maps that reconstruct Ñuflo de Chávez's expeditions show the route passing through Guarayos region, there is no direct mention of Guarayo people in the chronicles of the trip, contrasting with the extensive description of surrounding indigenous groups such as Chiquito, Chiriguano, Mojo, and others (Levillier 1976).

According to the interpretation of Levillier (1976), Chávez encountered the Guarayo indians north of latitude 16º South when he was attacked by an unidentified indigenous group living at a heavily fortified settlement. Chávez, uncertain of victory, turned away from the settlement and returned to Chiquitos.

In the late 17th century the Spaniards approach to conquest shifted from one of broad exploration to a more systematic effort at populating areas where they had been able to establish a presence. Because of its distance from Santa Cruz de al Sierra, the Guarayos region was not colonized and there is little mention of the area until the 18th century.

Missionary Activity

Religious missionaries entered South America with objectives quite different from those of the explorers—in place of gold they sought the souls of indigenous *infieles*. Unlike the explorers, who in most cases passed quickly over through the landscape, missionaries had sustained contact with local people. Jesuit missionaries arrived on the continent in the late 1500s and in the Bolivian lowlands the first *reducciones* (Jesuit and Franciscan missions) were established roughly a century later. In Mojos, the first mission (Loreto) was established in 1682; San Francisco Javier in Chiquitos was established in 1691.

Between 1700 and 1845, there were five attempts, first by Jesuits and later by Franciscans, to establish *reducciones* among the Guarayo. The first four failed at retaining significant numbers of people. It was only later (1845) that thousands of Guarayo were concentrated in several towns in the region, including the present-day capital, Ascención, founded by Franciscans in 1826.

Population Density

There are apparently no published estimates of population density in Guarayos before the missionary period. Nevertheless, as mentioned above, several lines of evidence indicate that the native population was high in pre-Columbian times. For example, near Guarayos in the savannas of Mojos, Jesuit missionaries reported 37 related yet distinct indigenous groups in 1696 (Chávez 1986). Denevan estimated a native population of 350,000 in the same region and calculated that that number decreased to 100,000 by the 1690s as a consequence of epidemic diseases (Denevan 1992a).

Spanish chronicles of expeditions from Paraguay to Santa Cruz and Mojos in the late 1500s and early 1600s reported encounters with hundreds of indigenous groups. Reports from this time stated that the Guaraní and Guaraní-related groups, including Chiriguano, Sirionó, and Itantines, tended to be the more populous and bellicose (Finot 1939, Pinckert-Justiniano 1991).

After Gregorio Salvatierra, a Franciscan missionary, visited four mission towns in 1794 (Asención, Yaguarú, Yotaú and Urubichá), he estimated a population between 3000 and 4000 in the region (Cardús 1886). D'Orbingy, who visited Asención de Guarayos in 1831, estimated 1,000 Guarayo Indians in the area (Orbigny 1835). During the mission period, the Jesuits concentrated hundreds of families in towns, but they repeatedly reported the existence of many "wild" Guarayo living in the forest who maintained only sporadic contact with people living in towns. The Jesuits carried out several recruitment expeditions into forested areas and reported dispersed families along their route and returned with groups of varied sizes, the last (1825) returning with 200 Guarayo (Cardús 1886).

The population estimates of D'Orbigny and Salvatierra were likely gross underestimates because they were based only on the established mission settlements, and did not include people dispersed through the forest. It also seems relevant to note that these censuses were carried out more than 200 years after the arrival of Europeans to the region, when populations were probably greatly diminished by introduced diseases such as smallpox and the flu. The impact diseases brought by Europeans was reported in Chiquitos by D'Orbigny who noted that half of the Chiquitano residing in San Javier died from smallpox in 1825. Similarly Cardús mentioned that a "malignous fever" attacked and killed hundreds of Guarayo in 1845.

Land and Resource Use

Archaeologists and ecologists are currently trying to understand land-use practices prior to European contact. Descriptions by Jesuits and Franciscans, admittedly biased by their belief that indigenous peoples were ignorant savages, and reports by D'Orbingy, provide the earliest reports of the land-use practices and customs. Unfortunately, the land-use practices they described already reflected European influences, the most important of these being the introduction of metal tools. Metal tools are several times more efficient for cutting trees than stone tools (the ratio varies from 10 to 1 to 23 to 1, Denevan 1992c), allowing faster forest clearing, and the development of long fallow shifting cultivation. Due to the inefficiency of stone axes, some authors claim that pre-Columbian agriculture was based in home gardens and permanent crop fields instead of modern shifting cultivation with short cropping periods followed by long forest fallows, which would be too labor intensive to be a common agricultural practice (Denevan 1998).

D'Orbigny, who visited Asención de Guarayos in 1823, provides the first description of anthropogenic soils, reporting "black fields ready to be planted". After his arrival he described the Guarayo living in mission towns with the Franciscans as having maintained more of their customs and otherwise were less influenced by Europeans than the Chiquitano. D'Orbigny asserts that agriculture was their main food producing activity, and that hunting was more of a past time than an essential activity (this contradicts the missionaries descriptions, who assert the Guarayo were mainly hunters). D'Orbigny's claims, however, are corroborated by the great number of religious ceremonies devoted to *Tamoi* (grandfather), the most important god of the Guarayo, who was believed to have taught them agriculture. When D'Orbigny arrived in the region, the Guarayo had a well-developed shifting cultivation system centered on squash, corn, yucca, papaya, pineapples, and sugar cane (an old world crop introduced by the Jesuits in the early 1800s) , using metal axes. Agricultural fields were managed by the whole community while they lived divided in small families in octagonal-shaped cabañas roofed with palm leaves, similar to those used by the Caribe of Central America. They reportedly planted near the houses a sacred tree called *turienda* (apparently *Ceiba pentandra*), which they claimed was used by their gods to come down and take them when they died. They wore clothes made of the bibosi tree bark (*Ficus* spp.) and painted their bodies with achiote (*Bixa orellana*; Orbigny 1835).

Cardús, a Franciscan missionary who visited the area between 1883 and 1884, provides a similar description of the Guarayo agricultural system (Cardús 1886). He described low, forested, rolling hills intermixed with forested wetlands to the south, extensive, flat, lowland forests to the north, and to the west, beyond several *leguas* (leagues, approximately four to seven kilometers) of forest, began the huge savannas of Mojos region. He also observed that the Río Blanco (Figure 1-1), was navigable to Carmen del Mojos whereas today, the river is navigable only seasonally, and then by small canoe. Cardús described the Guarayo as primarily hunters and fishers, with their principal crops being corn, yucca, plantain (an old world crop), beans, peanuts, and squash. Spider monkey was their preferred meat and *chicha*, a fermented beverage made of corn or yucca, was their most common beverage.

The different views on human cultures and ecology in the Guarayos region provided by early explorers, missionaries, and scientists, offer an opportunity to consider the dramatic changes that took place over the previous centuries. Although Guarayos was at first a region on the periphery of European activities in Bolivia, it was still affected, finally to a large degree, by the arrival of explorers and missionaries. Unfortunately, the accounts of D'Orbigny, Cardús, and others begin at least two centuries after the arrival of Europeans to the region, sufficient time for forests to regenerate on abandoned sites following the massive indigenous population declines that occurred throughout the Americas (Denevan 1992a, Block 1994). This lapse in time prevents us from understanding pre-colonial landscapes that may have been quite different from those D'Orbigny, Cardús, and others observed. For instance, if native populations were large before contact, the landscape was likely much less forested than it was more than a century after the population crash.

Study of the anthropogenic soils of La Chonta affords an opportunity to piece together the past at a much different level of detail than that made possible by historical and religious records. It allows us to estimate the area of long-abandoned settlements or cultivated plots, and the effects of human induced soil alterations on soil chemistry and plant species composition.

Methods

Study Site

This study was conducted in La Chonta, a lowland tropical forest in Guarayos Province, Department of Santa Cruz, Bolivia (15°47'S, 62°55'W, Figure 1-1). A 100,000 ha private timber concession since 1974, the area was selectively logged for mahogany *(Swietenia macrophylla*) and tropical cedar (*Cedrela odorata*) for the first decade after its establishment. When mahogany was depleted, the focus shifted to other species and today loggers extract up to a dozen species. La Chonta was certified by the Forest Stewardship Council as well managed in 1998. A long-term silvicultural research project was started in La Chonta in 2000 as part of the BOLFOR Sustainable Forest Management Project (Putz et al. *in press*).

The vegetation of La Chonta is classified as subtropical humid forest (Holdridge 1971), with mean annual temperature of 24.5°C and mean annual rainfall of ca. 1500 mm. The canopy is semideciduous and fairly open, with heights of mature forests of 20 to 25 m. Common canopy tree species are characteristic of humid forests and include *Hura crepitans* and *Pseudolmedia laevis* (Navarro and Maldonado 2002). Lianas are abundant and dominate disturbed areas (Alvira et al. 2003). The area has a long history of both human-induced and 'natural' fires, but there were no signs of recent fires in my study area. The region has numerous ephemeral streams, and the rivers Blanco and Negro border the peripheries of the concession (Figure 1-1).

Soil Sampling and Analysis

An area of 216 ha was surveyed for anthropogenic soils by sampling at 200 m intervals along walking trails separated by 150 m. The trails delimit research plots in La Chonta and are kept clear of vegetation; changes in soil color and type were easily recognized. Surface soil was cursorily examined and soil color was recorded using a Munsell Soil Color Chart. When soil color darkened markedly, sampling intervals were reduced to 100 m and examined more thoroughly for charcoal and pottery.

Soils were classified as *tierra negra* (TN) when extremely dark in color (7.5 YR 3/1 and 2.5/1; dark brown and very dark brown) and both charcoal and pottery sherds were present. Soils that were somewhat darkened (7.5 YR 4/3 - 3/2, brown to dark brown) but with little or no pottery were classified as *tierra morena* (MO). Soils with no apparent indicators of anthropogenic influences were classified as non-*tierra negra* (NTN), and are tentatively classified as inceptisols (Navarro 2002). When TN soils were encountered, their area was estimated by sampling in the four cardinal directions every 20 m with a soil auger until the patch limits were identified. Patch locations were recorded with a handheld Garmin GPS.

Soil samples were taken from each of the TN and MO patches, and the surrounding NTN soils. From the approximate center of each patch, soil samples were taken at two depths (0-10 and 40-50 cm) at the corners of a 10x10 m square. Samples from each of the depths were mixed together and 200 g of each was air dried in the field and stored for laboratory analysis.

As a preliminary archaeological assessment of the area, one test pit ($1x1m^3$) was excavated in the central area of each TN site to quantify the abundance of pottery sherds and to determine the depth of the TN soils. During the early phase of this study, two large charcoal fragments that were found intermixed with abundant pottery sherds at 10 and 20 cm depths in an anthropogenic soil patch (*tierra negra 3* Table 1-1) were submitted to Beta Analytic Laboratory for accelerator mass spectrometry (AMS) radio-carbon dating.

In the laboratory, soil organic matter was estimated using the weight loss on ignition method (Nelson 1996). Total phosphorous (P) was measured colorimetrically after sulfuric acid digestion (Olsen and Sommers 1982). Extractable phosphorous was measured colorimetrically after a Mehlich double-acid solution (Olsen and Sommers 1982). Finally, extractable calcium (Ca), magnesium (Mg), and potassium (K) were assayed using atomic absorption (AA) following extraction in a Mehlic double-acid solution (Thomas 1982). To compare soil types, the chemical data were analyzed with a two-way ANOVA model using soil type (TN, MO and NTN) and depth as factors and sites as replicates.

Results

Area, Shape, and Location of Anthropogenic Soil Patches

In an area of 216 ha, nine patches of *tierra negra* (TN, Table 1-1, Figure 1-2), three patches of *tierra morena* (MO), and six nearby (within 1 km) areas of non-*tierra negra* (NTN) soil were identified. The TN patches were commonly located on flat terraces within 200 m of streams that at least flow during the rainy season (Figure 1-3). TN patch sizes varied in La Chonta and were grouped in two categories: small circular patches

(0.3-2.5 ha), and larger, irregular patches (5-10 ha). Mapping of the larger areas was not completed because they extended past the perimeters of the research plots. Within TN sites, I found areas with higher concentration of charcoal and pottery sherds, probably corresponding to kitchen middens (S. Palma, *unpublished data*). The cumulative area of the most prominently affected anthropogenic soils (TN) accounts for approximately 20% of the study area (Table 1-1, Figure 1-2). The patches of MO were 0.3-1.0 ha and tended to surround the TN sites (Figure 1-3). I did not quantitatively measure areas of MO but estimate them to cover an additional 5% of the area.

The preliminary archaeological investigations carried out in TN soil pits revealed distinguishable layers, defined by abundant pottery sherds and charcoal, which differed between the small and large patches. In both patches sizes the surface 10 cm were dark in color but usually contained no pottery and charcoal, with the exception of areas disturbed by animals or roads. The small patches (0.3-1 ha) in general had one continuous stratum of dark soil from 10 to 30-45 cm depth with intermixed charcoal and pottery whereas the larger patches generally had two separated layers with anthropogenic traces, one at 10-40 cm depth and other at 45-75 cm depth. The 5 cm separation between the two anthropogenic layers in the large patches consisted of a layer of sandy-loam soil with large quartz crystals.

The density of buried pottery sherds in the intensively inventoried soil pits varied from 19 to 187 pieces per m^3. I also found solid pieces of macroscopic black carbon (between 1 and 5 cm size) from 10 to 75 cm soil depth in both the small and large patches. The two charcoal fragments found mixed with pottery in *tierra negra* site 3 at 10 and 20 cm below the surface were AMS dated from 330 ± 80 to 420 ± 60 years BP respectively.

Soil Chemistry

The pH of soils in La Chonta were all high, averaging 7.2 in the TN soils, 6.4 in the MO soils and 7.2 in the NTN (Table 1-2); pH was significantly higher in TN and NTN soils than in the MO soils ($P < 0.006$, Figure 1-4a). Organic matter content at 10 and 50 cm depth averaged 5.7% and 2.6% in TN soils, 4.8% and 2.1% in MO soils, and 4.7% and 2.1% in NTN soils, being significantly higher in the TN soils than the NTN soils ($P < 0.039$, Figure 1-4b).

Total phosphorous was relatively high in all three soil types while extractable phosphorous was relatively low. Total P was not significantly different among the three soil types and averaged 155±22-358±8 (Table 1-2) Extractable P content averaged 49.65 and 35.92 mg/kg (at 10 and 50 cm respectively) in TN soils, being significantly higher than MO soils at both depths and significantly higher than NTN at 50 cm ($P < 0.015$, Figure 1-4c).

Extractable Ca was extremely high in all La Chonta soils, averaging (at 10 and 50 cm depths, respectively) 3179 and 1428 mg/kg in TN soils, 1975 and 587 mg/kg in MO soils and 2435 and 805 in NTN soils, being significantly higher in TN soils than NTN and MO soils ($P < 0.002$, Figure 1-4d). Extractable K was significantly higher in NTN soils and TN soils when compared to MO soils ($P < 0.015$, Figure 1-4e), averaging 94.36 and 62.54 mg/kg in TN soils, 57 and 28.39 mg/kg in MO soils, and 91.82 and 55.24 mg/kg in NTN soils (at 10 and 50 cm, respectively).

All of the soil properties tested, with the exception of pH and total P, were significantly higher at 10 cm than at 50 cm depth (Table 1-3). Organic matter content, extractable P and extractable Ca were significantly higher in TN than MO and NTN at 50 cm depth ($P < 0.015$, $P < 0.001$, and $P < 0.0001$ respectively, Figure 1-4b, c, and d). Overall, the transitional MO soils had lower nutrient concentrations than NTN soils.

Discussion

Area, Shape, and Location of Anthropogenic Soil Patches

In contrast with the majority of anthropogenic soil areas in the Amazon Basin (Sombroek 1966, Smith 1980, Heckenberger et al. 1999, Woods et al. 2000, McCann et al. 2001), the anthropogenic soils of La Chonta are located in an area lacking big rivers or wetlands. In fact, researchers and logging crews currently working in the area are faced with the hardship of bringing barrels of water long distances to their camps. The closest rivers, Río Negro and Río Blanco, are 14-30 km from the TN areas I mapped (Figure 1-1) and the water flow in La Chonta streams has ceased completely during the latter portions of the dry seasons (between May and October). Ancient village sites in the Brazilian Amazon described to date are mostly associated with large rivers (Roosevelt 1989, Smith 1980, McCann et al. 2001). However, a large *terra preta* site (200 ha) relatively far away from rivers (15 kilometers from the Amazon River floodplain) was reported in Comunidade Terra Preta, at km 55 of the Juriti-Tabatinga road in Pará, Brazil (Smith 1999, p. 25). Further detailed analyses of the archaeology, pollen, and phytoliths in La Chonta are needed to determine if the water regime was the same when the area was last inhabited, and how the former inhabitants managed to provide themselves enough water to survive, given that I found no evidence of prehistoric wells or dams.

The processes of settlement, abandonment, and reoccupation of the large patches of TN may help explain the great differences in patch size. Apparently the larger patches (5-10 ha) were occupied more than once (S. Palma, *unpublished data*), which makes the size of the patches an inaccurate indicator of village size, as suggested by Meggers (1995) for TN areas in the Brazilian Amazon. Alternatively, the larger patches could represent old agricultural plots in which forms of indigenous agriculture not currently used may have been practiced. Denevan (1992c), for example, suggests that management of house gardens and permanent plots of mixed annuals and perennials were common indigenous pre-Columbian agricultural practices. Nevertheless, more archaeological research is needed to determine precisely the land-use practices carried in the large areas of TN and MO.

The two C-14 dates for charcoal that was mixed with pottery at 10 and 20 cm depth suggest *tierra negra* site 3 was inhabited between 300 and 400 years B.P, but do not indicate the prior duration of settlement. However, charcoal and pottery were present at deeper in the soil (to 75 cm) in other TN sites, consequently, a series of soil charcoal C-14 dates along several soil excavation units replicated in different archaeological sites in the area will be necessary to establish more precisely the sequence of human occupation of La Chonta.

In this study, charcoal was found at greater depths than those Glaser et al. (2000) reported in Brazil (30-40 cm depth). However, charcoal, presumably from wild fires, is commonly reported to one meter depth in neotropical forests soils (Saldarriaga et al. 1988, Horn 1992). The presence of charcoal and pottery sherds buried deep in the soil could also result from bioturbation, a process that is particularly strong in the tropics. In addition, repeated periods of afforestation and deforestation result in the burial of charcoal and pottery (Glaser et al. 2000).

Finally, *terra mulata* in Brazil have been described as large areas in which *terra preta* were embedded (Sombroek et al. 2002), but in La Chonta, MO areas appear to be smaller and only as a ring surrounding the TN areas. Further detailed mapping of MO areas in La Chonta are necessary to compare them with *terra mulata*, which is apparently the same sort of soil in Brazil.

Soil Chemistry

Perhaps the main difference between the *tierra negra* of La Chonta and *terra preta* soils reported in other parts of the Amazon Basin is the type of soils from which the soils are derived. All La Chonta soils have neutral pH contrasting with the typically acidic Amazonian soils (oxisols and ultisols). Therefore, even though reported pH values in Brazilian anthrosols (averaging 4.8-5.5; Smith 1980, Glaser et al. 2000, Sombroek et al. 2002) are higher than their surrounding oxisols, ultisols or inceptisols (< 4.8), they are much more acidic than the TN of La Chonta. The pH of TN of La Chonta was not significantly different from the NTN, which was also reported by Eden et al. (1984) for much more acidic *terra preta* and their surrounding inceptisols in Caquetá, Colombia (pH 4.3-4.8 for *terra preta* and 4.0-4.5 for inceptisols).

In La Chonta, soil organic matter (SOM) was significantly higher in TN soils than NTN soils, corresponding with the results of several other researchers working in the Brazilian Amazon (Smith 1980, Glaser et al. 2000, Sombroek et al. 2002). However, in La Chonta SOM did not differ between MO and NTN, contrasting with Brazilian *terra mulata,* which has higher SOM content, sometimes even higher that *terra preta* (Woods and McCann 1999, McCann et al. 2001, Sombroek et al. 2002).

Although total P is considered a good indicators of former human occupations (Eidt 1977), total P did not differ between TN, MO, and NTN in La Chonta. However, McGrath et al. (2001) had similar results, reporting no differences among Amazonian soils under different land-use practices (primary forest, secondary forest, and pasture; with values of total P ranging between 180 ± 41 to 231 ± 26 mg/kg).

In contrast with the results for total P, extractable P differed among the three soil types, being higher in TN than NTN and MO of La Chonta. The amounts of extractable P in TN (49.6 and 35.92 mg/kg at 10 cm and 50 cm respectively) were not as high as reported for *terra preta* in Brazil (358.1 and 619.2 mg/kg at 30 cm, Heckenberger et al. 1999; 175 mg/kg at 20 cm, Smith 1980; and 600 mg/kg, Woods and McCann 1999). While P is limiting in most tropical soils, occurring typically at less than 6 mg/kg (Kellman and Tackaberry 1997, McGrath et al. 2001, Fardeau and Zapata 2002), its presence at higher concentrations in TN, particularly deeper in the soil, positively influences soil fertility in TN. Not surprisingly, in present-day Brazil *terra preta* soils are valued as agricultural sites for both indigenous people and *mestizos*, and are sold in urban areas for spreading on yards to promote plant growth (Smith 1980).

Terra mulata has been reported as having slightly higher extractable P content than the surrounding non-anthropogenic soils in Brazil (McCann et al. 2001, Sombroek et al. 2002), but in La Chonta, MO soils had the same (at 50 cm) and less (at 10 cm) extractable P than NTN soils. One possible explanation for the relative lack of nutrients (particularly P and Ca) in MO soils may be that former inhabitants of La Chonta removed plant material and therefore nutrients from MO areas. Plant material may have been removed from the MO areas and incorporated into TN soils as green manure or through infield burning of vegetation. Certainly, the removal of plant material can locally diminish nutrients. However more studies in MO soils in La Chonta are necessary to test this hypothesis.

The high levels of Ca in the TN soils of La Chonta, coincide with those found by Heckenberger et al. (1999) (from 2626 to 3212 ppm at 20-50 cm depth) near the Negro and Xingu rivers in the Brazilian Amazon, and can be explained by additions of bones, shells, and the influence of ash deposition (Smith 1980, McCann et al. 2001). However, although significantly lower than in TN, extractable Ca was still very high for MO and NTN in La Chonta. These results can be explained by the nature of the parent material, in addition to the anthropogenic influences that might have affected MO and NTN areas, and require further study.

Implications of Anthropogenic Influences on La Chonta Forest

The large extent of anthropogenic soils in La Chonta should be taken into account by forest managers and researchers. The presence and extent of anthropogenic soils demonstrates that, in the past, the landscape of the region was dramatically different from what is found today and that the present forest developed in the wake of earlier human activities. This study, while not conclusive, shows that human settlements in La Chonta were quite large and of considerable duration. These settlements altered soil chemistry and their effects persist today.

Higher nutrient content deep in the anthropogenic soils of La Chonta are expected to strongly influence plant communities. The higher levels of extractable P in TN sites when compared with surrounding soils at 50 cm might be particularly influential. This difference is likely to be influencing present day plant species composition and growth.

In the future, careful studies of the larger TN areas, including comprehensive identification of concentrations of archaeological material, will be necessary to understand the ecological history of La Chonta at the landscape level. The present study concentrated on history and soil chemistry, which, integrated with additional archaeological studies, could contribute to a historical reconstruction of the area and a better understanding of current human-influenced landscapes.

In La Chonta, loggers should avoid disturbing archaeological sites until additional investigations are carried out. In addition, researchers should replicate experiments in areas with TN and NTN soils to understand the interactions between land-use history and the variables under examination. Interactions between TN soils and plant communities are still poorly understood and, considering the length of time needed for the formation of anthropogenic soils (1 cm/10 years, Smith 1980), silvicultural and research treatments that disturb TN soils should be minimized.

Table 1-1. Distribution of *tierra negra* (TN) sites in a 216 ha sample area

Site	Area	Geographic coordinates (UTM, zone 20)	
Tierra negra 1	2.4 ha	N 8266140	E 526015
Tierra negra 2	0.3 ha	N 8265393	E 525920
Tierra negra 3	1 ha	N 8265166	E 525950
Tierra negra 4	0.5 ha	N 8264084	E 521534
Tierra negra 5	10 ha	Not registered	
Tierra negra 6	10 ha	N 8267455	E 521670
Tierra negra 7	5 ha	N 8270277	E 520462
Tierra negra 8	1 ha	N 8269390	E 520130
Tierra negra 9	Undetermined	N 8263147	E524504

Table 1-2. Mean values (± one SE) of *tierra negra*, *tierra morena*, and non-*tierrra negra* soil properties at two depths (0-10 and 40-50 cm) with sites as replicates. Total P was measured colorimetrically after sulfuric acid digestion. Extractable P was measured colorimetrically, and Ca, Mg and K were measured and using atomic absorption (AA) after a Mehlich double-acid extraction

Soil property	*Tierra negra* (n = 10)		*Tierra morena* (n = 3)		Non- *tierra negra* (n = 6)	
	0-10 cm	40-50 cm	0-10 cm	40-50 cm	0-10 cm	40-50 cm
pH (in water)	7.3 ± 0.10	7.2 ± 0.10	6.6 ± 0.30	6.3 ± 0.30	7.3 ± 0.30	7.0 ± 0.20
% Organic matter	5.7 ± 0.40	2.6 ± 0.20	4.8 ± 0.80	2.1 ± 0.30	4.7 ± 0.30	2.1 ± 0.20
C/N ratio	10.77 ± 0.55	12.00 ± 0.64	10.23 ± 0.26	11.85 ± 0.07	10.13 ± 0.19	12.07 ± 0.32
Total P (μg/g)	203.17 ± 33.78	322.15 ± 41.33	170.62 ± 29.68	165.63 ± 53.74	155.31 ± 22.31	357.84 ± 88.12
Extractable P (mg/kg)	49.65 ± 16.36	35.92 ± 17.69	6.66 ± 1.44	2.84 ± 0.82	26.04 ± 9.82	4.34 ± 1.07
Extractable K (mg/kg)	94.36 ± 8.17	62.54 ± 7.92	57.00 ± 9.64	28.39 ± 6.42	91.82 ± 12.96	55.24 ± 8.86
Extractable Ca (mg/kg)	3179.75 ± 288.50	1428.95 ± 115.24	1975.96 ± 328.71	586.77 ± 161.63	2434.71 ± 333.62	805.14 ± 143.87
Extractable Mg (mg/kg)	87.00 ± 14.64	35.53 ± 3.75	58.18 ± 1.44	40.77 ± 7.17	60.12 ± 3.69	31.62 ± 5.77

Table 1-3. Statistical contrast of the three soil types at two depths

Soil property	Soils (*tierra negra*, *tierra morena,* and non-*tierra negra*)			Depth (0-10 cm and 40-50 cm)			Soils x Depth		
	df	F	P-value	df	F	P-value	df	F	P-value
pH (in water)	2	6.03	0.006	1	1.30	0.263	2	0.23	0.795
% Organic matter	2	3.60	0.039	1	72.91	< 0.0001	2	0.37	0.695
C/N ratio	2	0.21	0.812	1	8.63	0.006	2	0.24	0.791
Total P (ug/g)	2	1.55	0.230	1	5.81	0.022	2	1.53	0.234
Extractable P (mg/kg)	2	5.81	0.007	1	6.73	0.015	2	0.79	0.462
Extractable K (mg/kg)	2	4.83	0.015	1	12.64	0.001	2	0.06	0.942
Extractable Ca (mg/kg)	2	7.71	0.002	1	45.10	< 0.0001	2	0.18	0.834
Extractable Mg (mg/kg)	2	1.41	0.259	1	11.35	0.002	2	1.30	0.287

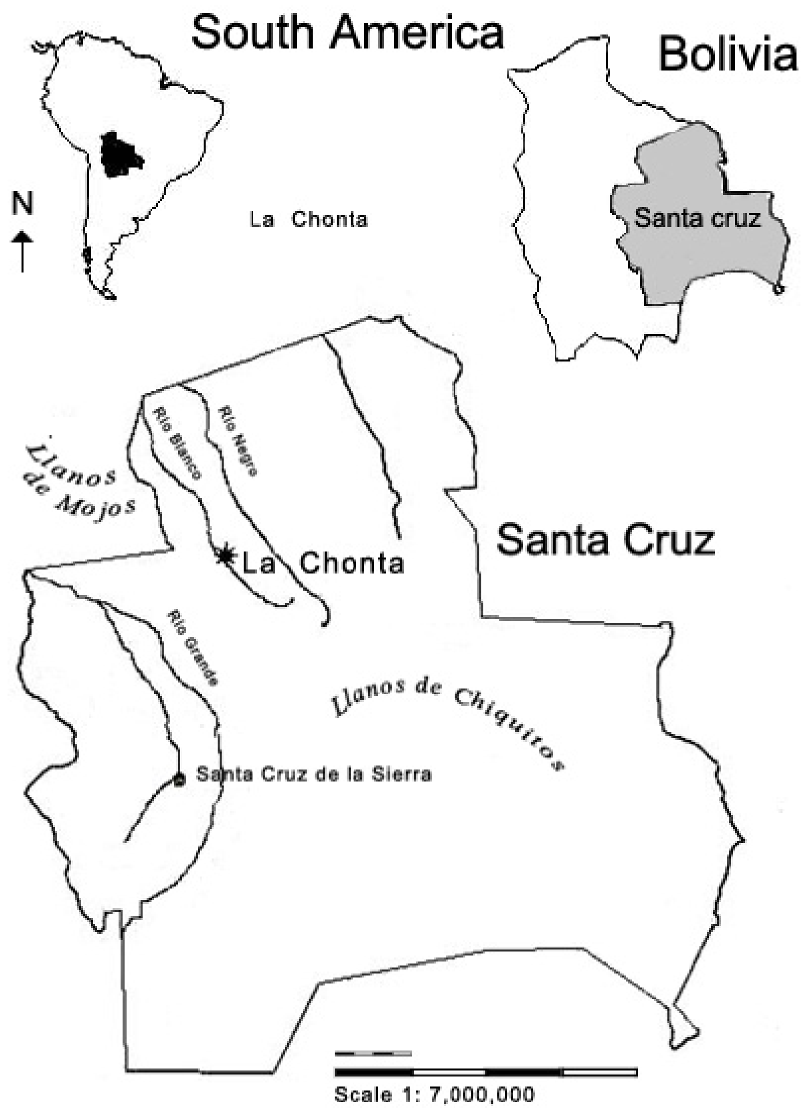

Figure 1-1. Location of the study site in lowland Bolivia

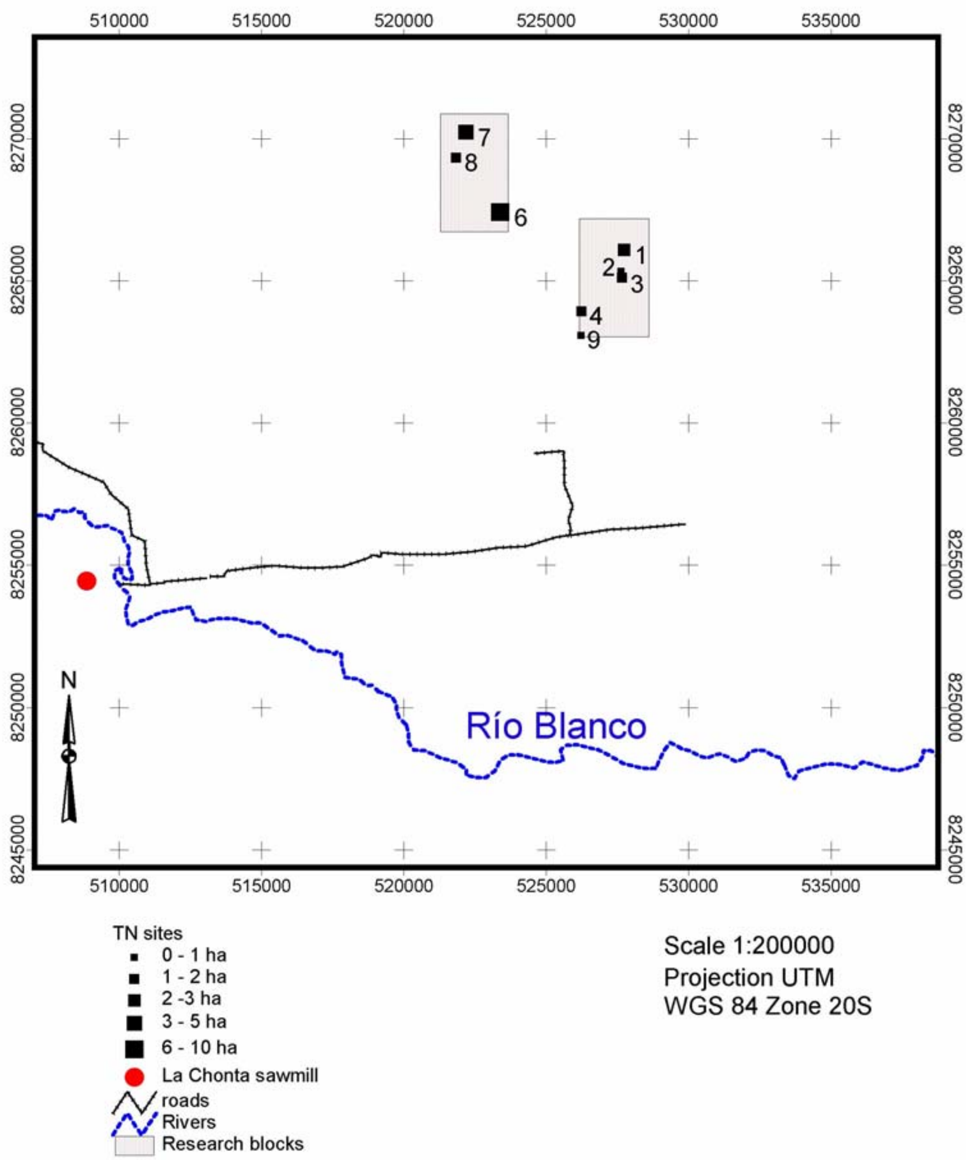

Figure 1-2. Location and size of the TN sites in La Chonta

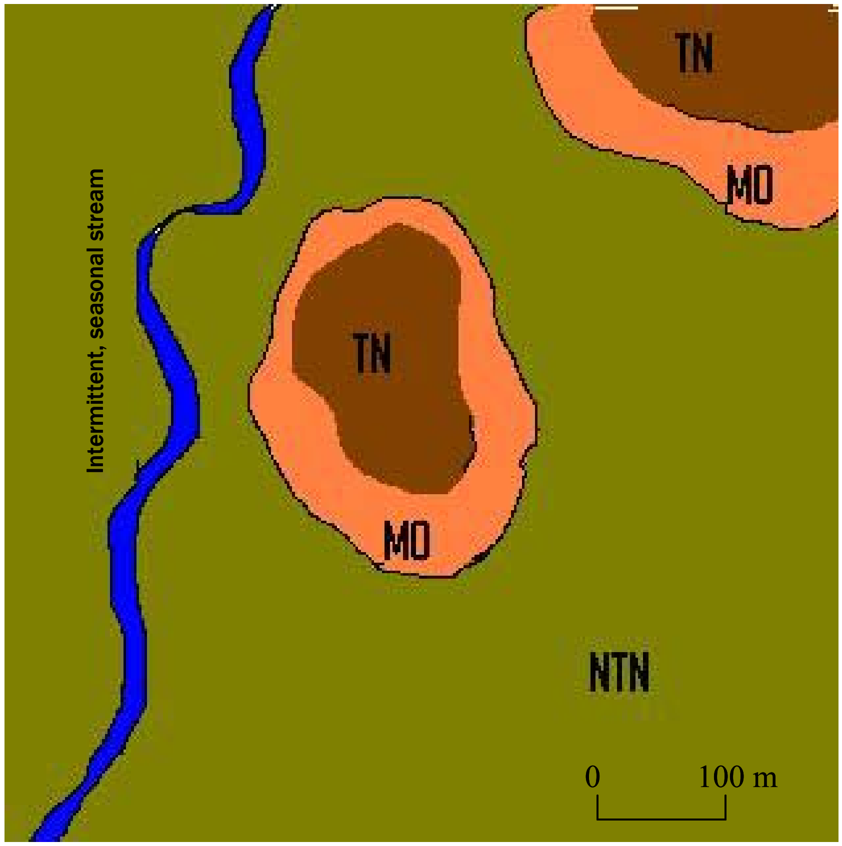

Figure 1-3. Spatial distribution of *tierra negra* (TN) in relation to *tierra morena* (MO) and *non-tierra negra* (NTN)

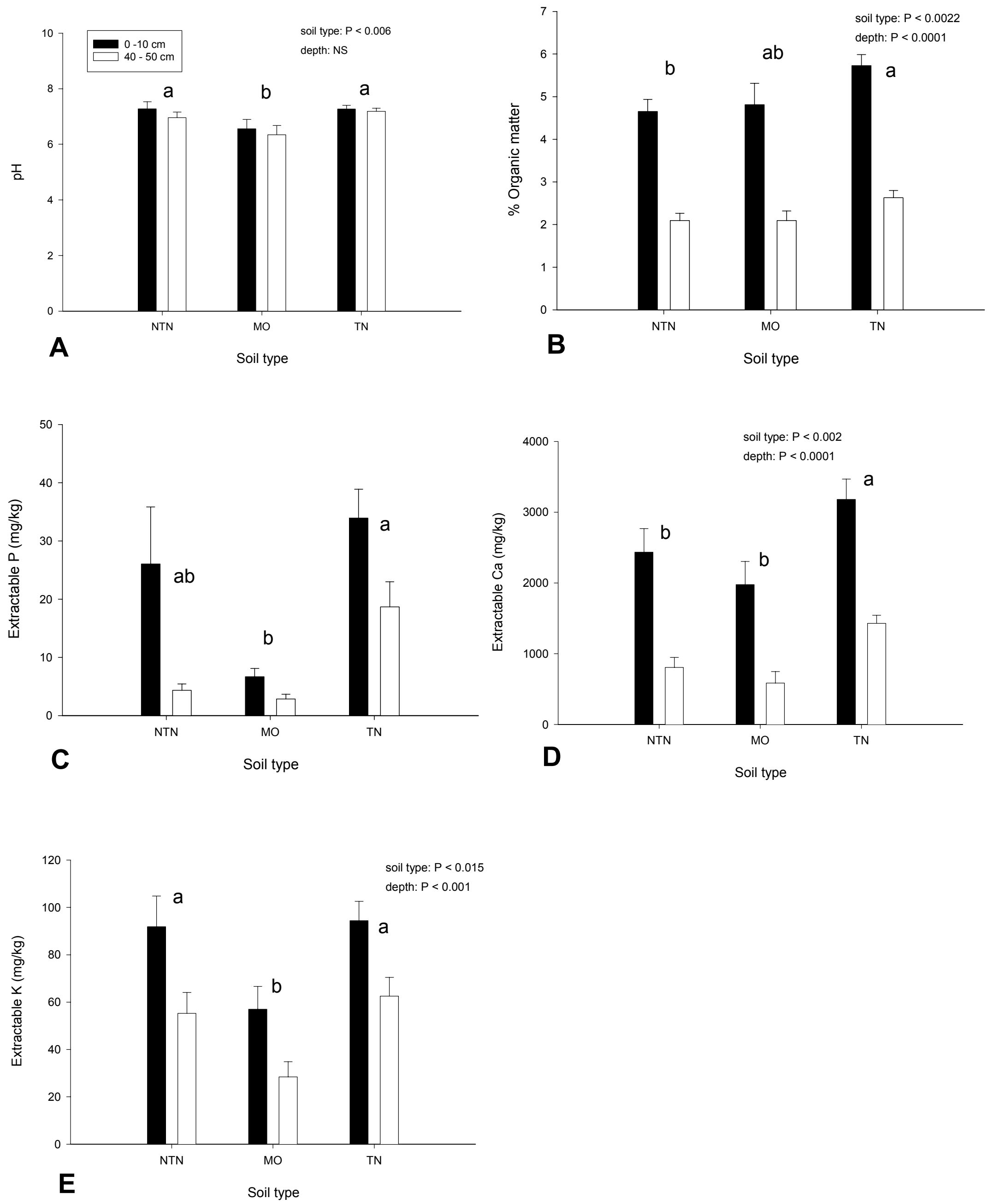

Figure 1-4. Mean values (+ 1 SE) for *tierra negra* (TN, N = 10), *tierra morena* (MO, N = 3,), and non-tierra negra (NTN, N = 6) at two different depths. A) pH. B) Organic matter content. C) Extractable phosphorous. D) Extractable calcium. E) extractable potassium. Different letters indicate overall significant differences among means of the three soil types.

CHAPTER 2
DISTRIBUTION OF USEFUL TREE SPECIES IN RELATION TO HISTORICAL HUMAN INFLUENCES ON THE FOREST OF A TIMBER CONCESSION IN LOWLAND BOLIVIA

Introduction

Enrichment of native plant communities with species used by humans (hereafter useful species) near settlements likely occurred prior to as well as after the advent of agriculture, when hunters and gatherers selected and favored certain plant species both purposefully by planting or inadvertently by consuming fruits and disposing of seeds in or near their settlements (Smith 1995, Peters 2000). Tropical fruits were harvested by humans and their seeds transported at least as long ago as 10,500 years B.P. (Roosevelt et al. 1996). These activities may have altered the distribution and enlarged the populations of selected plant species (Lentz 2000a) and are part of the process that transforms plants from wild to domesticated (Clement 1999). The alteration of forests and landscapes was even more dramatic after development of intensive agricultural systems, such as maize cultivation, which developed in the tropical lowlands of the Americas 6,000 - 7,000 years B.P. (Bush et al. 1989, Pearsall 1992, Piperno and Pearsall 1998).

Historical and archaeological records of pre-contact agriculture are scarce because of the severe depopulation and rapid reforestation that took place soon after European colonization of the Americas (Denevan 1992b, Block 1994). Using colonial documents and ethnographies of modern indigenous people to extrapolate pre-historic land-use practices can be inaccurate due to the effects of acculturation coupled with rapid environmental and demographic changes (Denevan 1992a, Lentz 2000b). During the last several decades, archaeological, ecological, paleobotanical, and geographical research carried out in the lowland tropics have revealed pre-Columbian agriculture of scales and intensities previously not considered (Denevan 1966, 1998, Roosevelt 2000). This study examines the influence of past land-use by native human populations on forest composition in the La Chonta timber concession in lowland Bolivia.

In modern times, as in the past, people increase the concentration of semi-domesticated and domesticated plants near their settlements by transplanting, planting, tending, and, in general, managing landscapes in favor of useful species (Posey 1985, Balée 1994, Dalle et al. 2002, Smith 2002). Moreover, a positive relationship between biodiversity and management of useful plants has been reported in certain tropical areas (Salick et al. 1999).

Accompanying the management of useful species, soils of ancient indigenous villages and their agricultural lands in tropical lowlands were dramatically changed through the addition of plant and animal refuse, charcoal and ash, and mulching, which resulted in darkened anthropogenic soils (referred as to *terra preta* in Brazil and *tierra negra* in Bolivia, black soil, and dark earth, Chapter 1). Anthropogenic soils persist for centuries after abandonment, acting as indicators of former villages (Smith 1980, Eden et al.1984, Denevan 1998, Heckenberger et al. 1999). Anthropogenic dark soils usually have higher organic matter and nutrient content than the surrounding soils even several centuries after abandonment (see Chapter 1).

The influence of historical land-uses on modern vegetation has been studied in several temperate forests (e.g., Peterken and Game 1984, Foster 1988, 1992, Zbigniew and Loster 1997, Motzkin et al. 1999) but there are few such studies in tropical forests (e.g., Foster et al. 1998, Dalle et al. 2002). Detecting changes in the distribution of species managed by humans in the past is particularly challenging in tropical regions because the vegetation and species are not well known, there is high diversity, dating tree age is difficult (but see Chambers et al. 1998, Martínez-Ramos and Alvarez-Buylla 1998), and many plant distributions are substantially influenced by stochastic forces (Hubbell and Foster 1986). Furthermore, animals other than humans disperse the seeds of the plants humans find useful (Andresen 1999, Galetti et al. 2001, Quiroga-Castro and Roldán 2001, Zuidema and Boot 2002). Nevertheless, soils and land-use history have been shown to play important roles in the distribution of tropical forests trees (Moran 1993, Clark et al. 1995, Clark et al. 1999, Lentz 2000b).

As in other Bolivian forests, many of the most important timber tree species are poorly represented among the smaller trees and regenerate poorly in the forest after logging in La Chonta (Mostacedo and Fredericksen 1999). In contrast, these same species seem to regenerate well in heavily disturbed areas such as along logging roads and in large logging gaps, especially where surface soils have been disturbed by harvesting equipment (Fredericksen and Mostacedo 2000, Fredericksen and Pariona 2002) or following large-scale natural disturbances (Gould et al. 2002). Past land-use practices by indigenous people in La Chonta including large-scale clearing and frequent burning (Chapter 1) may also have provided suitable habitats for colonization and recruitment by these poorly regenerating species. Several of these species may also have been cultivated in the past by indigenous people in the Amazon region such as *Bactris gasipaes* (Clement 1986, Mora-Urpí et al. 1997) and *Spondias mombin* (Smith et al. 1992, Smith 1995). Did individuals of these useful species or their parents regenerate in abandoned clearings and/or are they relicts of former indigenous cultivation? By investigating the relationship between these species and anthropogenic soils we can start to answer these questions.

In this study I compared the concentration of useful tree species in areas with anthropogenic and non-anthropogenic soils. I predicted that domesticated and semi-domesticated plant species are more abundant in areas with *tierra negra* than in the surrounding forest. I studied an array of purportedly domesticated and useful wild species including long-lived canopy tree species with dense wood (e.g., *Pouteria* spp.), pioneer species (e.g., *Pourouma cecropiaefolia*), and palms (e.g., *Attalea phalerata*).

Methods

Study Site

The study was carried out in La Chonta, a lowland tropical forest located in the Guarayos Province, Department of Santa Cruz, Bolivia (15°47'S, 62°55'W). The annual mean precipitation is ca. 1,500 mm with a severe dry season between May to October and the mean annual temperature of 24.3 ºC.

The vegetation of La Chonta is classified as subtropical humid forest (Holdridge 1971); common tree species include *Pseudolmedia laevis, Ocotea guianensis, Clarisia racemosa, Terminalia oblonga,* and *Hura crepitans* (Pizarro-Romero 2001, Fredericksen and Pariona 2002). Lianas are remarkably abundant in the forest (Alvira et al. 2003). The area has a history of human-induced disturbances indicated by the presence of extensive areas of anthropogenic soils (Chapter 1) but the sites examined have apparently not been inhabited for at least 300 years. Uncontrolled selective logging for mahogany (*Swietenia macrophylla*) and tropical cedar (*Cedrela odorata*) was carried out until 1996 when management plans were written and followed and current extraction of 18 species has occurred in the area since the 1970s.

La Chonta was formerly inhabited by Guarayo Indians (see Chapter 1), and is characterized by three different soils that they helped create: *Tierra negra* (TN) dark anthropogenic soils present in patches of 0.3->10 ha, surrounded by *tierra morena* (MO) a transitional anthropogenic soil that occurs adjacent to TN; and a matrix of non-anthropogenic soils (NTN), tentatively classified as inceptisols. The TN areas are likely former village sites or agricultural fields but the MO area's past land-use is unclear. The chemical properties differ between these soils; TN soils have higher organic matter content, extractable phosphorous (P), and extractable calcium (Ca), than NTN soils and higher pH and extractable P than MO soils. MO and NTN soils had similar organic matter and Ca content, and MO had significantly less extractable K than TN and NTN soils (see Chapter 1).

Species Selection

Based on a preliminary floristic inventory of the area coupled with literature search, seventeen tree species reportedly used by humans were selected for study (Table 2-1). These species are described as semi-domesticated or domesticated (mostly for their fruits or seeds) by tropical South American indigenous groups (Clement 1986, Smith et al. 1992, Balée 1994, Henderson 1995, Clement 1999) or are presently used by indigenous peoples in lowland Bolivia (Centurión and Krajlevic 1996, Vásquez and Coimbra 1996, DeWalt et al. 1999, Mostacedo and Uslar 1999, Paz et al. 2001). Information about uses and regeneration status was gathered for each species based on field observations, interviews with local foresters, and available literature (Table 2-1). Geographical distributions are based on the Missouri and New York Botanical Garden databases

(Solomon 2002, New York Botanical Garden 2003). Maximum stem diameters and growth rates are derived from unpublished BOLFOR databases (Table 2-2). Maximum age was calculated by dividing maximum DBH by the mean annual growth increment (MAI). The criteria for classifying species as domesticated or semi-domesticated were from Clement (1999) who defines them as follows:

> Domesticated species are those whose ecological adaptability has been reduced to a point that they can only survive in human-created environments, and if human interventions ceases, the population dies out in short order. Semi-domesticated species are those significantly modified by human selection and intervention, but that retain enough ecological adaptability to survive in the wild without human intervention.

Because edible plants are often dispersed to and planted in or near dwellings, ten of the seventeen useful plant species belong to this category. Camps, trails, and settlements were enriched with fruit and nut trees; a process that still takes place in Amazonian backyards and homegardens (Balée 1994, Smith 1995, Lamont et al. 1999). Five species are palms that are used in many ways and found in many present-day indigenous villages and abandoned village sites (Brücher 1989, Clark et al. 1995, Henderson 1995, Moraes-Ramirez 1996, Morcote-Rios and Bernal 2001). Most of the studied palm species regenerate at least sparsely in the forest, with the exception of *Bactris gasipaes*, which has not been observed as seedlings in La Chonta (T.S. Fredericksen 2002, *pers. comm.*) and is cultivated through tropical Latin America (Killeen et al. 1993, Postma and Verheij 1994, Clement 1999, Morcote-Rios and Bernal 2001).

Species Sampling

The total abundance of each selected species was recorded in 50 x 20 m plots in each soil type (TN, MO, and NTN) studied in Chapter 1. Plots were established in 14 NTN sites, 10 MO sites, and 14 TN sites. The area of each of the soil type site varies between 0.3 ha and >10 ha for TN sites, surrounded by MO sites of approximately 0.5 – 1 ha, all embedded in a matrix of NTN soils (Chapter 1). The number of plots per site (TN, MO, or NTN site) varied from one to five according the size of the site and the condition of vegetation (whether or not the area had been logged). One to three plots were established in 0.1-0.5 ha sites and five plots were established in sites >0.5 ha.

Data Analysis

The mean abundance of useful species in each site was calculated by averaging sample plot abundance data scaled up to 1 ha. To test whether species densities differed among soil types, Kruskal-Wallis tests were performed, using a probability of significance of 0.05 with a sequential Bonferroni correction for the error probability (Rice, 1989).

Results

The tree species I studied all occurred at low densities, but total abundance among the species also varied considerably. *Bactris gasipaes* (chonta de castilla, peach palm), *Astrocaryum aculeatum* (chonta de anillo), *Ceiba pentandra* (hoja de yuca), *Pourouma cecropiaefolia* (uvilla) and *Eugenia* sp. (arrayán) were all very scarce, with overall mean abundances between 0.02 to 0.09 individuals/ha. *Talisia sculenta* (pitón), *Spondias mombin* (ocorocillo, yellow mombim), *Batocarpus amazonicus* (mururé), *Syagrus sancona* (sumuqué), *Attalea phalerata* (motacú), *Inga* spp. (pacay), *Myrcia* sp. (sawinto), *Sapindus saponaria* (isotouvo), and *Astrocaryum murumuru* (chonta) were more common with overall mean abundances between 0.2 to 0.9 individuals/ha. *Pouteria nemorosa* (coquino), *Pouteria macrophylla* (lúcma) and *Ampelocera ruizii* (blanquillo) were the most abundant species, with 1.1-3.5 individuals/ha (Table 2-2).

The species vary in geographical distributions and growth characteristics. *Pourouma cecropiaefolia* is a geographically widespread, fast-growing tree, typical of pioneer species. *Spondias mombin, Inga* spp., *Ceiba pentandra,* and *Ampelocera ruizii* are widespread canopy trees with intermediate growth rates. Their sizes vary between 73 to 200 cm DBH and their maximum ages are estimated between 180 to 227 years. Finally, *Eugenia* sp., *Talisia sculenta, Batocarpus amazonicus, Myrcia* sp., *Sapindus saponaria*, *Pouteria nemorosa,* and *Pouteria macrophylla* are relatively slow-growing trees with widespread geographical distribution, except *Pouteria nemorosa* which is found only in Bolivia and Ecuador. Their sizes range between 51 and 150 cm DBH and their estimated maximum ages (249-468) are negatively correlated with their growth rates (Table 2-2). The distribution of the palms ranges from extremely widespread (*Bactris gasipaes*) to widespread (*Astrocaryum murumuru, Astrocaryum aculeatum,* found throughout the Amazon) to restricted *(Syagrus sancona, Attalea phalerata,* found in southwestern Amazon) (Table 2-2).

Contrary to my expectations, the densities of the seventeen species studied did not differ significantly among the three soil types (Figure 2-1) but they were trends that might indicate soil preferences or historical effects. Six species (*Inga* spp., *Spondias mombin, Astrocaryum aculeatum, Bactris gasipaes*, *Ceiba pentandra,* and *Pouteria nemorosa*) appear to be most abundant in MO areas, and *Pouteria macrophylla,* appears to be more abundant in NTN soils when compared to MO and TN soils, but the differences were not statistically significant due to high variances

When analyzing the differences between anthropogenic (TN and MO pooled together) and non-anthropogenic soils (NTN), the only species showing significant differences was *Pouteria macrophylla,* which was more abundant in NTN soils than in anthropogenic soils (MO and TN soils together, Mann-Whitney U = 254, P = 0.009, df = 1, Figure 2-1 O). Although not statistically significant probably due to small sample sizes, two species, *Astrocaryum aculeatum* and *Ceiba pentandra*, were only recorded in TN and MO soils and were not present in NTN soils (Figure 2-1 B and 2-1 G).

Discussion

Contrary to my expectations, the results showed few differences in the abundances of the 17 useful tree species studied between anthropogenic (TN and MO) and non-anthropogenic soils (NTN) in La Chonta, contradicting the original hypothesis (a concentration of useful species in anthropogenic soils). This unexpected result may be due to a misunderstanding of past land-use practices, but contemporary disturbances cannot be disregarded. It seems most likely that past inhabitants of La Chonta altered the forest beyond the TN areas, influencing both MO and NTN areas. This would be the case if TN areas were villages and surrounding areas (MO and NTN areas) were managed forest or agricultural plots. Alternatively, a former concentration of useful tree species in TN and MO areas may have been masked by modern disturbances, natural dispersal and other factors.

The overall low densities and high variability in the distributions of the species studied are consistent with other studies that report canopy species in tropical forests as rare, with densities of tress ≥ 10 cm DBH of < 1 individual/ha of (Hubbell 1979, Hubbell and Foster 1986, Clark and Clark 1992). Nevertheless, the six species that appear to be more abundant on MO soils than TN and NTN soils may have been concentrated there if the TN areas were indeed village sites that were mostly devoid of vegetation, and the MO sites were the surrounding agricultural plots.

Four of the six species that appear to be more abundant in MO areas (*Spondias mombin, Astrocaryum aculeatum, Bactris gasipaes*, and *Ceiba pentandra*) are present at overall low densities (0.21, 0.04, 0.02, and 0.05 trees/ha respectively), are widely distributed long-lived species, and regenerate poorly in La Chonta (Table 2-1, Table 2-2). In addition, they are all known to be cultivated near human settlements elsewhere in the tropics (particularly *Bactris gasipaes*, Brücher 1989, Smith et al. 1992, and Clement 1999). It is possible, therefore, were planted by the people who lived in La Chonta 300-400 years ago, but further studies at a bigger scale will be necessary to test this hypothesis.

While palms are influenced by several disturbance regimes (Anderson et al. 1991, McPherson and Williams 1998) they are commonly associated with human settlements (Clement 1999, Morcote-Rios and Bernal 2001). There are several reasons to expect that the *B. gasipaes* population of La Chonta is a relict of ancient cultivation. Despite maximum age estimations of 50-100 years for each mature stem (Brücher 1989, Smith et al. 1992, Mora-Urpí et al. 1997), the clone from which new stems emerge could be centuries old, perhaps planted by former inhabitants. In addition, it is the only species I studied that is considered fully domesticated (Clement 1999) and does not regenerate naturally in La Chonta. However, several authors (Clement 1986, 1999, Mora-Urpí et al. 1997) recognize that there are different varieties of *Bactris gasipaes,* comprising a continuum between domesticated and semi-domesticated varieties. In La Chonta, further studies of seed/fruit ratios will determine where *Bactris* falls in this continuum. Similar to *Bactris*, the small population of the semi-domesticated palm, *Astrocaryum aculeatum* (Clements 1999), may also be a relict from earlier plantings given that it is generally associated with human settlements (Wessels Boer 1965) and regenerates poorly in La Chonta (Table 2-1). The fact that *Bactris gasipaes* and *Astrocaryum aculeatum* are not significantly concentrated in the anthropogenic soils suggests in the past their management was not restricted to TN and MO sites.

Existing short-lived species (less than 100 years old) could not have been planted by former inhabitants of La Chonta because the area was abandoned more than 300 years ago. For example, the maximum age of *Inga* spp. in La Chonta is estimated to be 117 years, while in Brazil Laurence (*unpublished data*) estimated the age of three species of *Inga* to be between 50 to 160 years. While several species of *Inga* are considered semi-domesticated, in particular *Inga edulis*, (Clements 1999), they are also dispersed by monkeys (Andresen 1999) and regenerate well in La Chonta (Table 2-1). Consequently, the apparent concentration of *Inga* spp. on MO soils (Figure 2-1 H) may be the product of a secondary ecological adaptation rather than the result of enrichment by past inhabitants of La Chonta.

The species with abundant regeneration, overall high densities, and no apparent pattern of concentration according to soil type, such as *Ampelocera ruizii* and *Sapindus saponaria*, may be wild species that are used by people, but past uses apparently have not altered their present distribution in La Chonta. *Ampelocera ruizii* is not reported as domesticated or semi-domesticated in the literature and has a fairly narrow distribution, growing only in Brazil and the Bolivian lowlands (Table 2-1). In contrast, *Sapindus saponaria* is extremely widespread, and is reported to be used by several indigenous groups (Brüchner 1989). If the range *Sapindus saponaria* was expanded by humans, its regeneration status and distribution (Table 2-1) suggest that it has become wild in La Chonta.

The lack of apparent differences in the abundances of most of the species I studied on the different soil types may be explained by numerous interacting factors that are know to determine forest composition (topography, physiography, land use history, etc.) as well as stochastic forces (Hubbell and Foster 1986). Certainly, edaphic and historic factors alone are not enough to explain forest composition in La Chonta, but their interactions with several other factors might do so. Clark et al. (1999) for example, determined that the distributions of only 30% of the species they studied in a lowland forest in Costa Rica were correlated with edaphic conditions, and concluded that only mesoscale vegetation and soil sampling will estimate the true degree of edaphically influenced distributions. A larger scale study in La Chonta and its surroundings, integrating other environmental variables to the analysis may allow us to do the same.

One of the main factors influencing the results of this study might be the extended period post-abandonment forest dynamics in the area. The two C-14 dates of charcoal buried among pottery sherds in *tierra negra* site 3 (Chapter 1) suggest that the site was probably inhabited most recently 380 and 430 years BP. This extended time since abandonment might be sufficient to mask the effects of humans' enrichment with useful species in the anthropogenic soil areas. In this time period, two or three generations of the short-lived trees can have developed and biotic and abiotic seed dispersal processes may have extended the species' distribution range beyond the TN patches, if they were indeed initially concentrated there. In addition, disturbances such as fires and tree falls may have played a role in the distribution of useful species.

It is also possible that TN areas were maintained as permanently cleared areas in villages as they are and were in Amazonian Brazil (Heckenberger et al. 1999). If village sites were maintained clear of vegetation with a large central plaza and compacted soils (Heckenberger et al. 1999, Woods et al. 2000), it is likely that the perimeter of these areas (MO and NTN areas) represent the agricultural zone that was enriched with useful species. If this is true in La Chonta, the soils surrounding TN sites are those more affected by past agricultural practices and are areas where useful species would have been managed or cultivated. Consequently, NTN areas adjacent to TN areas might not constitute a good control for testing the influence of past land-use practices on species composition. A better control area would be a similar forest without a history of human disturbances, which will be difficult to find.

The results of this study suggest that short-lived species with good regeneration and no pattern of concentration in anthropogenic soils, while perhaps used by former inhabitants, are now wild species that do not reflect the influence of past human use. In contrast, large individuals of long-lived species with poor regeneration may in fact be remnants of former cultivation. The lack of significant concentrations of useful species in TN and MO soils suggests that species may have been cultivated or managed in adjacent NTN areas and that plant communities on all sites were influenced by human activities.

Table 2-1. Characteristics of tree species that are used by humans and selected for study in La Chonta.

Family	Scientific name	Common name	Use	Growth form	Geographical distribution	Regeneration status[a]
Anacardiaceae	*Spondias mombin**	Ocorocillo	Multiuse (edible fruit, roots and medicinal bark); cultivated.	Emergent	Mexico to Bolivia.	Poor
Arecaceae	*Astrocaryum aculeatum**	Chonta de anillo	Multi-use (edible fruits and seeds, oil, construction).	Subcanopy	Amazonia, from Colombia to Bolivia	Poor
Arecaceae	*Astrocaryum murumuru*	Chonta	Multi-use (edible fruits and seeds, oil, construction)	Canopy	Amazonia, from Colombia to Bolivia	Medium
Arecaceae	*Attalea phalerata*	Motacú	Multi-use (edible fruits and seeds, medicine, construction)	Canopy	South and West Amazonia, Peru, Brazil and Bolivia.	Good
Arecaceae	*Bactris gasipaes***	Chonta de castilla	Multi-use (edible fruit, medicine, bows, construction); cultivated.	Canopy	Central America to Bolivia.	Poor
Arecaceae	*Syagrus sancona*	Sumuqué	Multi-use (construction, fruits and seeds used to attract game); cultivated.	Emergent	Southwestern Amazon and Eastern Andes, from Colombia to Bolivia.	Medium
Bombacaceae	*Ceiba pentandra*	Hoja de yuca	Multi-use (religious, fiber, oil from seeds); cultivated.	Emergent	Pantropical.	Poor
Leguminosae (Mimosoideae)	*Inga* spp.*	Pacay	Edible fruit*; Inga edulis* cultivated	Subcanopy, pioneer	Genus is widespread in tropics and subtropics.	Good

Table 2-1, Continued

Moraceae	*Batocarpus amazonicus*	Mururé	Multi-use (edible fruit, dye, latex)	Canopy	Panama to Bolivia	Poor
Moraceae	*Pourouma cecropiaefolia*	Uvilla	Edible fruit, medicinal; cultivated.	Canopy, pioneer	Costa Rica to Bolivia.	Good
Myrtaceae	*Eugenia* sp.*	Arrayán	Edible fruit	Subcanopy	Pantropical	Good
Myrtaceae	*Myrcia* sp.	Sawinto	Edible fruit	Canopy	Amazonia, Bolivia and Brazil	Poor
Sapindaceae	*Sapindus saponaria*	Isotouvo	Soap from fruit, medicinal	Subcanopy	Arizona to Bolivia	Good
Sapindaceae	*Talisia sculenta*	Pitón	Edible fruit; cultivated.	Subcanopy	Amazonia, from Colombia to Bolivia.	Poor
Sapotaceae	*Pouteria macrophylla**	Lúcma	Edible fruit	Canopy	Bolivia, Brazil and Peru	Good
Sapotaceae	*Pouteria nemorosa*	Coquino	Edible fruit	Canopy	Disjunct, only in Ecuador and Bolivia	Good
Ulmaceae	*Ampelocera ruizii*	Blanquillo	Edible fruit	Canopy	Bolivia, Brazil and Peru	Good

[a]Good = seedlings, saplings (<1.50 m), juveniles (>1.50 m) and adults present in the forest; Medium = juveniles and adults present, regeneration scarce; Poor = only adults present, regeneration scarce. This classification is valid only for La Chonta.
* = Semi-domesticated; ** = Domesticated, according to (Clement 1999).

Table 2-2. Maximum diameters, mean growth rates for trees > 10 cm DBH , and mean annual diameter increment (MAI , based on 3 years of data) of the selected tree species in La Chonta, based on unpublished data from permanent sample plots of BOLFOR Project. Estimated maximum age was calculated by dividing maximum DBH by MAI.

Scientific name	Maximum DBH (cm)	Mean annual diameter increment (MAI, cm)	N (for MAI)	Estimated maximum age (years)	Overall mean abundance / ha (± one SE)
Spondias mombin	121	0.43	61	180	0.21 (± 0.04)
Astrocaryum murumuru	40	--	--	--	0.91 (± 0.12)
Astrocaryum aculeatum	16	--	--	--	0.04 (± 0.03)
Attalea phalerata	48	--	--	--	0.41 (± 0.07)
Bactris gasipaes	18	--	--	--	0.02 (± 0.01)
Syagrus sancona	26	--	--	--	0.37 (± 0.07)
Ceiba pentandra	200	0.88	15	227	0.05 (± 0.02)
Inga spp.	73	0.62	55	117	0.49 (± 0.12)
Batocarpus amazonicus	85	0.27	62	316	0.33 (± 0.08)
Pourouma cecropiaefolia	74	2.23	16	33	0.06 (± 0.03)
Eugenia sp.	37	0. 29	12	128	0.09 (± 0.03)
Myrcia sp.	83	0.30	209	276	0.60 (± 0.21)
Sapindus saponaria	51	0.12	166	427	0.83 (± 0.13)
Talisia sculenta	52	0.21	31	250	0.17 (± 0.05)
Pouteria macrophylla	99	0.26	100	382	1.49 (± 0.24
Pouteria nemorosa	150	0.32	219	469	1.12 (± 0.15)
Ampelocera ruizii	110	0. 61	410	180	3.51 (± 0.38)

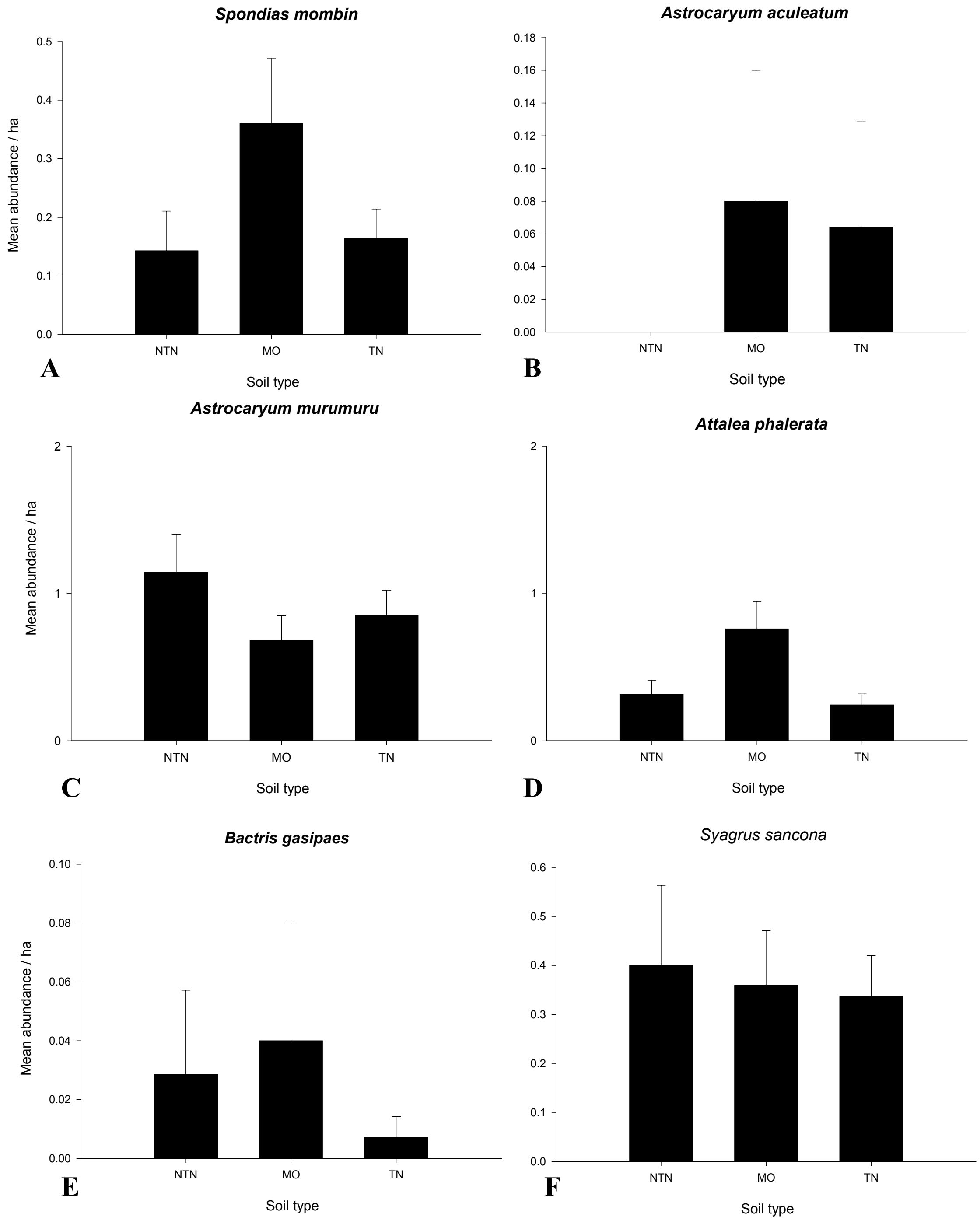

Figure 2-1. Comparisons of the relative abundances (± 1 SE) of the selected useful tree species among the three different soil types: non-*tierra negra* (NTN, N = 14), *tierra morena* (MO, N = 10), and *tierra negra* (TN, N = 14).

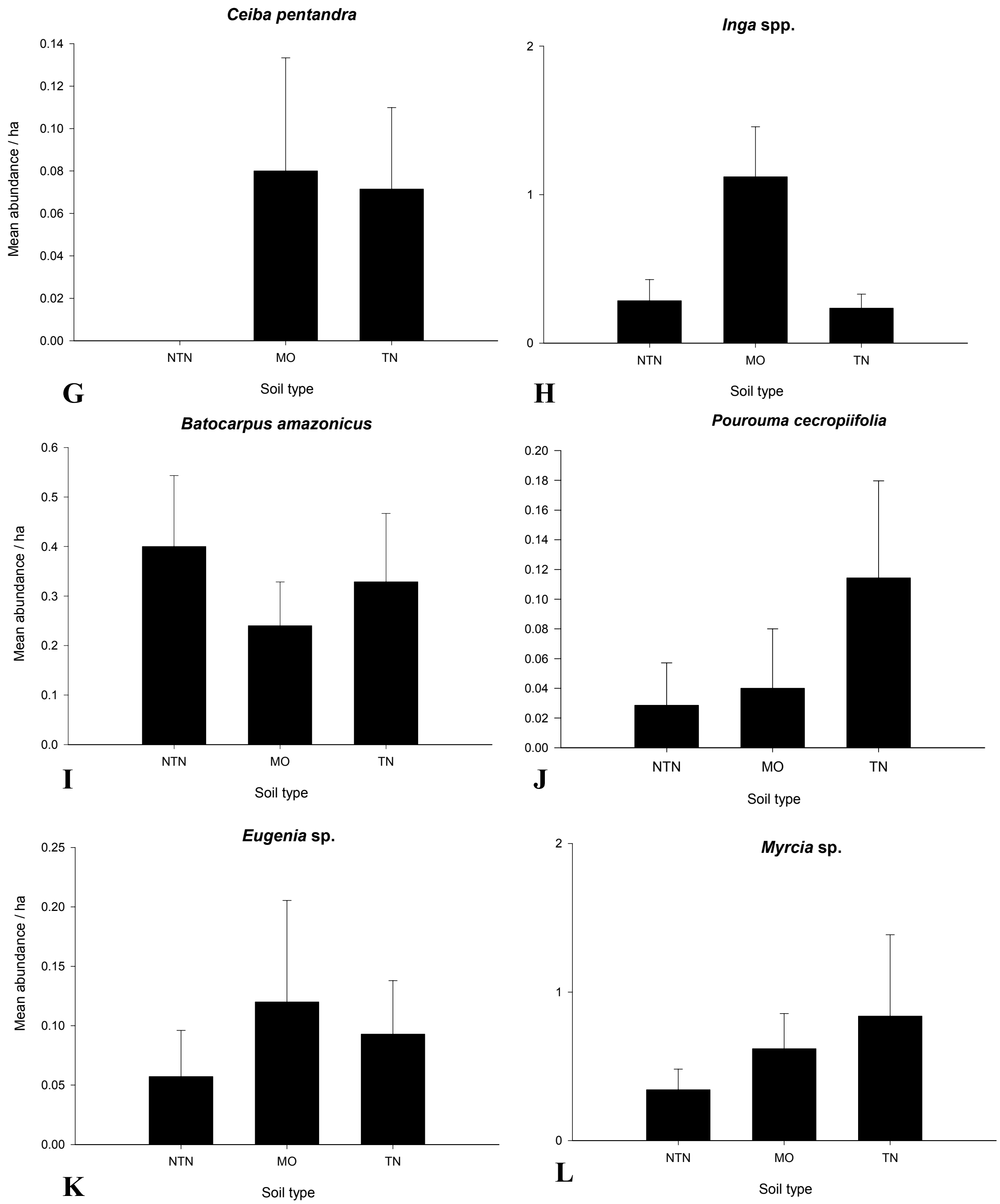

Figure 2-1. Continued

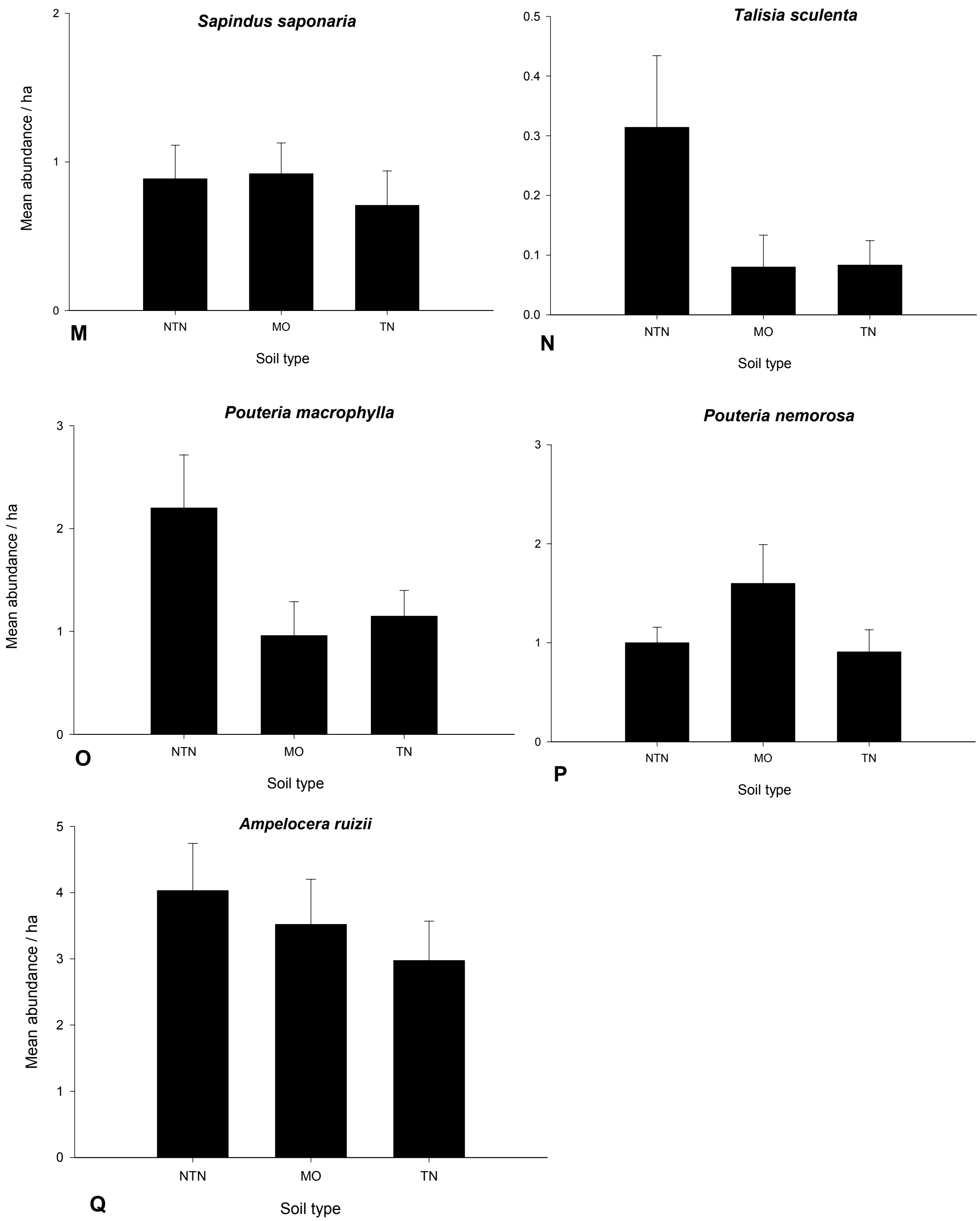

Figure 2-1. Continued

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BIOGRAPHICAL SKETCH

Clea Lucrecia Paz Rivera was born in La Paz, Bolivia. As a child, she lived in Perú, Mexico, and Colombia, while her mother, a sociologist, was in political exile. While living in these countries she developed a love and curiosity for the natural and cultural diversity of Latin America.

As an undergraduate she studied biological sciences at the Universidad Mayor de San Andrés in La Paz. Her undergraduate thesis focused on the effects of cattle grazing on floristic diversity in the savannas of Beni, Bolivia. She graduated with her *Licenciatura* in 1998. She the worked as an associate researcher at the Herbario Nacional de Bolivia, conducting floristic inventories in secondary forests in the Chapare region. She also collaborated in the initial phase of the Catalog of Vascular Plants of Bolivia. In 2000, the Herbarium nominated her for a LASPAU/Fulbright fellowship. The fellowship was granted and she began her graduate work in the University of Florida's Interdisciplinary Ecology Program in Spring 2001, hosted by the Department of Botany.

Upon completing her master's degree, Clea will return to her country with her husband and son. She intends to resume work at the Herbario Nacional de Bolivia and explore dissertation topics.