

## AN ABSTRACT OF THE THESIS OF

R. Flint Hughes for the degree of Doctor of Philosophy in Forest Science presented on September 9, 1997. Title: Effects of Deforestation and Land Use on Biomass, Carbon, and Nutrient Pools in the Los Tuxtlas Region, Mexico.

Abstract approved:

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Land-use change in forested regions of the tropics is currently one of the largest anthropogenic perturbations on earth; it is a force capable of altering biogeochemical cycles at local, regional, and global scales. However, significant uncertainties exist concerning the impact of land-use change on biomass and elemental pools of tropical forests. To evaluate the response of biomass and elemental pools to deforestation and land-use in the Los Tuxtlas Region, Mexico, total aboveground biomass (TAGB), C, N, S, and P pools were quantified along a land-use gradient that included primary forests, pastures, cornfields, and secondary forests. TAGB of primary forests averaged 403 Mg/ha; pastures and cornfields averaged 24 and 23 Mg/ha, respectively. Conversion of primary forests to pastures or cornfields resulted in declines of  $\approx 94\%$  of aboveground C pools,  $\approx 92\%$  of aboveground N,  $\approx 83\%$  of aboveground P, and between 89% and 95% of aboveground S. Soil pools of C, N, and S did not differ significantly between primary forests, pastures, and cornfields. Soil C to a 1 m depth ranged from 166-210 Mg/ha; N and S ranged from  $\approx 16,000$ -20,000 kg/ha and  $\approx 3400$ -3800 kg/ha, respectively.

In secondary forests, TAGB increased with increasing forest age; accumulations ranged from 4.8 Mg/ha in a 6-month-old site to 287 Mg/ha in a 50-year-old site. Results indicate that secondary forests will attain the equivalent of primary forest TAGB in 73 years. However, rates of TAGB accumulation were constrained by land-use history; rates decreased with increasing duration of land use prior to abandonment. Soil pools of secondary forests were not correlated to forest age or prior land-use history and did not differ significantly from soil pools of primary forests, pastures, or cornfields.

As a group, soils of primary and old secondary forest sites had significantly larger pools of available N and higher rates of nitrification and N mineralization than the combined group of pastures, cornfields, and recently abandoned sites.

Currently, the Los Tuxtlas Region functions as a net source of greenhouse gases. Regenerating secondary forests have the capacity to counterbalance emissions resulting from deforestation, but presently constitute only a small percentage of the the regional landscape.

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Effects of Deforestation and Land Use on Biomass, Carbon, and Nutrient Pools in the Los

Tuxtlas Region, Mexico

by

R. Flint Hughes

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Doctor of Philosophy

Presented September 9, 1997

Commencement June 1998

## **Acknowledgment**

This work has been made possible through funding by the United States Environmental Protection Agency and the National Aeronautics and Space Administration's Global Change Fellowship Program. I am grateful to J. Boone Kauffman for giving me the opportunity to pursue this project and for his advice and support throughout. I thank Annalee Hughes and the Sinaca family of Ejido Laguna Escondida for their indispensable assistance during all stages of the fieldwork. I also thank Victor Jaramillo, Rodolfo Dirzo, and David Perry for their helpful advice and assistance. Tomas Carmona and Franz Bongers provided previously unpublished data for the benefit of this project. Lisa Ellingson and Dian Cummings were instrumental in the laboratory analysis of samples. Mark Harmon, David Myrold, and John Selker provided thoughtful reviews of previous drafts of this thesis.

## **Contribution of Authors**

Dr. J. Boone Kauffman was involved in the design, analysis, and writing of each chapter of this dissertation. Dr. Victor Jaramillo of the Universidad Nacional Autonoma de Mexico (UNAM) was also involved in the design and analysis of research presented in Chapters 1 and 2.

## TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
TITLE PAGE; CHAPTER 2 The Impact of Deforestation and Land Use on Biomass, Carbon, and Nutrient Dynamics in Tropical Evergreen Forest Systems of the Los Tuxtlas Region, Mexico	4
ABSTRACT	5
INTRODUCTION	6
STUDY AREA	9
METHODS	11
RESULTS	22
DISCUSSION	33
TITLE PAGE; CHAPTER 3 Biomass, Carbon and Nutrient Accumulation in Tropical Evergreen Secondary Forests of the Los Tuxtlas Region, Mexico	41
ABSTRACT	42
INTRODUCTION	43
STUDY AREA	46
METHODS	48
RESULTS	56
DISCUSSION	70
TITLE PAGE; CHAPTER 4 Dynamics of Available Soil Nitrogen in Response to Land-Use Change in Tropical Evergreen Forest Ecosystems of the Los Tuxtlas Region, Mexico	79
ABSTRACT	80
INTRODUCTION	80
STUDY AREA	82
METHODS	84
RESULTS	86
DISCUSSION	93
CHAPTER 5 CONCLUSIONS	96
BIBLIOGRAPHY	99

## LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
2.1	Plot layout used to sample total aboveground biomass in primary forest sites of the Los Tuxtlas Region, Mexico.	13
2.2	Plot layout used to sample total aboveground biomass in pasture sites of the Los Tuxtlas Region, Mexico.	16
2.3	Plot layout used to sample total aboveground biomass in cornfield sites of the Los Tuxtlas Region, Mexico.	17
2.4	Average mass of C, N, and S of soil to 1 m in depth in forest, cornfield, and pasture sites of the Los Tuxtlas Region, Mexico.	32
2.5	Ecosystem pools (i.e., aboveground biomass and soil pools) of C, N, and S in forest, cornfield, and pasture sites of the Los Tuxtlas Region, Mexico.	33
3.1	Plot design for sampling secondary forests in the Los Tuxtlas Region, Mexico.	51
3.2	The relationship between annual rates of total aboveground biomass accumulation and duration of land use in secondary forests of the Los Tuxtlas Region, Mexico.	59
3.3	Estimates of total aboveground biomass (TAGB) accumulation during secondary forest succession in the Los Tuxtlas, Region, Mexico.	60
3.4	Dynamics of TAGB along a land-use gradient in the Los Tuxtlas Region, Mexico.	73
3.5	Dynamics of carbon (A) and nitrogen (B) in total aboveground biomass and soil along a land-use gradient in the Los Tuxtlas Region, Mexico.	77
4.1	Concentrations of available N to a 10 cm depth in soils at sites along a land use gradient in the Los Tuxtlas Region, Mexico.	90
4.2	Potential rates of net nitrification and N mineralization in soils to a 10 cm depth at sites along a land-use gradient in the Los Tuxtlas Region, Mexico.	91
4.3	Bulk soil pools of ammonium and nitrate to a 10 cm depth at sites along a land-use gradient in the Los Tuxtlas Region, Mexico.	92
4.4	Potential rates of net nitrification and N mineralization in soils to a 10 cm depth along a land-use gradient in the Los Tuxtlas Region, Mexico.	93

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1 Land-use histories of pastures and cornfields.	12
2.2 Equations used to determine components of aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico.	14
2.3 Total aboveground biomass (Mg/ha) in primary forest, cornfield, and pasture sites of the Los Tuxtlas Region, Mexico.	23
2.4 Stem density (stems/ha) and basal area (m <sup>2</sup> /ha) of woody species in primary forests of the Los Tuxtlas Region, Mexico.	24
2.5 Mean concentrations of C, N, S, and P in components of aboveground biomass in forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico.	25
2.6 Mass of C, N, S, and P in aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico.	26
2.7 Comparison of elemental ratios in primary forest, pasture, and cornfield sites of the Los Tuxtlas Region, Mexico.	28
2.8 Soil nutrient concentrations in forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico.	29
2.9 Mass of C, N, S, and P in soils of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico.	31
3.1 Names and land-use histories of secondary forest sites.	49
3.2 Equations used to determine components of aboveground biomass of secondary forest sites in the Los Tuxtlas Region, Mexico.	53
3.3 Wood densities in woody debris of young and old secondary forests of the Los Tuxtlas Region, Mexico.	53
3.4 Aboveground biomass pools (Mg/ha) in secondary forests of the Los Tuxtlas Region, Mexico.	58
3.5 Stem density and basal area of woody species in secondary and primary forests of the Los Tuxtlas Region, Mexico.	61
3.6 Concentrations of N, C, S, and P in various components of vegetation in secondary forests of the Los Tuxtlas Region, Mexico.	63
3.7 Concentrations of C, N, S, and P in soils of secondary forests of the Los Tuxtlas Region, Mexico.	65
3.8 Aboveground pools of C, N, S, and P in secondary and primary forests in the Los Tuxtlas Region, Mexico.	67

## LIST OF TABLES CONTINUED

<u>Table</u>		<u>Page</u>
3.9	Soil pools of C, N, S, and P in secondary forests of the Los Tuxtlas Region, Mexico.	69
4.1	Concentrations (mg/kg) of available N in soils of primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites of the Los Tuxtlas Region, Mexico.	87
4.2	Rates of nitrification and N mineralization in soils to a 10 cm depth of primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites of the Los Tuxtlas Region, Mexico.	88
4.3	Soil bulk densities, soil pools of available N, and rates of transformation of available N in soils to a 10 cm depth in primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites of the Los Tuxtlas Region, Mexico.	89

## CHAPTER 1 INTRODUCTION

Land-use change in tropical forested ecosystems has become one of the largest anthropogenic perturbations on earth; it is a force capable of altering biogeochemical cycles at local, regional, and global scales. Worldwide, deforestation and subsequent land use in the tropics is responsible for an estimated annual C flux of  $\approx 1.6 \times 10^{15}$  g to the atmosphere (Houghton 1994). This value represents approximately 25% of the annual total net C emissions; the remaining 75% is contributed by the combustion fossil fuels (Schlesinger 1997). Unfortunately, while the emission of CO<sub>2</sub> from fossil fuel burning is one of the best known values of the global C cycle (Subak et al. 1993), tremendous uncertainties exist concerning the contribution of land-use change in forested regions of the tropics to that cycle (Schimel et al. 1995). Such uncertainties pertain to both the extent and impact of land-use change in the tropics. Further information concerning the dynamics of biomass, C, and nutrient pools in response to deforestation and land use is required to reduce uncertainties associated with the impacts of land-use change on emissions of C and other elements from forested regions of the tropics, particularly those regions that have experienced, or are currently experiencing, high rates of land-use change.

In Mexico, approximately 90% of the nation's original forested land has been deforested (Rzedowski 1978). During the 1980's, deforestation and associated biomass burning accounted for an estimated 41% of Mexico's total net C emissions, and the vast majority of deforestation occurred in tropical forests of that nation. Most of this deforestation has taken place in order to covert forested lands to pastures and croplands. Masera et al. (1992) estimated that annual rates of deforestation of tropical evergreen forests in Mexico averaged approximately 2%. In certain regions, such as the Los Tuxtlas

Region in the state of Veracruz, deforestation rates have recently been as high as 4.3% (Dirzo and Garcia 1992 and Riley et al. 1997).

The Los Tuxtlas Region of Mexico represents the northernmost extent of intact moist evergreen forest in tropical America, and is a tropical region rich in biological diversity. Unfortunately, it is also among the most heavily deforested areas of Mexico. By the mid-1980's, approximately 84% of the Los Tuxtlas Region had been deforested (Dirzo and Garcia 1992). As in other regions of Mexico, the establishment of cattle pastures is currently the primary cause of deforestation in the Los Tuxtlas Region, although conversion of forest to croplands (e.g., cornfields) is also common. Primary and secondary forests are present within the landscape, but are becoming increasingly scarce as human population pressure and land-use change increase (Guevara et al. 1997, Dirzo and Garcia 1992).

Despite the dramatic land-use/land-cover changes that have occurred, and are continuing to occur, in the Los Tuxtlas Region, relatively little information exists concerning the ecosystem-level dynamics of biomass, C, and nutrient pools in response to such changes in this region. Previous studies have quantified biomass and elemental pools in vegetation and soils at various points along land-use gradients in forested ecosystems elsewhere in the tropics (e.g., Kauffman et al. 1995, Kauffman et al. in press, see review by Brown and Lugo 1990). However, to use direct measures of the dynamics of biomass and elemental pools in response to land use from one region to estimate the response to land-use change in other regions risks substantial error due to the inherent variability of both the ecosystems and the land-use patterns associated with those systems. Uncertainties regarding the impacts of land-use change on forested ecosystems in specific regions of the tropics are significantly reduced by direct quantification of pertinent ecosystem properties within those regions.

The objectives of this study were to investigate the impacts of deforestation and land-use change on biomass, carbon, and nutrient pools in vegetation and soils of the

heavily deforested region of Los Tuxtlas, Mexico. To accomplish these objectives we quantified total aboveground biomass (TAGB), pools of C, N, S, and P in both vegetation and soils, and pools and transformation rates of available N in soils at sites that constitute a land-use gradient in the region. These sites include primary forests, pastures, cornfields, and secondary forests. By quantifying the above parameters along a land-use gradient in the Los Tuxtlas Region, the potential impacts of land-use change in tropical landscapes on global biogeochemical cycles of will be better described and more thoroughly understood.

## **CHAPTER 2**

**The Impact of Deforestation and Land Use on Biomass, Carbon, and Nutrient Dynamics in  
Tropical Evergreen Forest Systems of the Los Tuxtlas Region, Mexico.**

**R. Flint Hughes**

**Keywords:** Deforestation, Mexico, carbon pools, nutrients, land use, Los Tuxtlas, pastures, tropical forests, cornfields, greenhouse gas flux.

## Abstract

Deforestation of tropical evergreen forests has become a major contributor to increasing levels of greenhouse gases in the atmosphere. However, large uncertainties currently exist concerning the quantities of C and other elements lost to the atmosphere due to the conversion of primary forests to pastures and agricultural lands. To estimate elemental loss from forests due to land-use change in the heavily deforested Los Tuxtlas Region of Mexico, total aboveground biomass (TAGB) as well as carbon and nutrient pools in aboveground vegetation and soils were quantified along a land-use gradient that included primary forest, pasture, and cornfield sites. TAGB of primary forests in the Los Tuxtlas Region averaged 403 Mg/ha; pasture and cornfield sites averaged 24 and 23 Mg/ha, respectively. Approximately 80% of TAGB of forest sites was accounted for by trees >30 cm dbh, and trees >70 cm dbh comprised  $\approx 44\%$  of TAGB. Conversion of forest sites to pasture or cornfield sites resulted in declines of  $\approx 95\%$  of aboveground C pools,  $\approx 91\%$  of aboveground N pools,  $\approx 83\%$  of aboveground P pools, and between 89% and 95% of aboveground S pools. In contrast to aboveground pools, we did not detect a significant difference between primary forests, pastures, and cornfields with regard to soil pools of C, N, and S to a 1 m depth. Average C mass in soils of forest, pasture, and cornfield sites ranged between 166-210 Mg/ha; mass of N and S in soils ranged from  $\approx 16,000 - 20,000$  kg/ha and  $\approx 3400 - 3800$  kg/ha, respectively. Changes in aboveground biomass pools of C and nutrients dominated those of soil pools along the land-use gradient. Approximately 50% of the total ecosystem pool of C was lost as a result of deforestation and land use. Because the vast majority (>90%) of N and S pools were present in the relatively stable pools of the young volcanic soils in the Los Tuxtlas Region, less than 10% of total ecosystem pools of N and S were lost due to land-use change.

## Introduction

Deforestation of tropical evergreen forests (TEF's) is occurring at unprecedented rates and is altering biogeochemical cycles at local, regional, and global scales. While TEF's comprise only 11% of the earth's land area, they have accounted for ~60% of the carbon in aboveground biomass pools of the world's forests and 37% of the total terrestrial NPP of the earth (Whittaker and Likens 1975, Potter et al. 1993, Dixon et al. 1994, Dixon and Wisniewski 1995). The conversion of TEF's to pastures or croplands has resulted in increased emissions of CO<sub>2</sub> and other greenhouse gases such as CO, CH<sub>4</sub>, N<sub>2</sub>O, and SO<sub>2</sub> (Levine 1990, Kauffman and Uhl 1990, Ward et al. 1992, Vitousek and Matson 1992), and decreased stores of C, N, S, and P in biomass. During the 1980's the estimated rate of deforestation in tropical forest ecosystems was  $15.4 \times 10^6$  ha/year, and associated C emissions were  $1.6 \pm 1.0$  Gt/yr (Dixon et al. 1994, Schimel et al. 1995). Similarly, N-volatilization resulting from the combustion of TEF's has accounted for an annual loss of 10 to 20 Tg N from tropical ecosystems - a loss equivalent to 6 to 20% of the total amount of N fixed annually by earth's terrestrial systems (Crutzen and Andreae 1990). In addition, atmospheric concentrations of N<sub>2</sub>O have been increasing annually by 0.2 - 0.3%; a large portion of this increase is linked to biomass burning associated with deforestation during the past four decades (Dixon and Wisniewski 1995). In general, forest ecosystems contain large pools of C, N, S, and P, and reduction in the extent of forested lands through processes such as tropical deforestation invariably results in significant alteration of the global cycling of these elements.

Although the links between tropical deforestation and increased fluxes of radiatively active gases to the atmosphere are well acknowledged, significant uncertainties exist concerning the magnitude of such fluxes (Schimel et al. 1995). These uncertainties are due, in part, to a scarcity of information concerning the size of C, N, S, and P pools in TEF's, the losses of such pools during the conversion of TEF's to pasture and agricultural

lands, and the sizes of such pools that are sustained by converted lands during periods of management.

Few site specific studies have directly measured total above ground biomass (TAGB) or the size of elemental pools in intact TEF's (see reviews by Kauffman and Uhl 1990, Hao et al. 1990, and Brown et al. 1989). Direct measures of TAGB in tropical evergreen forests range from 143 to 1174 Mg/ha (Fearnside 1992, Golley 1983). Using tree volume data from forest inventories, Brown (1997) estimated a range of TAGB values between 182 and 860 Mg/ha for moist forests in tropical America. Less information is available on the pools of biomass, C, and nutrients in pastures and cultivated systems of the tropics. TAGB of pastures converted from TEF's in the Brazilian Amazon ranged from 53 to 119 Mg/ha (Kauffman et al. in press). Total aboveground C pools of these pastures ranged between 26 and 59 Mg/ha, and aboveground N pools ranged between 304 and 661 kg/ha. Other estimates of TAGB in pasture and agricultural lands converted from TEF's ranged from 0.7 to 20 Mg/ha (Buschbacher 1984, Fearnside 1996).

Information concerning the response of pools of soil C, N, S, and P pools to deforestation and land use in TEF systems is highly variable. Houghton et al. (1983) assumed a 25% reduction of soil C when TEF's are converted to pasture, and 50% reduction when they are converted to cultivated systems. Other studies report losses of 4 to 54% in soil C as TEF's are converted to agriculture (Harcombe 1980, Brown et al. 1984, Tiessen et al. 1994). Conversion of TEF's to pasture have been variously shown to result in decreases (Chone et al. 1991, Veldkamp 1994, Trumbore et al. 1995), increases (Lugo and Brown 1992, Fisher et al. 1995) and no change (Reiners et al. 1994, Townsend and Vitousek 1995, Kauffman et al. in press) in the size of soil C pools.

Unfortunately, using direct measures of TAGB and elemental pools from one region to estimate effects of land-use change in other regions risks great error due to the inherent variability of both TEF ecosystems and land-use patterns associated with those systems. Conversely, regional scale estimates tend to be coarse-grained in approach and

often do not include measures of locally important C and nutrient pools such as residual wood debris (Brown 1996). Additional site specific studies of the impacts of land-use change are needed to reduce uncertainties in estimating emissions of radiatively active gases from regions that are undergoing, or have undergone, conversion of forest systems to managed systems.

In Mexico, deforestation and forest burning during the 1980's accounted for 41% of that nation's total C emissions, with  $\approx 75\%$  of deforestation occurring in tropical forests (Masera et al. 1992). Historically, tropical evergreen forests covered  $1.97 \times 10^8$  ha of Mexico; currently, only 10% of this area remains forested (Rzedowski 1978). Masera et al. (1992) estimated that deforestation of TEF's averaged  $\approx 2\%$  per year during the 1980's, with substantially higher rates in certain areas (e.g., 4.3%, 4.5%, and 12.4% in the Los Tuxtlas Region of Veracruz and the Selva Lacondona and Palenque Regions of Chiapas, respectively). Despite the high rate and widespread nature of deforestation of TEF's in Mexico, no studies have yet been conducted to quantify C and nutrient pools in intact forest sites or the dynamics of these pools during land-use change. Such studies are vital to understanding and quantifying overall elemental fluxes from Mexico as a result of deforestation and land use in that nation.

The Los Tuxtlas Region of Mexico supports the northernmost extent of intact moist evergreen forest in the neotropics and is an area rich in biological diversity - the richest in North America - harboring a unique assemblage of species of both tropical and temperate origin, including numerous endemics (Dirzo et al. 1997). It is also among the most heavily deforested areas in Mexico. By the mid-1980's, 84% of the Los Tuxtlas Region had been deforested, with the highest rates of deforestation occurring during the past 30 years (Dirzo and Garcia 1992). Establishment of cattle pastures is currently the primary cause of deforestation in the region, although conversion of forest to cultivated lands (principally cornfields) is also common (Masera et al. 1992, Guevara et al. 1997). According to estimates by Riley et al. (1997), between 1986 and 1990  $\approx 2 \times 10^4$  ha were converted from

forest lands to non-forest lands with an associated carbon loss of  $\approx 1.5 \times 10^6$  Mg. If current deforestation rates continue, less than 9% of the forests in the Los Tuxtlas Region will remain by the year 2000 (Dirzo and Garcia 1992).

The objective of this study was to quantify the changes in TAGB, C, N, S, and P pools associated with land-use change in the Los Tuxtlas Region, Mexico. Specifically, we wished to estimate declines of stored C, N, S, and P due to the conversion of forests to pastures and cornfields within the region. To accomplish this goal, we quantified biomass, C, N, S, and P pools in aboveground vegetation and soils of forest, pasture, and cornfield sites located in the Los Tuxtlas Region.

### Study Area

All study sites were located within a 10 km radius around the Los Tuxtlas Biological Station (LTBS) managed by Universidad Nacional Autónoma de México (UNAM) (18°35'N, 95°05'W). This 700 ha reserve is located on the northeastern slope of Volcán San Martín in the Sierra de Los Tuxtlas - a series of recently formed volcanoes rising from the Gulf Coast plain in the state of Veracruz, Mexico. Currently, the LTBS is bordered by pastures or farmland managed by private owners or agricultural cooperatives known as ejidos.

The climate of the study area is classified as hot and humid (Holdridge et al. 1971, García 1970); mean annual temperature is 27°C, and mean annual rainfall is 4700 mm. Precipitation varies seasonally with  $\approx 60\%$  of annual precipitation occurring between June and October (Bongers et al. 1988). A relatively dry season occurs between March and May in which monthly rainfall usually does not exceed 150 mm. Temperature varies between a maximum (32°C) during mid-Summer and a minimum (16°C) during December and January (Ibarra-Manríquez and Sinaca-Colín 1987).

The topography of the Los Tuxtlas Region is characterized by undulating hills gradating to steep slopes. Volcán San Martín was last active in 1793 and recent volcanism is evidenced by pyroclastic deposits and volcanic material throughout the region. Soils are

classified as well drained, coarse textured, vitric Andosols mixed with volcanic ash (FAO/UNESCO 1975). In general, forest soil horizons are poorly developed, contain high levels of organic matter, and are weakly acid (pH ranges from 6.1 - 6.5) (Bongers 1988, Chizon 1984).

Potential vegetation of the study area is classified as "selva alta perennifolia" (tall evergreen forest) by Gomez-Pompa (1973), and is characterized by a closed canopy 30 to 35m in height. Dominant tree species include *Nectandra ambigens*, *Pseudolmedia oxyphyllaria*, *Poulsenia armata*, and *Ficus* spp. The understory is dominated by native palms *Astrocaryum mexicanum* and *Chamaedorea* spp. All primary forest sites sampled in this study supported selva alta perennifolia vegetation and showed no signs of anthropogenic disturbance (e.g., tree stumps).

Pastures are typically dominated by either native grass species (e.g., *Paspalum conjugatum*, *Axonopus compressus* and *Panicum* spp.) or exotic African grasses such as *Cynodon plectostachyis* and *Panicum maximum*. Cultivated tree species, such as *Citrus sinensis*, and native tree species, (e.g., *Pouteria sapota*, *Ficus* spp. and *N. ambigens*) are often maintained in pastures to provide fruit or shade. Although broadleaf herbicide is sometimes applied to inhibit non-grass vegetation, pastures are typically maintained by manual removal of woody species and fire (Guevara et al. 1992). Inorganic fertilizers were not applied to any of the pasture sites sampled in this study (personal communication with landholders).

Corn (*Zea maize*) is the predominant crop cultivated by farmers in the Los Tuxtlas Region. Cornfields are typically cultivated during each wet season although farmers may occasionally cultivate corn during the dry season as well. In contrast to many other regions of the tropics where periods of cultivation are typically short (2 to 5 years) and are interspersed with lengthy fallow periods, slash and burn cultivation in the Los Tuxtlas Region is typically long-lived: cornfields have been cultivated for up to 45 consecutive years by landholders. Consequently, agriculture in this region is best characterized as

semi-permanent rather than shifting cultivation. According to landholders, fertilizers were not applied to the cornfield sites sampled in this study.

## Methods

TAGB and pools of C, N, S, and P were quantified in four forest, seven pasture, and four cornfield sites. Forest sites have the following names: Selva Lava (SL), Selva Norte (SN), Selva Bongers (SB), and Selva Plana (SP). Pasture sites ranged from 8 to 40 years of management since deforestation, and cornfield sites ranged from 3 to 45 years of management since conversion (Table 2.1). Land-use histories of both pasture and cornfield sites were determined from interviews with the respective landholders of each site. Pools of C, N, and S were quantified in soils to a 1 m depth at 3 forest (SN, SB, and SP), 4 pasture (P-8, P-9, P-33a, and P-33b), and 3 cornfield (C-5, C-32, and C-45) sites. Pools of P were also quantified in soils, but only to a depth of 10 cm, and only at 3 forest (SN, SB, and SP) and 2 pasture (P-8 and P-33a) sites.

### Plot Layout - Primary Forests

TAGB, C, and nutrient pools of forests were quantified using a nested plot design. At each site, diameter at breast height (dbh) was measured for all trees >30 cm dbh present within a 105 x 75 m plot (i.e., 0.7875 ha). A 25 x 105 m subplot was established within the central portion of the larger plot; the dbh of all trees 10-30 cm dbh were measured within this subplot (Figure 2.1). In cases where individual trees had large buttresses, diameter was measured above the buttress. In addition to dbh, genus and species of each tree >10 cm dbh was recorded as well.

Biomass of wood debris was measured along sixteen 15 m sampling planes (Van Wagner 1968, Brown and Roussopoulos 1974) placed at 15 m intervals along each of two 105 m transects; transects extended in randomly selected directions from their origins

Table 2.1. Land-use histories of pastures and cornfields. Numbers in the label of each site indicate the number of years of land use following deforestation. Land-use period refers to time prior to sampling. The chronology of each site's land-use history reads from left to right. All sites supported primary forest vegetation prior to the onset of land use.

<b>Pastures</b>	<b>Land Use History</b> (years prior to sampling)	<b>land-use period</b> (years)
P-8	8 yrs. pasture	8
P-9	1 yr. cornfield; 8 yrs. pasture	9
P-10	1 yr. cornfield; 9 yrs. pasture	10
P-28	9 yrs. cornfield; 5 yrs. 2nd. growth forest; 14 yrs. pasture	28
P-33a	27 yrs. cornfield; 6 yrs. pasture	33
P-33b	3 yrs. cornfield; 30 yrs. pasture	33
P-40	40 yrs. pasture	40
<b>Cornfields</b>		
C-3	3 yrs. cornfield	3
C-5	5 yrs. cornfield	5
C-32	32 yrs. cornfield	32
C-45	45 yrs. cornfield	45

on the 105 m transects (Figure 2.1). Diameter was recorded for all wood > 7.6 cm diameter that crossed each 15 m transect; wood was divided into sound and rotten classes based on degree of decomposition. Wood pieces 2.54 - 7.6 cm diameter were counted along a 10 m section of each transect.

Biomass of wood debris was calculated at each 15 m transect using planar intersect techniques (Table 2.2). An average value for specific gravity (Sg) of each of the 3 particle classes (2.45-7.6 cm diam., >7.6 cm diam. sound, and >7.6 cm diam. rotten) was determined from samples collected randomly in 3 of the 4 forests (SN, SB, and SP). Average values for small, large sound, and large rotten particles were 0.37, 0.42, and 0.23 g/cm<sup>3</sup>, respectively. The quadratic mean diameter for small wood particles was determined from a sample of 120 pieces collected from 3 of the 4 forests. Wood density and quadratic mean diameter values determined from the forest sites were used to calculate wood debris biomass in cornfield and pasture sites. Bias due to slope was corrected for as outlined in Van Wagner (1968) and Brown and Roussopoulos (1974); percent slope was measured

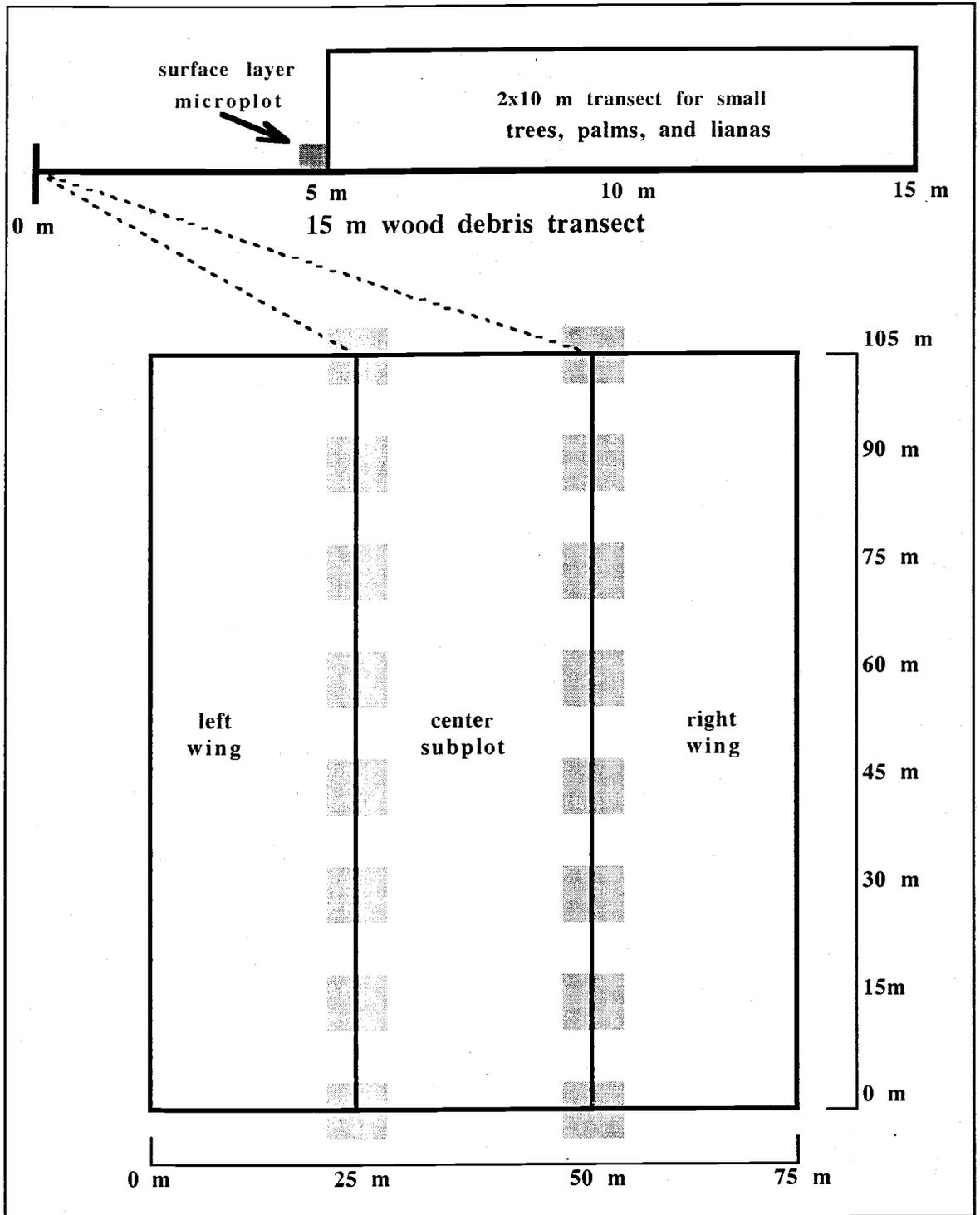


Figure 2.1. Plot layout used to sample total aboveground biomass in primary forest sites of the Los Tuxtlas Region, Mexico.

Table 2.2. Equations used to determine components of aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. All biomass is expressed as dry weight (Mg).

parameter	equation	C F	R <sup>2</sup>
height of trees >10cm dbh <sup>1</sup>	= 4.722 ln(D <sup>2</sup> ) - 13.323	none	0.70
biomass; trees >10cm dbh <sup>2</sup>	= (exp (-2.409+0.9522 ln (D <sup>2</sup> HSg))) CF/10 <sup>3</sup>	1.031	0.99
biomass; <i>Cecropia</i> >10cm dbh (wood bio.) <sup>3</sup>	= {exp (-3.78 + 0.95 ln (D <sup>2</sup> ) + 1.00 ln(H))}/10 <sup>3</sup>	none	0.88
biomass; <i>Cecropia</i> >10cm dbh (leaf bio.) <sup>3</sup>	= {-0.56+0.02 (D <sup>2</sup> )+0.04 (H)}/10 <sup>3</sup>	none	0.98
biomass; standing dead trees >10cm dbh <sup>1</sup>	=π((D/2) <sup>2</sup> )H(0.42)	none	
biomass; trees <10cm dbh <sup>1</sup>	= (exp (4.9375 + 1.0583 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.143	0.93
biomass; dead trees <10cm dbh <sup>1</sup>	= (exp (4.6014 + 1.1204 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.112	0.95
biomass; palms <sup>1</sup>	= (exp (3.6272 + 0.5768 ln (D <sup>2</sup> H))) CF/10 <sup>6</sup>	1.022	0.73
biomass; palms <sup>1</sup>	=(EXP(5.7236 + 0.9285 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.050	0.39
biomass; dead palms <sup>1</sup>	= (exp (-0.5285 + 0.9907 ln (D <sup>2</sup> H)))/10 <sup>6</sup>	none	0.98
biomass; lianas <sup>4</sup>	=(10 <sup>0.12 + 0.91 LOG10(BA)))/10<sup>3</sup></sup>	none	0.82
biomass; tree leaves <sup>5</sup>	=exp(-1.897+0.836 ln (D <sup>2</sup> H))/10 <sup>3</sup>	none	0.85
biomass; sapling wood <sup>1</sup>	= exp (4.7472 + 1.0915 ln (D <sup>2</sup> ))/10 <sup>6</sup>	1.132	0.93
biomass; sapling leaves <sup>1</sup>	= exp (3.0473 + .07778 ln (D <sup>2</sup> ))/10 <sup>6</sup>	1.450	0.71
biomass; liana leaves <sup>4</sup>	=(0.109 BA)-0.376)/10 <sup>3</sup>	none	none
biomass; wood debris 2.45-7.6 cm diam. <sup>6</sup>	= Sg x ((π <sup>2</sup> x N x S x Cs x d <sup>2</sup> )/8L) x 10 <sup>2</sup>	none	none
biomass; wood debris >7.6 cm diam. <sup>6</sup>	= Sg x ((π <sup>2</sup> x sumD <sup>2</sup> x S x Cs x d <sup>2</sup> )/8L) x 10 <sup>2</sup>	none	none
<b>Definitions for symbols used to represent the various components in the above equations:</b>			
D = diameter breast height (cm).		Cs = slope correction factor (square root of (1+(% slope/100) <sup>2</sup> )).	
H = height (m).		N = number of wood particles intersected per transect.	
Sg= wood density (g/cm <sup>3</sup> ).		S = secant of wood particle tilt.	
BA = basal area (cm <sup>2</sup> ).		d = quadratic mean diameter of wood particles (cm).	
CF = correction factor = exp(MSE/2).		sumD <sup>2</sup> = sum of wood particle diameters <sup>2</sup> (cm <sup>2</sup> ).	
Sg = specific gravity of wood (g cm <sup>-3</sup> ).		L = transect length (cm).	
Sources are indicated by superscript number following the description of each parameter: 1 = this study; 2 = Brown and Lugo 1989; 3 = Uhl et al. 1988; 4 = Putz 1983; 5 = Crow 1978; 6 = Van Wagner 1964.			

along each wood debris transect. Because the vast majority of wood particles lay directly on the forest floor, particle tilt was assumed to be negligible, and its secant was assumed to be 1.

The dbh of trees, lianas, and palms at least 1.3 m in height but <10 cm dbh was measured for all individuals within 2 x 10 m transects located adjacent to each of the 16 wood debris transects (Figure 2.1). At SL and SP forest sites, both height and dbh were recorded for all palms; at SN and SB sites, the dbh of palms alone was measured.

Biomass of seedlings (i.e., vegetation <1.3 m in height) and forest floor litter (i.e., fallen leaves, fruits, seeds, bark, and wood <2.45 cm diam.) was destructively sampled in 50 x 50 cm microplots placed at the 5 m point along each wood debris transect line (n = 16 per site; Figure 2.1).

#### Plot Layout - Pastures

At each pasture site, a 60 x 90 m plot was established in which dbh of all trees, lianas, and palms >1.3 m in height was measured (Figure 2.2). Wood debris was sampled along 15 m transects placed at 10 m intervals along 3 parallel transects 90 m in length established within the 60 x 90 m plot (n = 30). Wood debris was sampled in the manner described for wood debris of forest sites. The combined biomass of litter, graminoids, and seedlings was destructively sampled in 25 x 25 cm microplots located at the 2 m point along each wood debris transect (n = 30 microplots per site).

#### Plot Layout - Cornfields

At each cornfield site, dbh of all trees, lianas, and palms >1.3 m in height was measured within one 30 x 60 m plot; this plot size was representative of the approximate size of most cornfields encountered in the study area (Figure 2.3). Corn biomass was quantified in 5 x 5 m microplots located on five 25 m transects running perpendicular to the 60 m side of the plot at 15 m intervals (3 microplots per transect; 5 transects per plot). All corn stalks within each microplot were counted, and an average dry weight value for each corn stalk was obtained through the measurement of 20 stalks (i.e., stem, leaves, grain, and cob) randomly collected from each site. Wood debris was measured along 15 m transects placed at a randomly selected corner of each 5 x 5 m microplot (n = 15); methods followed those described for forest sites. The combined biomass of litter and seedlings was measured in a 50 x 50 cm microplot placed at a randomly selected corner of each 5 x 5 m microplot (n = 15).

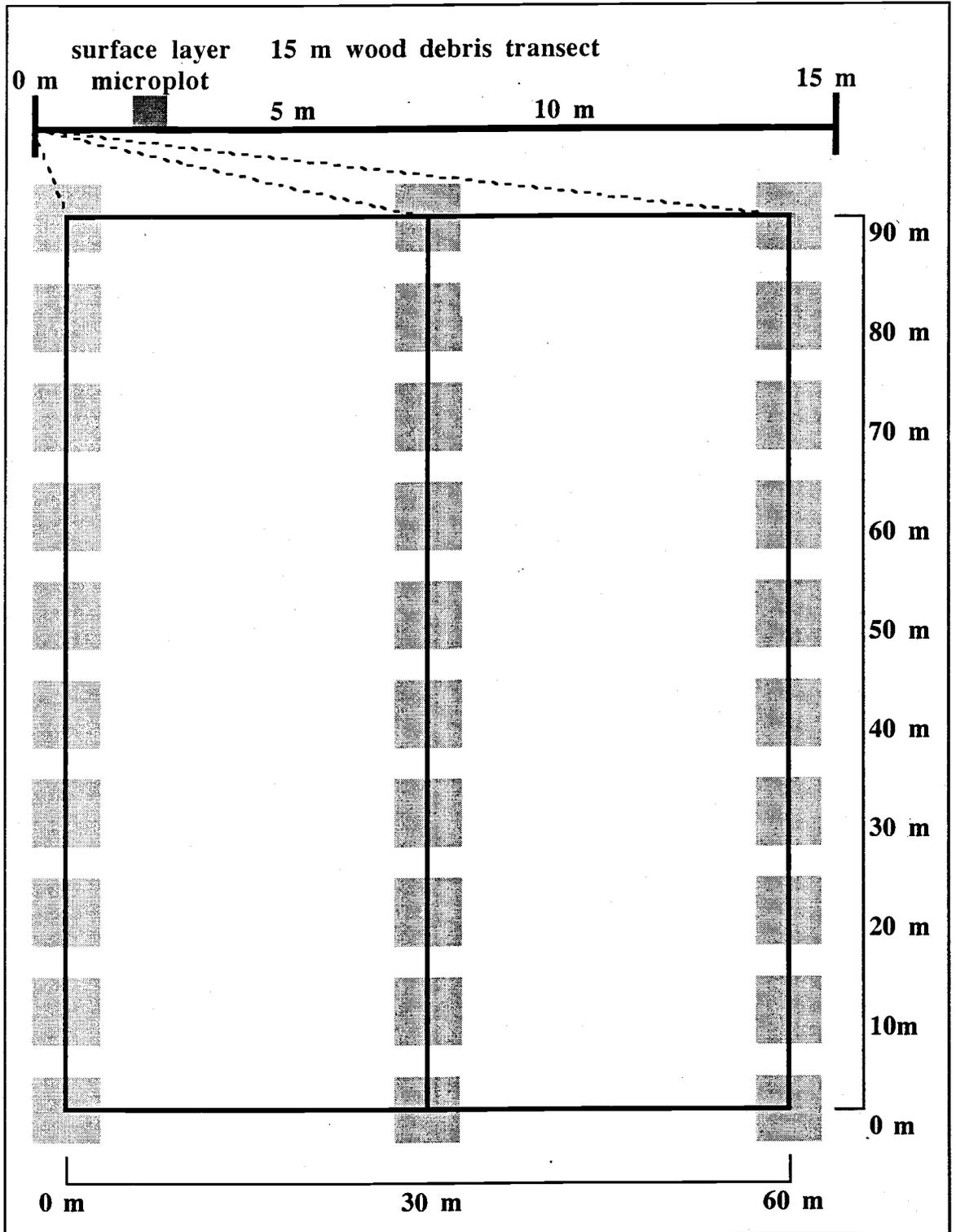


Figure 2.2. Plot layout used to sample total aboveground biomass in pasture sites of the Los Tuxtlas Region, Mexico.

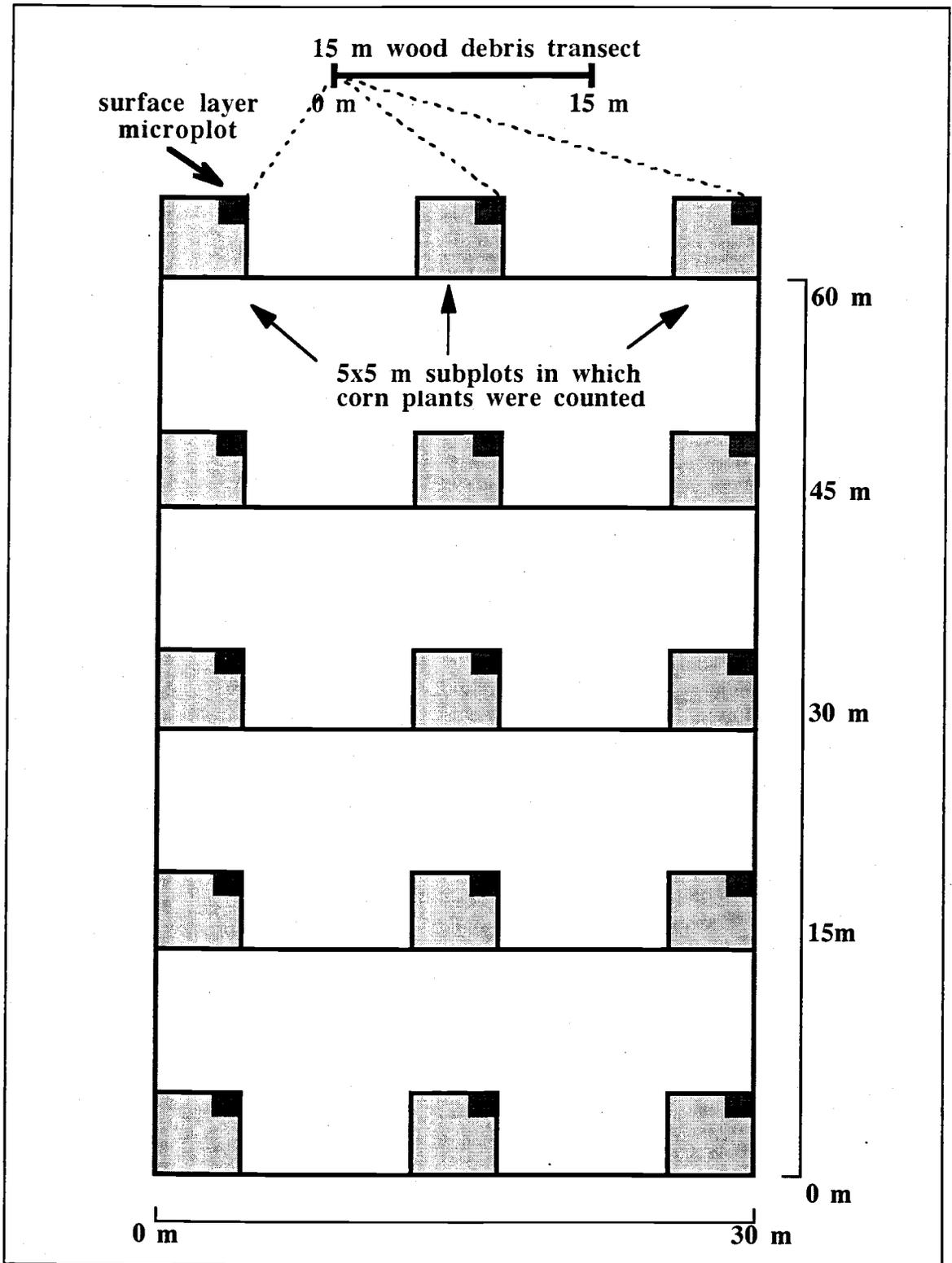


Figure 2.3. Plot layout used to sample total aboveground biomass in cornfield sites of the Los Tuxtlas Region, Mexico.

### Soil Sampling

Pools of C, N, S, and P in mineral soil were determined from 5 samples collected at 10 m intervals along a 50 m transect established in the center of each plot that was sampled. Samples were collected from 0-2.5 cm, 2.5-10 cm, 10-30 cm, 30-50 cm, and 50-100 cm depths. Surface samples (i.e. 0-2.5 cm and 2.5-10 cm depths) were collected in the following manner: at each sample point 4 subsamples were collected 1 m from the sampling point in each cardinal direction and composited into one sample. Soils at depths of 10-30 cm, 30-50 cm, and 50-100 cm were collected at each sample point along the 50 m transect in the following manner: one of the four subsample sites from which surface soils had been collected was randomly selected, and samples of subsurface soil were collected from that point ( $n = 5$  per site). Bulk density of soils was determined at each site from samples of known volume collected at 5 points located within each site. These samples were collected at 0-10, 10-30, 30-50, and 50-100 cm depths ( $n = 5$  per depth).

### Calculations

Biomass of trees  $>10$  cm dbh was calculated using an allometric equation developed by Brown et al. (1989) for tropical moist forest systems. This model uses dbh, height, and wood density to predict tree biomass (Table 2.2). In addition to dbh, each tree  $>10$  cm dbh was identified to species in order to assign species specific wood density values to each individual. The majority of wood density values were provided by Carmona-Valdovinos (unpublished data) and Barajas-Morales (1987) and were determined from samples obtained from trees of the Los Tuxtlas Region. Remaining wood density values were obtained from Reyes et al. (1992) and Brown (1997). In cases where density values were not available for particular species, mean values derived from congeners were used; where mean congener values were not available, a mean value ( $0.58 \text{ g/cm}^3$ ) for species from the Los Tuxtlas Region was used (Barajas-Morales 1987). Heights of trees  $>10$  cm dbh were determined via a predictive model which used dbh as the independent variable and was

developed from a sample of 553 trees of varying species located in and around the LTBS (Table 2.2).

Correction factors were included in the majority of allometric models to account for bias introduced during conversion from logarithmic to arithmetic units (Newman 1993, Baskerville 1972). In certain cases correction factors were not employed because either they were not available from cited sources or they failed to improve the predictability of the respective models based on the difference of the expected versus observed values (Table 2.2).

Due to the unusual form of *Cecropia obtusifolia*, genus specific models for wood and leaf biomass developed by Uhl et al. (1988) were employed to predict biomass of this species (Table 2.2). Volume of standing dead trees >10 cm dbh was calculated by treating each individual as a cylinder; the mean value for the density of sound wood debris >7.6 cm diam. was used to calculate biomass (Table 2.2). Biomass of standing dead trees was included in wood debris biomass at each site.

Biomass of trees at least 1.3 m in height but <10 cm dbh was calculated using a regression equation developed from measures of 66 trees harvested in and around the LTBS; dbh of these trees ranged from 0.4 to 9.9 cm. Biomass of dead trees was determined from a regression model of dbh versus main stem biomass of those 66 trees.

Biomass of palms was calculated using a regression equation developed from dry weights of 15 *Astrocaryum mexicanum* individuals harvested from the study area. The dbh of the harvested palms ranged from 4.1 to 6.2 cm, and height ranged from 1.5 to 5.8 m. In two of the forest sites (SN and SB) dbh was the only variable measured to predict biomass (Table 2.2). Palm biomass of the other two sites was determined from a regression model using dbh and height as independent variables (Table 2.2). Biomass of dead palms was calculated from a regression model based on the main stem biomass of the 15 sampled palms. Liana biomass was calculated from a regression model developed by

Putz (1983) which used basal area as the independent variable to predict biomass (Table 2.2).

Surface layer biomass was defined as litter and vegetation <1.3 m in height. At forest sites, the litter and seedling components were collected separately. At cornfield and pasture sites, litter, graminoid, and seedling biomass components were sampled together.

Concentrations of C, N, S, and P in trees >10 cm dbh were determined from samples of wood and sun leaves collected from randomly selected individuals at the SB and SP forest sites. Wood samples were collected from trees at 1.3 m in height using increment borers inserted to the center of each trunk to ensure that the entire bole was represented by each sample. Five composite samples, each consisting of subsamples taken from eight trees, were collected at each site. Leaf samples were collected by climbing into the tree canopy and cutting leaf bearing branches with pruning shears attached to an extension pole. Five composite samples, each consisting of leaves taken from five trees, were collected at each site.

Pools of C, N, S, and P of all biomass components were calculated by multiplying mass of each component by its respective C and nutrient concentration. Because the concentrations of C, N, S, and P in wood and leaf tissue did not differ between the two forest sites (t-test,  $P > 0.05$ ), samples from the two sites were pooled, and subsequent mean values were used to determine C and nutrient pools of leaf and wood biomass of all trees >10 cm in forest, cornfield, and pasture sites. Leaf biomass of each tree >10 cm dbh was determined using a regression equation developed by Crow (1978). Wood biomass of each tree was calculated by subtracting leaf biomass from total tree biomass.

Carbon and nutrient concentrations in leaf and wood tissue of trees <10 cm dbh were determined from samples of 25 randomly selected individuals at two of the forest sites (SB and SP). Samples were composited to provide five leaf and five wood samples per site. Again, because no differences were detected between sites for any of the elements (t-

test,  $P > 0.05$ ), sample concentrations were pooled, and resulting means used to calculate elemental pools in trees  $< 10$  cm dbh at all sites.

C, N, S, and P pools in palms were calculated by multiplying palm biomass by C and nutrient concentrations measured in stem tissue sampled from 15 randomly selected *A. mexicanum* individuals. C and nutrient pools of leaf and wood biomass in lianas were calculated using concentrations in leaf tissue of trees  $> 10$  cm dbh and concentrations in wood tissue of trees  $< 10$  cm dbh, respectively.

Elemental concentrations of each of the three wood debris classes were determined from 25 subsamples each for sound and rotten wood debris classes  $> 7.6$  cm dbh, and 45 subsamples for wood 2.45-7.6 cm dbh randomly collected within forest sites. Subsamples were composited to provide five samples for each wood debris class.

Elemental concentrations of surface layer pools were determined from five composited samples obtained from biomass samples. At one pasture site (P-10), C and nutrient concentrations of surface layer biomass were not determined, and mean values from the other six pasture sites were used. Elemental concentrations of corn plant, corn grain, and corn cob biomass were determined at each cornfield site from five composited tissue samples obtained from 20 corn plants selected at random in each site.

The mass of C, N, S, and P in soils was calculated by multiplying the mean concentrations of those elements sampled at each depth by the corresponding mean soil bulk density value determined for each depth at each site.

### Lab Analysis

All soil and vegetation samples were oven dried to a constant weight at a temperature of  $\approx 60^\circ$  C. Vegetation samples were ground to pass through a 40 mesh screen (0.5 mm) using a Udy Mill. Soil samples were sieved to remove roots  $> 2$  mm diameter and ground to pass through a 60 mesh screen (250 micrometer pore size). Total C, N, and S concentrations in vegetation and soil samples were determined by the induction furnace method using a Carlo-Erba NA Series 1500 NCS analyzer (Nelson and Sommers 1982).

Total P concentrations were determined using a Kjeldahl digestion procedure followed by colorimetric analysis (Olson and Sommers 1982).

### Statistical Analysis

Differences in TAGB, C, N, S, and P pools between forest, pasture, and cornfield sites were analyzed using single classification analysis of variance tests and Tukey-Kramer post hoc tests (Sokal and Rohlf 1969).

## **Results**

### Total Aboveground Biomass

TAGB averaged 403 Mg/ha in primary forests and was approximately twenty-fold greater than TAGB of both pastures and cornfields ( $P = 0.000$ ). Mean values of TAGB in pasture and cornfield sites were 24 and 23 Mg/ha, respectively, and did not differ significantly from one another ( $P = 0.999$ ). Conversion of forest to pasture or agriculture resulted in declines of nearly 95% of TAGB, or 380 Mg/ha (Table 2.3).

Large tree biomass accounted for the majority of TAGB in forests. On average, trees >30 cm dbh comprised  $\approx 80\%$  of TAGB, and trees >70 cm dbh comprised  $\approx 45\%$  of TAGB (Table 2.3). In contrast, the combined biomass of surface layer (i.e. litter, graminoids, and seedlings <1.3 m in ht.), wood debris, palm, liana, and trees <10 cm dbh accounted for only  $\approx 9\%$  of primary forest TAGB. Overall, TAGB was highly variable among sites, ranging from 320 to 545 Mg/ha.

Total stem density of trees in forests was highest in the smaller dbh classes whereas total basal area was highest in the large dbh classes (Table 2.4). Stems <10 cm dbh accounted for  $\approx 94\%$  of the mean total stem density. In contrast, trees >30 cm dbh accounted for 72% of the total basal area of forests.

TAGB of cornfields and pastures was also highly variable among sites. TAGB of cornfields ranged from 4.7 - 41.9 Mg/ha. In pastures TAGB ranged from 6.5 - 47.7 Mg/ha. Wood debris and large trees were the most substantial and variable biomass

Table 2.3. Total aboveground biomass (Mg/ha) in primary forest, cornfield, and pasture sites of the Los Tuxtlas Region, Mexico. Mean  $\pm$  one standard error is presented for each cover type. Tree biomass is divided into classes based on diameter at breast height (dbh) measured in centimeters. The surface layer category represents the sum of litter and seedling components of TAGB.

Forests	litter	seedling	surface layer	dead wood	palm	liana	tree <10	tree 10-30	tree 30-70	tree >70	total
SL	7.1	2.4	9.5	22.9	5.9	0.9	13.6	57.3	128.9	114.5	353.6
SN	6.3	0.8	7.2	9.1	5.8	6.6	4.3	27.3	134.3	125.7	320.2
SB	5.3	0.6	5.9	2.7	7.2	2.1	1.7	48.8	142.6	182.0	392.9
SP	5.8	0.6	6.4	22.6	1.9	3.3	4.3	51.7	170.4	284.2	544.7
mean	6.1 $\pm$ 0.4	1.1 $\pm$ 0.4	7.3 $\pm$ 0.8	14 $\pm$ 5.1	5.2 $\pm$ 1.2	3.2 $\pm$ 1.2	6.0 $\pm$ 2.6	46 $\pm$ 6.6	144 $\pm$ 9.2	177 $\pm$ 39	403 $\pm$ 50

Corn-fields	surface layer	corn plant	corn cob	corn grain	wood debris	palm	liana	tree <10	tree >10	total
C-3	4.5	6.4	0.5	1.3	20.6	0.0	0.0	0.0	0.6	33.7
C-5	2.1	2.7	0.2	0.5	33.6	0.6	0.0	0.0	2.1	41.9
C-32	2.1	6.3	0.7	1.7	0.0	0.0	0.0	0.0	0.0	10.8
C-45	1.5	2.6	0.2	0.4	0.0	0.0	0.0	0.0	0.0	4.7
mean	2.6 $\pm$ 0.7	4.5 $\pm$ 1.1	0.4 $\pm$ 0.1	1.0 $\pm$ 0.3	14 $\pm$ 8.3	0.2 $\pm$ 0.2	0.0	0.0	0.7 $\pm$ 0.5	23 $\pm$ 8.9

Pastures	surface layer	wood debris	palm	liana	tree <10	tree >10	total
P-8	4.7	1.4	0.0	0.1	1.4	21.6	29.3
P-9	10.2	1.3	0.0	0.0	0.2	36.1	47.7
P-10	12.1	15.9	0.0	0.0	0.0	1.3	29.3
P-28	4.6	2.3	0.0	0.0	0.2	2.2	9.4
P-33a	8.0	0.0	0.0	0.0	0.1	0.0	8.2
P-33b	5.4	0.0	0.0	0.0	0.7	0.3	6.5
P-40	7.5	1.9	0.0	0.0	0.4	27.7	37.6
mean	7.5 $\pm$ 1.1	3.3 $\pm$ 2.1	0.0	0.0 $\pm$ 0.0	0.4 $\pm$ 0.2	13 $\pm$ 5.8	24 $\pm$ 6.1

components in cornfields and pastures. Woody biomass ranged from 0 - 38 Mg/ha and 0 - 36 Mg/ha in pastures and cornfields, respectively. In contrast, non-woody biomass (i.e., the surface layer and corn biomass) ranged from 5 - 13 Mg/ha in cornfields and from 5 - 12 Mg/ha in pastures. On average, corn biomass accounted for  $\approx$ 25% of TAGB in cornfields. In pastures, surface layer biomass accounted for  $\approx$ 30% of TAGB. Palm and liana biomass was negligible or nonexistent in both pasture and cornfield sites (Table 2.3).

Table 2.4. Stem density (stems/ha) and basal area (m<sup>2</sup>/ha) of woody species in primary forests of the Los Tuxtlas Region, Mexico. Size classes refer to diameter at breast height (1.3 m) measured in centimeters.

forest site	density (stems/ha)				total >10	basal area (m <sup>2</sup> /ha)				
	0-10	10-30	30-70	>70		0-10	10-30	30-70	>70	total
SL	7031.3	468.6	67.3	15.24	551.1	7.2	10.8	12.4	9.8	40.2
SN	6968.8	186.7	95.2	21.6	303.5	4.2	4.5	15.0	11.7	35.4
SB	5406.3	247.6	87.6	22.9	358.1	3.1	6.8	14.4	16.0	40.3
SP	7000.0	274.3	110.5	27.9	412.7	2.6	7.3	18.2	22.7	50.8
mean±se	6602±399	294±61	90±8.9	22±2.6	406±53	4.3±1.0	7.3±1.3	15±1.2	15±2.8	42±3.3

### Elemental Concentrations of TAGB

Concentrations of C in the various components of aboveground biomass ranged between 43% and 50%. Woody components tended toward higher C concentrations, whereas C concentrations in leaf, herb, surface layer, and corn grain were lower (Table 2.5). In contrast to C, concentrations of N, S, and P were generally higher in tree leaf, herb, surface layer, and corn grain components and lower in woody components (Table 2.5).

### Mass of Aboveground C and Nutrient Pools

Distributions of C pools were similar to those of TAGB. Total aboveground C pools of forest sites ranged from 155 - 264 Mg/ha. Trees >30 cm dbh accounted for 80% of the total aboveground C pool of forest sites, and variation in total C between sites was primarily due to variation in the mass of C in trees >70 cm (Table 2.6). Aboveground C mass was significantly higher in primary forests relative to cornfields and pastures ( $P = 0.00$ ); C mass did not differ between pastures and cornfields ( $P = 1.00$ ). Conversion of forests to pastures or cornfields resulted in a loss of 94% of aboveground C mass, or 184 Mg/ha. Total C mass was  $\approx 11$  Mg/ha in both pastures and cornfields, and wood debris and large trees accounted for the majority of aboveground C mass in each land-cover type.

Table 2.5. Mean concentrations of C, N, S, and P in components of aboveground biomass in forest, pastures, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are mean  $\pm$  standard error.

vegetation type	C (%)	N (mg/g)	S (mg/g)	P (mg/g)
litter- forest sites	46.15 $\pm$ 0.88	17.29 $\pm$ 1.16	1.59 $\pm$ 0.16	0.70 $\pm$ 0.07
herbs - forest sites	42.52 $\pm$ 0.24	19.05 $\pm$ 1.01	2.88 $\pm$ 0.16	1.18 $\pm$ 0.13
surface layer - pasture sites	43.68 $\pm$ 0.33	13.34 $\pm$ 0.74	2.27 $\pm$ 0.38	1.73 $\pm$ 0.27
surface layer - cornfield sites	42.48 $\pm$ 0.46	14.06 $\pm$ 0.84	1.29 $\pm$ 0.26	1.42 $\pm$ 0.34
palm (trunk only)	47.32 $\pm$ 0.30	7.00 $\pm$ 1.29	1.10 $\pm$ 0.16	1.00 $\pm$ 0.18
trees <10cm - leaf	43.05 $\pm$ 0.84	26.04 $\pm$ 0.98	4.05 $\pm$ 0.30	1.48 $\pm$ 0.14
trees >10cm - leaf	46.25 $\pm$ 0.51	25.14 $\pm$ 0.76	2.99 $\pm$ 0.17	1.35 $\pm$ 0.11
trees <10cm - wood	45.82 $\pm$ 0.25	8.01 $\pm$ 0.28	1.53 $\pm$ 0.19	0.73 $\pm$ 0.07
trees >10cm - wood	48.58 $\pm$ 0.13	3.20 $\pm$ 0.18	0.45 $\pm$ 0.10	0.19 $\pm$ 0.02
corn plant	44.59 $\pm$ 0.29	9.34 $\pm$ 1.13	0.83 $\pm$ 0.16	1.36 $\pm$ 0.29
corn cob	45.97 $\pm$ 0.13	5.97 $\pm$ 1.06	0.43 $\pm$ 0.17	1.01 $\pm$ 0.29
corn grain	44.43 $\pm$ 0.54	16.69 $\pm$ 0.64	1.12 $\pm$ 0.15	2.11 $\pm$ 0.12
wood debris diameter class (cm)				
2.55-7.6	49.16 $\pm$ 0.28	4.93 $\pm$ 0.31	0.49 $\pm$ 0.04	0.25 $\pm$ 0.02
>7.6 sound	50.12 $\pm$ 0.33	3.73 $\pm$ 0.43	0.19 $\pm$ 0.02	0.36 $\pm$ 0.19
>7.6 rotten	49.29 $\pm$ 0.63	5.64 $\pm$ 0.68	0.42 $\pm$ 0.09	0.31 $\pm$ 0.06

Total aboveground pools of N in forests, pastures, and cornfields averaged 1705, 161 and 152 kg/ha, respectively. Mass of N was significantly higher in forests than pastures and cornfields ( $P = 0.00$ ), but did not differ between pastures and cornfields ( $P = 1.00$ ). Reductions of N due to forest conversion were slightly lower than reductions in C; N pools of pastures and cornfields represented  $\approx 9\%$  of those in forests.

Partitioning of N among components of aboveground biomass in pastures and cornfields was distinctly different from that of C and biomass. For example, whereas the surface layer made up only 29% the total C pool in pastures, it constituted 58% of the total N pool. Similarly, combined pools of surface layer and total corn biomass made up 34% of total C but 63% of N in cornfield sites. In forests N, like C, was concentrated in tree biomass; trees >10 cm dbh accounted for 91% of N and 82% of C in TAGB of forest sites (Table 2.6).

Table 2.6. Mass of C and N in aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are mean  $\pm$  one standard error. In forest sites litter and seedling biomass pools were sampled separately. The surface layer category represents the sum of these two compartments.

<b>carbon (Mg/ha)</b>			
<b>biomass compartment</b>	<b>forest</b>	<b>pasture</b>	<b>cornfield</b>
surface layer	3.3 $\pm$ 0.4	3.3 $\pm$ 0.5	1.1 $\pm$ 0.3
litter	2.8 $\pm$ 0.2		
seedlings	0.5 $\pm$ 0.2		
wood debris	7.1 $\pm$ 2.5	1.6 $\pm$ 1.1	6.8 $\pm$ 4.1
corn biomass			2.6 $\pm$ 0.6
palm	2.5 $\pm$ 0.5	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1
liana	1.5 $\pm$ 0.6	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
tree <10cm	2.7 $\pm$ 1.2	0.2 $\pm$ 0.1	0.0 $\pm$ 0.0
tree 10-30cm	22.4 $\pm$ 3.2	0.9 $\pm$ 0.3	0.3 $\pm$ 0.2
tree 30-70cm	69.9 $\pm$ 4.5	2.2 $\pm$ 1.3	0.0 $\pm$ 0.0
tree >70cm	85.7 $\pm$ 18.8	3.1 $\pm$ 2.0	0.0 $\pm$ 0.0
<b>total</b>	<b>195.1 <math>\pm</math> 24.2</b>	<b>11.3 <math>\pm</math> 3.0</b>	<b>10.9 <math>\pm</math> 4.4</b>

<b>nitrogen (kg/ha)</b>			
<b>biomass compartment</b>	<b>forest</b>	<b>pasture</b>	<b>cornfield</b>
surface layer	126 $\pm$ 10	93 $\pm$ 9	35 $\pm$ 8
litter	105 $\pm$ 5		
seedlings	21 $\pm$ 8		
wood debris	60 $\pm$ 20	15 $\pm$ 10	53 $\pm$ 32
corn biomass			61 $\pm$ 17
palm	36 $\pm$ 8	0 $\pm$ 0	1 $\pm$ 1
liana	28 $\pm$ 11	0 $\pm$ 0	0 $\pm$ 0
tree <10cm	56 $\pm$ 24	4 $\pm$ 2	0 $\pm$ 0
tree 10-30cm	192 $\pm$ 28	8 $\pm$ 2	3 $\pm$ 2
tree 30-70cm	554 $\pm$ 37	17 $\pm$ 10	0 $\pm$ 0
tree >70cm	653 $\pm$ 140	24 $\pm$ 16	0 $\pm$ 0
<b>total</b>	<b>1705 <math>\pm</math> 165</b>	<b>161 <math>\pm</math> 24</b>	<b>152 <math>\pm</math> 43</b>

Table 2.6 continued. Mass of S and P in aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are mean  $\pm$  one standard error. In forest sites litter and seedling biomass pools were sampled separately. The surface layer category represents the sum of these two compartments.

<b>sulfur (kg/ha)</b>			
<b>biomass compartment</b>	<b>forest</b>	<b>pasture</b>	<b>cornfield</b>
surface layer	12.9 $\pm$ 1.6	16.8 $\pm$ 3.6	3.3 $\pm$ 1.1
litter	9.7 $\pm$ 0.8		
seedlings	3.1 $\pm$ 1.3		
wood debris	3.7 $\pm$ 1.2	1.0 $\pm$ 0.7	3.0 $\pm$ 1.8
corn biomass			4.5 $\pm$ 0.7
palm	5.7 $\pm$ 1.3	0.0 $\pm$ 0.0	0.2 $\pm$ 0.2
liana	5.1 $\pm$ 2.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
tree <10cm	10.3 $\pm$ 4.4	0.8 $\pm$ 0.3	0.0 $\pm$ 0.0
tree 10-30cm	25.7 $\pm$ 3.7	1.0 $\pm$ 0.3	0.4 $\pm$ 0.3
tree 30-70cm	75.0 $\pm$ 4.9	2.3 $\pm$ 1.4	0.0 $\pm$ 0.0
tree >70cm	89.0 $\pm$ 19.2	3.3 $\pm$ 2.1	0.0 $\pm$ 0.0
<b>total</b>	<b>227.4 <math>\pm</math> 22.5</b>	<b>25.2 <math>\pm</math> 4.4</b>	<b>11.4 <math>\pm</math> 2.4</b>

<b>phosphorus (kg/ha)</b>			
<b>biomass compartment</b>	<b>forest</b>	<b>pasture</b>	<b>cornfield</b>
surface layer	5.6 $\pm$ 0.8	12.4 $\pm$ 1.9	4.1 $\pm$ 2.0
litter	4.3 $\pm$ 0.5		
seedlings	1.3 $\pm$ 0.5		
wood debris	4.9 $\pm$ 1.8	1.1 $\pm$ 0.7	4.7 $\pm$ 2.9
corn biomass			7.9 $\pm$ 1.6
palm	5.4 $\pm$ 1.2	0.0 $\pm$ 0.0	0.2 $\pm$ 0.2
liana	2.4 $\pm$ 0.9	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
tree <10cm	4.5 $\pm$ 2.0	0.4 $\pm$ 0.1	0.0 $\pm$ 0.0
tree 10-30cm	11.2 $\pm$ 1.6	0.4 $\pm$ 0.1	0.9 $\pm$ 0.7
tree 30-70cm	32.5 $\pm$ 2.1	1.0 $\pm$ 0.6	0.0 $\pm$ 0.0
tree >70cm	38.5 $\pm$ 8.3	1.4 $\pm$ 0.9	0.0 $\pm$ 0.0
<b>total</b>	<b>105.0 <math>\pm</math> 9.2</b>	<b>16.8 <math>\pm</math> 2.4</b>	<b>17.8 <math>\pm</math> 4.9</b>

Total aboveground pools of S in forests, pastures, and cornfields sites were 227, 25, and 11 kg/ha, respectively. Mass of aboveground S in pastures and cornfields was significantly lower compared to that in primary forests ( $P = 0.00$ ), but did not differ between each other ( $P = 0.64$ ). In pastures, the surface layer contained the majority of the S (67%), and the majority of S in cornfields was distributed between the surface layer and

corn biomass components (68% of total). S mass of forests was concentrated in trees >10 cm dbh (83% of total).

Total aboveground mass of P averaged 105 kg/ha in forests and was significantly higher than P mass in either pastures or cornfields ( $P = 0.00$ ). Site conversion resulted in an average decline of 83% of aboveground P pools; mass of P in pastures and cornfields was 17 and 18 kg/ha and did not differ between these cover types. In forests,  $\approx 78\%$  of the total pool of P was concentrated in trees >10 cm dbh. In contrast,  $\approx 74\%$  of the aboveground P of pastures was in the surface layer, and 67% of total P of cornfields was in the surface layer and corn biomass (Table 2.6).

Conversion of primary forests resulted in substantial shifts in elemental ratios of TAGB (Table 2.7). Ratios of C:N in TAGB of primary forest sites averaged nearly twice those of pasture and cornfield sites. In addition, ratios of C:P were approximately 3 times higher in forests relative to pastures and cornfields, and ratios of N:P were 50% higher in forests relative to pastures and 100% higher in forests relative to cornfield sites.

Table 2.7. Comparison of elemental mass ratios in primary forest, pasture, and cornfield sites of the Los Tuxtlas Region, Mexico. Within each elemental ratio comparison, cover types that share the same letter were not significantly different from one another ( $P < 0.1$ ).

cover type	C:N	C:P	C:S	N:P	N:S	P:S
forests	114 $\pm$ 3 a	1845 $\pm$ 72 a	853 $\pm$ 22 a	16 $\pm$ 0.2 a	8 $\pm$ 0.0 a	0.5 $\pm$ 0.0 a
pastures	63 $\pm$ 10 b	643 $\pm$ 149 b	441 $\pm$ 76 b	10 $\pm$ 0.9 b	7 $\pm$ 0.7 a	0.8 $\pm$ 0.1 b
cornfields	62 $\pm$ 15 b	543 $\pm$ 154 b	845 $\pm$ 272 a,b	8 $\pm$ 0.8 b	13 $\pm$ 1.5 b	1.5 $\pm$ 0.1 c

### Soil Nutrient Concentrations

At each soil depth, concentrations of C, N, S, and P in forest, pasture, and cornfield soils did not differ significantly (Table 2.8). In all land-cover types, soil C concentrations decreased with depth; concentrations ranged from 7.8% to 1.1%. In general, concentrations of N, S, and P were distributed throughout the soil profile in a

manner similar to soil C: concentrations decreased with increasing depth and did not differ significantly between forests, pastures, and cornfields at any soil depth (Table 2.8).

Table 2.8. Soil nutrient concentrations in forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are mean  $\pm$  one standard error. Phosphorus concentrations were determined only for surface soil layers and were not measured in cornfield sites. P-values were derived from single classification analysis of variance tests of the three land-cover types at each soil depth.

depth (cm)	carbon (%)			P-value
	forest	pasture	cornfield	
0-2.5	7.8 $\pm$ 1.7	6.5 $\pm$ 0.9	5.4 $\pm$ 0.8	0.40
2.5-10	5.0 $\pm$ 1.5	4.6 $\pm$ 0.5	4.6 $\pm$ 0.8	0.95
10-30	3.5 $\pm$ 1.4	2.5 $\pm$ 0.6	3.5 $\pm$ 0.7	0.67
30-50	2.6 $\pm$ 1.1	1.6 $\pm$ 0.4	2.3 $\pm$ 0.4	0.55
50-100	1.9 $\pm$ 0.8	1.1 $\pm$ 0.2	1.7 $\pm$ 0.3	0.51
depth (cm)	nitrogen (mg/g)			P-value
	forest	pasture	cornfield	
0-2.5	7.04 $\pm$ 1.66	6.17 $\pm$ 1.01	5.10 $\pm$ 0.91	0.58
2.5-10	5.00 $\pm$ 1.62	4.43 $\pm$ 0.56	4.63 $\pm$ 0.91	0.92
10-30	3.57 $\pm$ 1.58	2.56 $\pm$ 0.74	3.69 $\pm$ 0.92	0.71
30-50	2.43 $\pm$ 1.01	1.47 $\pm$ 0.42	2.21 $\pm$ 0.45	0.55
50-100	1.66 $\pm$ 0.68	1.05 $\pm$ 0.22	1.54 $\pm$ 0.36	0.58
depth (cm)	sulfur (mg/g)			P-value
	forest	pasture	cornfield	
0-2.5	0.83 $\pm$ 0.18	0.79 $\pm$ 0.10	0.74 $\pm$ 0.09	0.90
2.5-10	0.65 $\pm$ 0.17	0.61 $\pm$ 0.08	0.70 $\pm$ 0.07	0.85
10-30	0.52 $\pm$ 0.18	0.40 $\pm$ 0.06	0.58 $\pm$ 0.05	0.48
30-50	0.44 $\pm$ 0.17	0.32 $\pm$ 0.11	0.46 $\pm$ 0.08	0.66
50-100	0.42 $\pm$ 0.17	0.33 $\pm$ 0.08	0.41 $\pm$ 0.08	0.85
depth (cm)	phosphorus (mg/g)		P-value	
	forest	pasture		
0-2.5	1.27 $\pm$ 0.04	1.42 $\pm$ 0.14	0.27	
2.5-10	1.34 $\pm$ 0.11	1.34 $\pm$ 0.18	1.00	

#### Mass of C and Nutrients in Soils

Mass of C, N, S, and P in soil pools did not differ significantly between the forest, pasture, and cornfield sites that we sampled (Table 2.9). In addition, mass of these

elements did not differ between land-use types at any soil depth. Total mass of soil C to a 1 m depth in forests, pastures, and cornfields averaged 210, 167, and 200 Mg/ha, respectively (Table 2.9). Total soil N to a 1 m depth ranged between 15,974 and 19,850 kg/ha for the 3 land cover types. Total soil S to a 1 m depth ranged between 3,358 and 3,835 kg/ha. The lack of statistical difference between land-cover types was due to a high variation within forest and cornfield sites. Although the average mass of C, N, and S was lower in pastures than in forests and cornfields, the high variability among forest and cornfield sites resulted in a lack of significance among land-cover types (Figure 2.4). Comparing elemental mass in soils to a 1 m depth of pastures and cornfields >30 years in age (i.e., P-33a, P-33b, C-32, and C-45) to that in soils to a 1 m depth of pastures and cornfields <10 years in age (i.e., P-8, P-9, and C-5), no significant difference was found between the two groups with regard to C ( $P = 0.18$ ), N ( $P = 0.22$ ) and S ( $P = 0.11$ ).

In all land-cover types, approximately 50% of soil C and N occurred between 0-30 cm;  $\approx 30\%$  of C and N was located in the 50-100 cm depth. Approximately 40% of soil S was located within the 0-30 soil depth range, and 30 - 50% was located between 50 and 100 cm (Table 2.9).

#### Ecosystem Pools of C, N, and S

Total ecosystem pools (excluding root biomass) of C in forests, pastures, and cornfields averaged 413, 177, and 209 Mg/ha, respectively. While C in forests was distributed equally between soil and aboveground vegetation pools, soil pools accounted for the majority of total ecosystem C in pastures and cornfields (Figure 2.5). Ecosystem pools of C were significantly higher in forest sites than in both pasture ( $P = 0.049$ ) and cornfield ( $P = 0.019$ ) sites. Ecosystem pools of N averaged 22, 16 and 20 Mg/ha for forests, pastures, and cornfields and did not differ among the three land cover types ( $P = 0.59$ ). On average, 96% of N in each of the 3 land cover types was concentrated in soil pools. Ecosystem pools of S ranged from 3 to 4 Mg/ha and did not differ among forest,

pasture, and cornfield sites ( $P = 0.83$ ). Soil pools accounted for 98% of total ecosystem S mass in each of the land cover types (Figure 2.5).

Table 2.9. Mass of C, N, S, and P in soils of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are mean  $\pm$  one standard error. Mass of C, N, and S are to a 1 m depth; mass of P is to a 10 cm depth. P mass was not quantified in cornfield sites. P-values were derived from single classification analysis of variance tests of the three land-cover types at each soil depth.

carbon (Mg/ha)				
depth (cm)	forest	pasture	cornfield	P-value
0-2.5	15.4 $\pm$ 0.8	13.6 $\pm$ 1.2	12.6 $\pm$ 3.0	0.59
2.5-10	28.5 $\pm$ 3.6	28.9 $\pm$ 2.0	32.5 $\pm$ 8.4	0.83
10-30	53.0 $\pm$ 12.6	43.1 $\pm$ 3.2	60.4 $\pm$ 12.0	0.43
30-50	40.3 $\pm$ 11.1	28.1 $\pm$ 2.4	42.8 $\pm$ 6.7	0.30
50-100	73.1 $\pm$ 21.8	52.9 $\pm$ 5.9	52.0 $\pm$ 26.2	0.67
<b>total to 1m</b>	<b>210.3 <math>\pm</math> 49.2</b>	<b>166.6 <math>\pm</math> 9.0</b>	<b>200.3 <math>\pm</math> 47.6</b>	<b>0.65</b>
nitrogen (kg/ha)				
depth (cm)	forest	pasture	cornfield	P-value
0-2.5	1,382 $\pm$ 83	1,280 $\pm$ 158	1,204 $\pm$ 325	0.85
2.5-10	2,866 $\pm$ 417	2,771 $\pm$ 248	3,290 $\pm$ 951	0.79
10-30	5,358 $\pm$ 1,454	4,291 $\pm$ 558	6,465 $\pm$ 1,686	0.47
30-50	3,818 $\pm$ 1,072	2,607 $\pm$ 258	4,174 $\pm$ 820	0.30
50-100	6,426 $\pm$ 1,895	5,026 $\pm$ 516	4,865 $\pm$ 2,475	0.78
<b>total to 1m</b>	<b>19,850 <math>\pm</math> 4,863</b>	<b>15,974 <math>\pm</math> 1,224</b>	<b>19,922 <math>\pm</math> 5,399</b>	<b>0.70</b>
sulfur (kg/ha)				
depth (cm)	forest	pasture	cornfield	P-value
0-2.5	164 $\pm$ 9	165 $\pm$ 17	174 $\pm$ 38	0.95
2.5-10	380 $\pm$ 34	380 $\pm$ 30	491 $\pm$ 97	0.35
10-30	802 $\pm$ 139	704 $\pm$ 66	1,013 $\pm$ 116	0.17
30-50	703 $\pm$ 169	542 $\pm$ 86	874 $\pm$ 138	0.24
50-100	1,584 $\pm$ 455	1,568 $\pm$ 182	1,283 $\pm$ 649	0.86
<b>total to 1m</b>	<b>3,632 <math>\pm</math> 800</b>	<b>3,358 <math>\pm</math> 316</b>	<b>3,835 <math>\pm</math> 862</b>	<b>0.87</b>
phosphorus (kg/ha)				
depth (cm)	forest	pasture	P-value	
0-2.5	267 $\pm$ 40	316 $\pm$ 31	0.45	
2.5-10	864 $\pm$ 192	894 $\pm$ 120	0.92	
<b>total to 10 cm</b>	<b>1,131 <math>\pm</math> 231</b>	<b>1,210 <math>\pm</math> 151</b>	<b>0.82</b>	

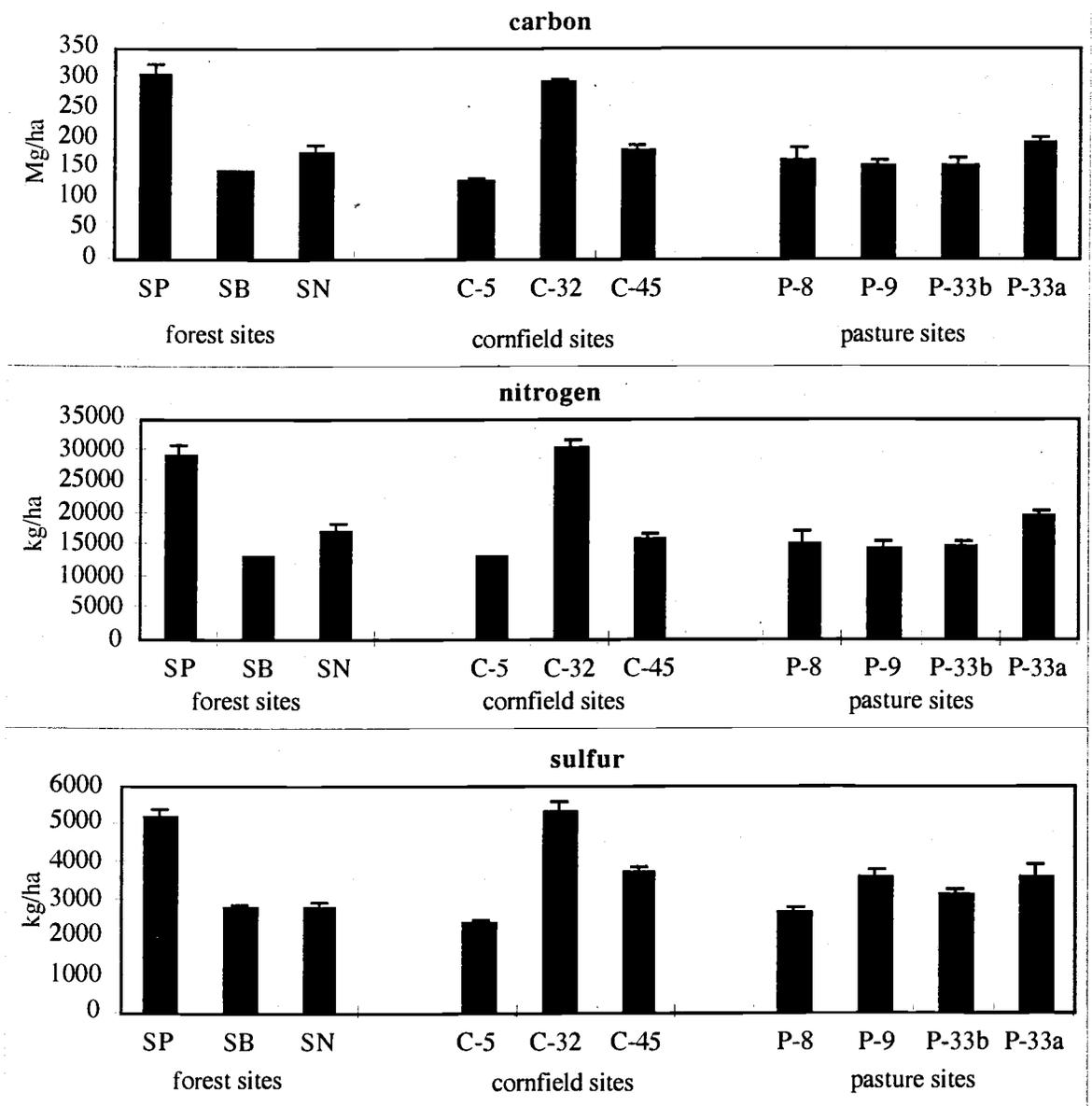


Figure 2.4. Average mass of C, N, and S of soil to a 1 m depth in forest, pasture, and cornfield sites of the Los Tuxtlas Region, Mexico. Error bars represent one standard error of the mean (n = 5).

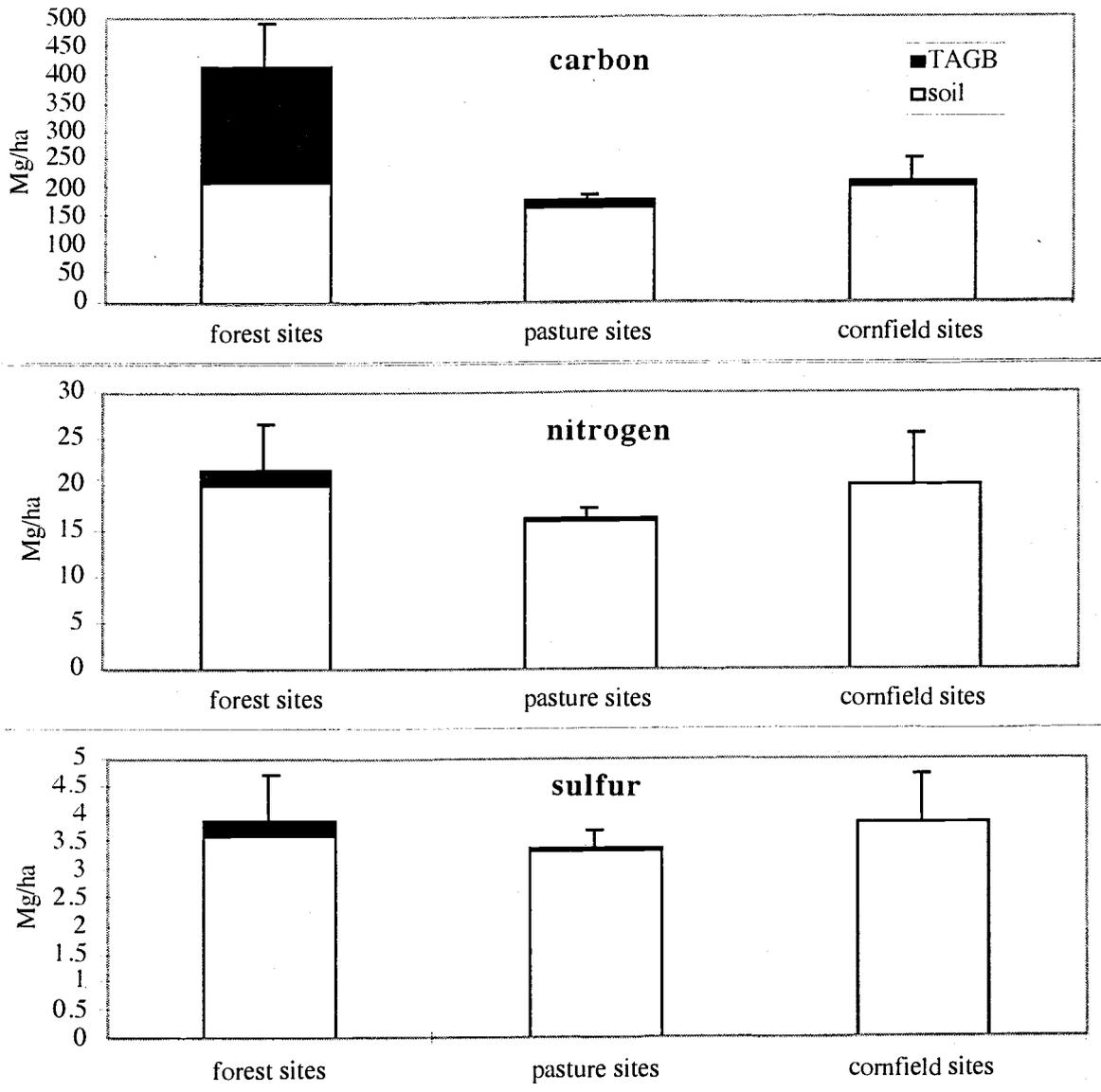


Figure 2.5. Ecosystem pools (i.e., aboveground biomass and soil pools) of C, N, and S in forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Error bars represent one standard error from the mean of the combined aboveground and soil pools.

## Discussion

### Pools of TAGB in Forests

The average value of TAGB of forests measured in this study (403 Mg/ha) is high relative to of TEF sites measured elsewhere in tropical America. Cummings (1998) report

a mean value of 345 Mg/ha for 20 forest sites in the state of Rondonia, Brazil. Uhl et al. (1988) reported TAGB values of 333 and 363 Mg/ha for 2 primary forest sites in the eastern Amazon Basin, and Jordan (1989) reported a value of 264 Mg/ha for TEF's growing on oxisol soils in the Venezuelan Amazon. Measures of TAGB in TEF sites of Puerto Rico, Costa Rica, and Panama were 365, 382, and 326 Mg/ha, respectively (Ovington and Olson 1970, Werner, unpublished data cited by Jordan 1989, Golley et al. 1975). Brown (1997) presented TAGB estimates based on forest inventories of 22 moist forests in Tropical America; only 3 of these forests had TAGB pools that were equivalent to, or higher than, the average TAGB of forest sites in the Los Tuxtlas Region. Because biomass pools of primary forests in the Los Tuxtlas Region were large relative to other forest systems in tropical America, biomass losses following deforestation and land use would be expected to be relatively large as well.

The broad range of primary forest TAGB in this study (320-545 Mg/ha) demonstrates the potential for high variability among forest sites in relatively close proximity to one another. In the Los Tuxtlas Region this variability is likely due to edaphic conditions at each site; the two sites with relatively low TAGB (i.e., SL and SN), were located on very rocky and very steep slopes, respectively. In contrast, the site with the largest TAGB (SB) was located on relatively flat substrate near the margins of a large lake.

Variation among the four forest sites was primarily due to variation in trees >70 cm dbh; this vegetation component represented the largest contribution to TAGB and was also highly variable among those sites. On average, trees >70 cm dbh accounted for 44% of TAGB of the four forest sites, and the standard error represented 22% of the mean for this biomass component. TAGB was dominated by trees >30 cm dbh which represented  $\approx 80\%$  of TAGB. This dominance of primary forest TAGB by large tree biomass is more pronounced in Los Tuxtlas than in forests of the Brazilian Amazon where trees >30 cm dbh accounted for only  $\approx 58\%$  of TAGB, and trees >70 cm dbh accounted for only 20% of TAGB (Cummings 1998).

The structural characteristics of trees in forests of the Los Tuxtlas Region underscored the importance of large trees within these sites. Average stem density (406 stems/ha) and basal area (37.4 m<sup>2</sup>/ha) of trees >10 cm dbh in the 4 forest sites were comparable to results of Bongers et al. (1988) who reported a density of 346 stems/ha and a basal area of 34.9 m<sup>2</sup>/ha for trees >10 cm sampled at one forest site in the Los Tuxtlas Region. However, mean basal area of all trees >10 cm dbh of forest sites in the Los Tuxtlas Region was somewhat higher than trees >5 cm dbh (32.1 m<sup>2</sup>/ha) in mature forest sites of the Venezuelan Amazon (Saldarriaga 1988). Furthermore, mean basal area of trees >70 cm dbh in Los Tuxtlas forests (15.1 m<sup>2</sup>/ha) was more than double that of trees >60 cm dbh in the Venezuelan forests (7.3 m<sup>2</sup>/ha).

In contrast to the large tree components of primary forest TAGB, combined biomass of the surface layer, dead wood, trees <10 cm dbh, palms, and lianas accounted for a relatively small portion of forest TAGB ( $\approx 9\%$ ), and did not vary greatly between the 4 forest sites; combined pools of these components ranged between 7 and 15% of TAGB. Wood debris, in particular, proved to be a minor component of forest biomass, accounting for, on average, only 3% of TAGB.

#### Mass of C, N, S, and P of Forest Sites

Our results indicate that mass of C in intact forests of the Los Tuxtlas Region was much larger than had been previously thought. Mass of C in aboveground biomass and soils of forests averaged 195 and 210 Mg/ha, respectively. These values are substantially higher than previous estimates of C in TAGB (144 Mg/ha) and soils (66 Mg/ha) of TEF's in Mexico (Masera et al., 1992). In addition, they are substantially higher than values for aboveground biomass (150 Mg/ha) and soil (104 Mg/ha) used by Riley et al. (1997) to model landscape level C dynamics in the Los Tuxtlas Region. We measured losses of approximately 95% of aboveground C as a result of conversion of forest to non-forest vegetation in the Los Tuxtlas region. This loss constitutes 184 Mg/ha of C and is 2.5 times higher than estimates of C loss due to land-use change in the Los Tuxtlas Region made by

Masera et al. (1992) and Riley et al. (1997). These studies estimated that deforestation and land-use change would result in losses of only 67 and 75 Mg/ha of C, respectively.

Pools of soil carbon in forests of the Los Tuxtlas Region were large relative to C pools in forest soils measured elsewhere. At 210 Mg/ha, the average C mass of forest soils sampled to a 1 m depth in this study was between 39% and 233% higher than C mass in tropical soils of a variety of soil textures and located in a variety of climatic regimes (Brown 1993). Sanchez (1982) reported C mass to a 1 m depth for a variety of soil orders from the tropics (i.e., Oxisols, Mollisols, Alfisols and Ultisols) ranging from 64 to 113 Mg/ha. The large amount of C in soils from the Los Tuxtlas Region is likely related to their recent volcanic origin. Volcanically derived soils (i.e., Andosols) commonly contain significant amounts of allophane - a mineral capable of sequestering large quantities of soil organic matter (Sollins et al. 1988). Pools of soil C in the Los Tuxtlas Region are similar in magnitude to those of volcanic soils of tropical moist forests in Hawai'i (Crews et al. 1995, Townsend et al. 1995) and in Costa Rica (Veldkamp 1994). In general, tropical Andosols are characterized as being fertile and having excellent physical properties which make them suitable for land-use. As a result, Andosols are commonly foci of land-use change in the tropics (Sanchez 1989).

In contrast to the roughly equal distribution of C mass between TAGB and soil pools, the majority of the N mass in forest sites was located in soil pools. Mass of N in TAGB was 1,705 kg/ha and was lower, on average, than that of forests in the Brazilian Amazon (i.e., 2055 kg/ha; Kauffman et al. 1995), but was within the range of total N pools in aboveground biomass of moist tropical forests reviewed by Vitousek and Sanford (1986). At  $\approx 20,000$  kg/ha, N mass was ten times higher in soils to a 1 m depth than in TAGB pools of forest sites. In addition, N mass in forest soils of the Los Tuxtlas Region was two to three times the amount of soil N to a 1 m depth found in tropical soils reported by Sanchez et al. (1983). As with soil C, the large soil N pools in the forests of Los Tuxtlas are likely due to the inherent capacity of Andosols to sequester large quantities of

soil organic matter. Crews et al. (1995) reported similar values for N mass in Andosols of Hawai'i that support tropical evergreen forests.

Mass of P in aboveground biomass of forests in the Los Tuxtlas Region (105 kg/ha) was nearly 60% higher than forests of Brazil (67 kg/ha; Kauffman et al. 1995), but was at the low end of the range of tropical forests on moderately fertile soils of Panama, Venezuela, and Ghana (i.e., 112 - 290 kg/ha; see review by Vitousek and Sanford 1986). The relatively large pools of aboveground P in Los Tuxtlas forests coincide with large pools in soils; total P in surface soils was nearly tenfold higher than in surface soils of forests in the Amazon reported by Kauffman et al. (1995) and was comparable to mass of total P in soils of moist forests of Hawai'i (Crews et al. 1995).

#### Aboveground Pools of Biomass, C, N, S, and P in Pastures and Cornfields

In Los Tuxtlas, pasture TAGB was generally higher than the 8 - 20 Mg/ha range of pasture biomass used to model C and nutrient dynamics following deforestation elsewhere in tropical America (Fearnside 1992, Buschbacher 1984), but lower than values reported by Kauffman (in press) for young pastures of the Amazon Basin (53 and 119 Mg/ha). The higher values seen in Amazonian pastures were due to larger amounts of downed woody debris at these sites relative to pastures in the Los Tuxtlas Region.

In cornfields, the average TAGB - 23 Mg/ha - was substantially higher than estimates for TAGB in cultivated sites (0.7 - 10 Mg/ha) used to model C dynamics resulting from land-use change (Fearnside 1996, Houghton et al. 1983). In addition, vegetative biomass of corn (4.5 Mg/ha) at sites in the Los Tuxtlas Region was higher than that of unfertilized cornfields ( $\approx 2.8$  Mg/ha) converted from TEF's in the Uxpanapa Region of Veracruz (Caamal and del Amo 1987). However, total corn biomass, as well as corn grain biomass, was much lower in Los Tuxtlas sites (5.8 and 1.0 Mg/ha, respectively) relative to fertilized cornfields in Poza Rica, Veracruz (12-24 and 5-7 Mg/ha, respectively; Goldsworthy et al. 1974). Although TAGB pools of crops are small relative to those of forests, their variability across landscapes and regions is potentially very high. Increased

resolution of cropland biomass pools and dynamics are likely to greatly improve models of ecosystem dynamics resulting from land-use change.

Differences in the mass of aboveground C among cornfield sites were largely due to the presence or absence of wood debris, and differences between aboveground C mass in pastures were largely due to live standing trees >10 cm dbh. In young cornfields, woody debris accounted for  $\approx 70\%$  of TAGB and C pools, but was nonexistent in old cornfields. Wood debris has been shown to be an important component in other croplands and pastures in tropical America as well. For example, wood debris accounted for between 47% and 87% of TAGB in pastures of the Brazilian Amazon (Kauffman et al., in press).

In pasture sites of Los Tuxtlas, remnant trees >10 cm dbh accounted for a substantial portion of TAGB and C pools. On average, they comprised over 50% of TAGB and C pools, and accounted for  $\approx 75\%$  of these pools in 3 of the 7 pastures sampled. In addition to being important C and nutrient pools, remnant trees in pastures of Los Tuxtlas have been shown to be important foci for the regeneration of woody species (Guevara et al. 1992), as well as providing forage and shade for cattle, fruit for human consumption, and fencing material for small landholders. Together, wood debris and remnant trees represent potentially significant portions of aboveground biomass and elemental pools of pastures and croplands. Consequently, quantification of the fate of these biomass components is critical to understanding ecosystem dynamics following deforestation in tropical landscapes such as the Los Tuxtlas Region.

In addition to the absolute losses of C, N, S and P associated with deforestation and land use, our results also indicate significant shifts in the relative concentrations of those elements in aboveground biomass following land-use change. Conversion of forests to pastures and cornfields in the Los Tuxtlas Region led to a significant reductions in the C:N and C:P ratios in aboveground biomass due to the reduction of woody vegetation in pastures and cornfields relative to forests.

### Pools of C, N, and S, in Soils of Pastures and Cornfields

Although the mean values for C and N mass in soil pools were lower by 20% in pastures compared to forests, these differences were not statistically significant (Table 2.8). In addition, the mass of C, N, and S in soils of cornfield sites were essentially equivalent to those in soils of forest sites. Mass of S and P in soils of pastures also did not differ significantly from those in soils of forest sites. Consequently, our results cannot be used to support previous estimates that C mass in soils would be reduced 20 to 50% following deforestation and land use (Schlesinger 1984, Detwiler 1986, Riley 1997). Although our sample sizes were relatively small and values were highly variable, mass of C, N, S in soils were also not significantly different among sites that differed in type or duration of land use; soil pools did not differ between pastures and cornfields, nor did they differ between younger and older sites. The lack of change of elemental pools in soils following deforestation and land use is likely due to the inherent capacity of Andosols to retain large amounts of soil organic matter in spite of prolonged periods of land use (Vitousek and Sanford 1986, Sanchez 1989, Veldkamp 1994).

Overall, deforestation and land use in the Los Tuxtlas Region resulted in declines of 95% of aboveground biomass, 94% of C, 91% of N, between 89 - 95% of S, and 83% of P in aboveground pools. Losses of C resulting from deforestation and subsequent land-use represented nearly half ( $\approx 184$  Mg/ha) of total ecosystem pools. These losses are high because nearly 50% of the total ecosystem C was stored in TAGB, and approximately 95% of TAGB is eventually lost during the conversion of forests to pastures or cornfields. In contrast, although reductions in the quantities of aboveground N, S, and P during conversion of forests to pastures or cornfields were large, the fractions of total ecosystem N, S, and P that were lost were relatively small. This is due to the fact that the vast majority of N, S, and P was located in soil pools and was not significantly altered by land-use change (Figure 2.5). These results are similar to findings of other studies that changes in aboveground biomass pools tended to dominate those of soil pools of C and nutrients

during deforestation and land-use processes (Trumbore et al. 1995, Kauffman et al. in press).

While losses of N, S, and P due to reductions in TAGB were small relative to total ecosystem pools, losses of these nutrients due to soil erosion may be substantially higher. Deforestation and land use in tropical America typically leads to increased soil erosion; Lal (1984) estimates that lands converted from TEF's lose approximately 1 cm of topsoil each year. If this estimate is accurate for the Los Tuxtlas Region, an area in which the potential for erosion is high (i.e., cultivated slopes commonly exceed 30%), over a ten year period erosional losses of N, S, and P would be equivalent to  $\approx 2.5$  times the pools of these elements contained in TAGB pools of primary forests. Thus, although losses due to soil erosion may not be as apparent as combustion losses during conversion of forest to non-forest vegetation, the impacts of erosion are potentially significant in terms of cumulative nutrient loss following land conversion as well as the impact of such losses on potential site productivity.

Assuming estimates made by Dirzo and Garcia (1992) that  $\approx 91\%$  of the 850 km<sup>2</sup> northern Los Tuxtlas Region will be deforested by the year 2000, and assuming that all of this deforested land is converted to pasture and cultivated land, we calculate eventual total regional losses of 30 Tg of biomass, 14 Tg of C, 0.12 Tg of N, 0.016 Tg of S, and 0.007 Tg of P. Unless profound changes in land-use practices are implemented and the annual 3% rate of deforestation documented by Riley et al. (1997) is reduced, the Los Tuxtlas Region will continue to function as a significant net source of C, N, and S to the atmosphere.

## CHAPTER 3

Biomass, Carbon, and Nutrient Accumulation in Tropical Evergreen Secondary Forests of the Los Tuxtlas Region, Mexico.

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**Keywords:** Secondary Forests, Mexico, Carbon Accumulation, Nutrient Dynamics, Biomass, Los Tuxtlas, Tropical Ecosystems, Greenhouse Gas Flux.

### Abstract

Secondary forests have the capacity to function as large terrestrial sinks for C, N, and S by accumulating biomass, C, and nutrient pools lost due to deforestation and land use in tropical forested regions. However, few studies have quantified that capacity. In the Los Tuxtlas Region of Mexico, a region that has been heavily deforested over the past three decades, pools of biomass, C, N, S, and P were quantified in 11 secondary forest sites ranging from 6 months to 50 years since abandonment. Total aboveground biomass (TAGB) increased with increasing site age; accumulations ranged from 4.8 Mg/ha in a recently abandoned site to 287 Mg/ha in the 50-year-old secondary forest site. Results indicate that secondary forests will reach the TAGB of primary forests of the Los Tuxtlas Region in approximately 73 years. In addition, rates of TAGB accumulation were negatively correlated to the prior land-use history of each secondary forest; as periods of land use prior to abandonment increased, rates of TAGB accumulation decreased.

Aboveground C pools ranged from 2.1 Mg/ha in the youngest forest to 136.1 Mg/ha in the oldest forest. Aboveground N pools ranged from 73 to 1167 kg/ha; aboveground S and P pools ranged from 9.3 to 146.7 kg/ha and from 4.9 to 147 kg/ha, respectively. Soil pools of C, N, and S in secondary forest sites remained relatively stable throughout the successional chronosequence; as a group, they did not differ with respect to forest age or prior land-use history, and did not significantly differ from soil pools of primary forest, cornfield, and pasture sites in the Los Tuxtlas Region. Soil C, N, and S pools of secondary forests averaged  $\approx 200$  Mg/ha,  $\approx 20$  Mg/ha, and  $\approx 3.4$  Mg/ha, respectively.

Dynamics of total ecosystem C were characterized by increasing contributions from aboveground pools with increasing forest age. In contrast, changes in ecosystem pools of N and S during secondary succession were relatively small because the vast majority (>90%) of N and S was located in stable soil pools. Overall, our results indicate that

secondary forests have the potential to act as large sinks for C and nutrients, but that rates of accumulation will be reduced by the duration of prior land-use.

### Introduction

Secondary forests are rapidly becoming among the most common land-cover types in tropical forest regions. It has been estimated that secondary forests now occupy approximately 40% of the total forest area of the tropics and that  $\approx 9 \times 10^6$  ha of secondary forests are formed annually (Brown and Lugo 1990). While secondary succession has always been an integral process in tropical forest ecosystems following natural disturbances (e.g., hurricanes, land slides, and tree falls due to senescence), current increases in secondary forest cover result from anthropogenic disturbances throughout the tropics such as logging activities and conversion of primary forests to pasture and agricultural lands (Brown and Lugo 1990, Skole and Tucker 1993). Fearnside (1996) estimated that by 1990, secondary forests occupied  $\approx 48\%$  of the original area converted from primary forest to pastures or croplands in the Brazilian Amazon.

Tropical secondary forests, particularly during the early stages of succession, have been generally characterized as communities dominated by relatively few fast growing, heliophytic, r-selected, pioneer species (Budowski 1965). Total stem density and leaf area index (LAI) of secondary forests are typically high, while the wood density ( $\text{g/cm}^3$ ) and basal area of dominant species are typically low (Ewel 1980, Brown and Lugo 1990). In general, secondary forests are capable of rapid rates of total net aboveground primary production and biomass accumulation, particularly during the initial stages of succession; previous studies have documented accumulations of up to 100 Mg/ha after the first 15 years of succession (see reviews by Brown and Lugo 1990, Ewel 1980, and Lugo and Brown 1992). Consequently, secondary forests have the potential to assimilate and store relatively large fractions of the carbon and nutrients that are lost during deforestation and land-use phases (Kauffman et al. 1995, Kauffman et al. in press, Hughes see chapter 1). Lugo and Brown (1992) estimated that forest fallow (i.e., secondary forests) may sequester between

0.6 and 1.4 Pg of C each year throughout the tropics, or 40 to 90% of the estimated annual C emissions resulting from biomass burning in tropical ecosystems.

Numerous studies have also documented that secondary forests have the capacity to increase quantities of soil organic matter by increased above and below ground litter inputs, and are generally considered to operate as sinks for both potentially limiting nutrients and C (Aweto 1981, Brown et al. 1984, Lugo et al. 1986, Ramakrishnan and Toky 1981). In contrast, Vitousek (1991) cautioned that while tree regeneration on deforested land results in potentially rapid net C and nutrient accumulation and storage, this storage is likely to be an ephemeral effect due to the shifting nature of land use in the tropics which determines the long-term fate of that fixed C. Indeed, numerous studies have noted the transitory nature of secondary forests within the tropical landscape. In the Brazilian Amazon, for example, secondary forests typically exist as 4- to 10- year old fallows whose accumulated biomass is returned to the atmosphere when the site is converted back to pasture or agriculture via burning (Kauffman et al. in press, Skole et al. 1994).

Rates of secondary forest regrowth following anthropogenic disturbance have been shown to be influenced by the type, duration, and intensity of land use (Quintana-Ascencio 1996, Uhl et al. 1988, Uhl 1987), the proximity of secondary forests to primary forest vegetation (Purata 1986), and the soil fertility status of a given site (Werner 1984, Ewel 1980). However, studies that have quantified rates of biomass accumulation of secondary forests in relation to their age and prior land-use history are relatively rare, and studies that involve the late successional stages of such forests are even rarer. Brown and Lugo (1990) list only 18 studies that quantified biomass pools in secondary forests throughout the world's tropical regions; only 6 of those studies included secondary forests >20 years in age. Given the growing prevalence, diversity, and functional importance of secondary forest systems in the tropics, a greater understanding of biomass, C, and nutrient pool dynamics in these systems is needed.

In Mexico, current rates of deforestation in tropical evergreen forests are high; during the 1980's, approximately 5,000 km<sup>2</sup> of tropical forests were deforested annually (Masera 1995). Despite the need for accurate information concerning rates of biomass, C, and nutrient accumulations in secondary forests of Mexico, only one study (Williams-Linera 1983) has quantified biomass and nutrient dynamics in secondary forests of the Mexican tropics.

As part of their study to estimate regional C dynamics resulting from land-cover change in the Los Tuxtlas Region of Mexico, Riley et al. (1997) modeled C dynamics of secondary forests under the assumption that it would take secondary forests 40 years to accumulate the C pools equivalent to those of intact forest sites. However, these estimates were derived from values of C mass in vegetation and soil pools of secondary forest vegetation outside of Mexico. Clearly, models that predict rates of C and nutrient sequestration by secondary forests in tropical Mexico would be improved by the availability of direct measures of biomass, C, and nutrient pools specific to extensively deforested landscapes such as the Los Tuxtlas Region. Conversion of primary forests to pastures and cornfields in this region has been shown to result in dramatic reductions in total aboveground biomass, C, N, S, and P pools; declines ranged from 85 to 95% of the original pools contained in primary forest vegetation (Hughes see chapter 1). However, questions remain as to the accumulation rates of biomass, C, N, S, and P pools in secondary forests and the possible constraints on those rates following the abandonment of pastures and cultivated sites in the Los Tuxtlas Region.

The objectives of this study were to quantify total aboveground biomass, forest structure, species richness of trees >10 cm dbh, and pools of C, N, S, and P in vegetation and soils in secondary forest sites representing a successional chronosequence in the Los Tuxtlas Region. For comparison, values for tropical primary forest biomass, structure, C, and nutrient pools of the Los Tuxtlas Region (Hughes see chapter 1) were utilized to represent the potential maxima of each of those parameters for secondary forests in this

region. I used this secondary forest chronosequence to quantify potential rates of biomass, C, N, S, and P accumulation, to document the manner in which partitioning of these pools within the various forest components changes through time, and to evaluate the influence of prior land-use history on accumulation rates.

### Study Area

All study sites were located within or very near the Los Tuxtlas Biological Station (LTBS) administered by the Universidad Nacional Autonoma de Mexico (UNAM) (18°35'N, 95°05'W). The LTBS is located in the northeastern portion of the Los Tuxtlas Region in the state of Veracruz, Mexico. This region is defined by the Sierra de Los Tuxtlas - a series of volcanoes constituting the easternmost portion of the Trans-Mexican Volcanic Belt (Nelson and Gonzalez-Caver 1992). All secondary forest sites were located on the lower, southeastern slopes of the San Martin volcano between 100 and 300 m in elevation. Lava flows from San Martin are classified as basanite and alkali basalt. Volcanism in the Los Tuxtlas Region began approximately 7 million years ago and has continued up to the recent past with extensive activity during the last several thousand years (Nelson and Gonzalez-Caver 1992). Historical eruptions occurred as recently as 1664 and 1793; the former eruption resulted in extensive ash deposition and lava flows within and along the margins of the LTBS, and the latter explosive eruption likely resulted in extensive ash deposition and destruction of the tropical forests located along the slopes of the San Martin volcano (Mooser 1958). The topography of the region is characteristic of recent volcanism with undulating hills grading to steep slopes; cinder cones of various sizes are numerous, and maars (i.e. water filled craters) are common.

Soils have been classified as well-drained, coarse textured, vitric Andosols mixed with volcanic ash (FAO/UNESCO 1975). Forest soils are poorly developed, contain high concentrations of organic matter, total N, P, and K, and are weakly acid (pH range 6.1 - 6.5) (Bongers et al. 1988, Chizon 1984).

The climate is classified as hot and humid (Holdridge et al. 1971, Garcia 1970); the mean annual temperature is 27°C and mean annual precipitation is >4000 mm (Soto and Gama 1997). Precipitation is highest between June and February and is interrupted by a dry season between March and May during which time monthly rainfall does not exceed 150 mm. Monthly temperatures range from a minimum of 16°C during December and January to a maximum of 32 °C during July and August (Ibarra-Manriquez and Sinaca-Colin 1987).

The potential vegetation throughout the study area has been classified as tall evergreen forest (Miranda and Hernandez-X 1963) and is characterized by an overstory tree canopy 30 to 35 m in height with occasional emergent trees exceeding 40 m. Common canopy tree species include *Nectandra ambigens*, *Pseudolmedia oxyphyllaria*, *Poulsenia armata*, and *Ficus* spp.; the understory vegetation is dominated by the native palms *Astrocaryum mexicanum* and *Chamaedorea* spp.

These low elevation tall evergreen forests now comprise only a small fraction of the landscape of the Volcan San Martin, and large, intact portions are limited to the forest reserve of the LTBS. Land-use change (i.e. conversion of forests to pastures and croplands) in the Los Tuxtlas Region has been both rapid and extensive; Dirzo and Garcia (1992) reported annual deforestation rates of over 4% in the Los Tuxtlas Region during the period between 1967 and 1986, and estimated that ≈84% of the area had been deforested by the end of that period. As a result, the general study area appears as a matrix of land cover types in which pasture and agricultural lands dominate, with scattered fragments of primary and secondary forests present but limited in extent.

As in many other parts of the tropics, land use in the Los Tuxtlas Region is initiated by cutting and burning the primary forest followed by establishment of either agricultural crops (e.g. corn, rice, beans) or pasture grasses (e.g., *Paspalum conjugatum*, *Axonopus compressus*, *Cynodon plectostachiys* and *Panicum maximum*). Land-use cycles and patterns are highly variable; deforested sites may be used exclusively for crop production,

exclusively as pasture, or in an alternating sequence of these two land-use types depending on the decisions/actions of the respective landholders (for further discussion, see Guevara et al. 1997).

Following abandonment of pasture and cultivated sites, early successional tree species colonize the sites. Young secondary forests (i.e. <15 years since abandonment) are characterized by species such as *Cecropia obtusifolia*, *Miconia argentea*, *Heliocarpus appendiculatus*, *Piper* spp., *Bursera simarubua*, and *Trichospermum mexicanum*. As secondary forests develop, *Lonchocarpus unifoliolatus*, *Ficus* spp., *Croton schiedeianus*, *Rollinia* spp., *Myriocarpa longipes*, and *Omphalea oleifera* become characteristic species of the overstory canopy community (Ibarra-Manriquez et al. 1997).

## Methods

We sampled 11 secondary forest sites for this study ranging in age from 6 months to 50 years since abandonment (Table 3.1). The land-use history and time since abandonment (i.e. the age of the secondary forest) of each site were determined from interviews with the local agriculturists who had managed the sites in question. Total aboveground biomass (TAGB) and pools of C, N, S, and P in TAGB were quantified at each of the 11 secondary forest sites. In addition, we quantified pools of C, N, and S in soils to a 1 m depth at eight of the eleven sites (S-4, S-8a, S-8b, S-16, S-20a, S-20b, S-26, S-30). We also determined soil P to a depth of 10 cm at two sites (S-16 and S-20a).

### Plot Design

TAGB, C, and nutrient pools of secondary forest sites were quantified using of a nested plot design. A 60 x 50 m plot was established at each site in which the diameter at breast height (1.3 m in ht., dbh) was measured for all trees and dead snags >10 cm dbh (Figure 1). The genus and species of each tree >10 cm dbh was recorded as well. Downed wood debris was sampled along 15 m transects placed at 15 m intervals along

Table 3.1. Names and land-use histories of secondary forest sites. Land-use period denotes the duration of land use following deforestation and prior to abandonment. Abandonment period refers to the time following cessation of land use and prior to sampling. In cases where sites experienced a series of land-use periods, the chronology of initial to subsequent land use moves from left to right. Numbers in each site name indicate the number of years of secondary succession experienced by that site. Sites which had the same number of years of secondary succession are distinguished from each other by a lower case letter following each number. All sites supported primary forests prior to the onset of land use.

Site Name	Land Use History (years prior to abandonment)	Land-Use Period (years)	Abandonment Period (years)
S-0.5	20 yrs as a cornfield, 8 years as a pasture, and 2 years as a cornfield	30	0.5
S-4	1 year as a cornfield	1	4
S-8a	5 years as a cornfield, 2 years as a pasture	7	8
S-8b	15 years as a cornfield, 10 years as a pasture, 2 years as a cornfield	27	8
S-10	15 years as a cornfield, 15 years as a pasture	30	10
S-16	5 years as a cornfield	5	16
S-20a	13 years as a cornfield	13	20
S-20b	1 year as a cornfield	1	20
S-26	2 years as a cornfield	2	26
S-30	15 years as a cornfield	15	30
S-50	site was a cornfield for an indeterminate period	-	50

each of three 60 m transects located on the edges and down the center of the plot ( $n = 15$ ; Figure 3.1). Each 15 m transect extended in a randomly selected direction from its point of origin along the transects. The diameters were recorded for all large wood pieces (i.e.  $>7.6$  cm in diameter) that crossed each 15 m transect; pieces were divided into sound and rotten classes based on their degree of decomposition. Wood particles 2.54 - 7.6 cm diam. were counted along a 10 m section of each 15 m transect.

The dbh of trees, lianas, and palms at least 1.3 m in height but  $<10$  cm dbh was measured for all individuals within 2 x 10 m belt transects located adjacent to each of the 15 wood debris transects. Biomass pools of seedlings (i.e., vegetation  $<1.3$  m in height) and forest floor litter (i.e., fallen leaves, fruits, seeds, bark, and wood  $<2.45$  cm diam.) were destructively sampled in 50 x 50 cm micro plots placed at the 5 m point along each wood debris transect line ( $n = 15$  per site). Because the S-10 site more closely resembled a

pasture than a forest site, methods to quantify TAGB in pastures described by Hughes (see chapter 1) were used at this site.

At each site, pools of C, N, S, and P in soils were determined from samples collected at 10 m intervals along a 40 m transect established in the center of the 60 x 50 plot. Samples were collected at the following depths: 0-2.5 cm, 2.5-10 cm, 10-30 cm, 30-50 cm, and 50-100 cm. Surface samples (i.e. 0-2.5 cm and 2.5-10 cm depths) were collected in the following manner: at each sample point along the 50 m transect, samples were obtained by compositing four subsamples collected 1 m from the sampling point in each cardinal direction ( $n = 5$  per site). Soils at depths of 10-30 cm, 30-50 cm, and 50-100 cm were collected by randomly selecting for sampling one of the four holes from which surface soils had been collected ( $n = 5$  per site).

Bulk density of soils was determined for each depth at each site from samples of known volume collected at five points located within each site. Samples were collected at 0-10, 10-30, 30-50, and 50-100 cm depths ( $n = 5$  per depth).

### Methods of Quantification

Biomass of trees  $>10$  cm dbh was calculated using an allometric model created by Brown et al. (1989) for tropical moist forest systems. This model uses tree dbh, height, and wood density ( $\text{g}/\text{cm}^3$ ) to predict biomass (table 3.2). Tree height was determined via regression analysis using dbh as the independent variable. This model was developed from a sample of 553 trees of varying species sampled for this study and from data in Bongers et al. (1988). Species specific wood density values were obtained for each tree species from Carmona-Valdovinos (unpublished data), Reyes et al (1992), Barajas-Morales (1987), and Brown (1997). In cases where density values were not available for particular species, mean values derived from congeners were used; where mean congener values were unavailable for a particular species, we used the mean value of  $0.58 \text{ g}/\text{cm}^3$  for tree species of the Los Tuxtlas Region determined by Barajas-Morales (1987). Correction factors

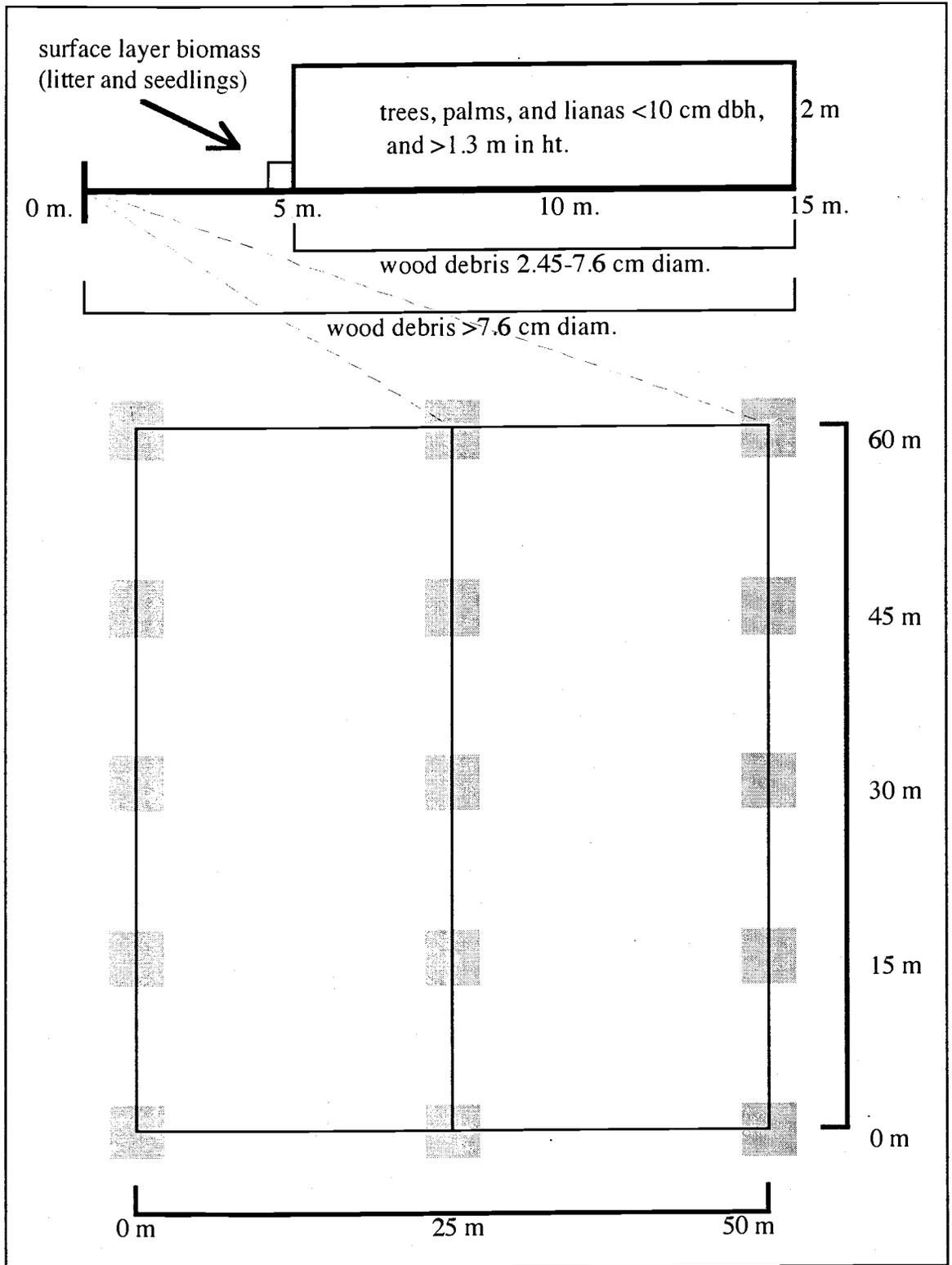


Figure 3.1. Plot design for sampling secondary forests in the Los Tuxtlas Region, Mexico.

(CF) were used in the majority of models to predict biomass in order to account for bias introduced during conversion from logarithmic to arithmetic units (Newman 1993, Baskerville 1972). In certain cases correction factors were not employed because either they were not available from cited sources or they failed to improve the predictability of the respective models based on the difference of the expected versus observed values (Table 3.2).

Genus specific models for wood and leaf biomass developed by Uhl et al. (1988) were used to predict biomass of *Cecropia obtusifolia* (Table 3.2). For standing dead trees >10 cm dbh, height as well as dbh was measured, and their volumes were calculated as cylinders. A mean wood density value of 0.42 g/cm<sup>3</sup> derived from samples of sound wood debris pieces (see below) was used to convert volume of standing dead trees to biomass. Biomass of downed wood debris was calculated at each 15 m transect using the planar intersect technique (Van Wagner 1968; Brown and Roussopoulous 1974). An average value for specific gravity of each of the three measured particle classes (2.45-7.6 cm diam., >7.6 cm diam. sound, and >7.6 cm diam. rotten) was determined for both young (<15 years old) and old (>15 years old) secondary forest sites. Samples were collected at random within young and old secondary forest sites, and mean values were used to calculate biomass for all sites within the two successional subcategories (i.e., <15 years old and >15 years old; Table 3.3). Bias due to slope was corrected for at all sites as outlined in Van Wagner (1968) and Brown and Roussopoulous (1974); percent slope was measured along each wood debris transect at each site. Because the vast majority of wood pieces lay directly on the forest floor, particle tilt was assumed to be negligible.

Biomass of trees that were at least 1.3 m in height but <10 cm dbh was calculated using a regression equation developed from measures of 66 trees harvested in and around the LTBS (Table 3.2). Biomass of dead trees at least 1.3 m in height but <10 cm dbh was calculated using a regression model of dbh versus main stem biomass of those 66 trees.

Table 3.2. Equations used to determine components of aboveground biomass of secondary forests in the Los Tuxtlas Region, Mexico. All biomass is expressed as dry weight (Mg).

parameter	equation	C F	R <sup>2</sup>
height of trees >10cm dbh <sup>1</sup>	= 4.722 ln(D <sup>2</sup> ) - 13.323	none	0.70
biomass; trees >10cm dbh <sup>2</sup>	= (exp (-2.409+0.9522 ln (D <sup>2</sup> HSg))) CF/10 <sup>3</sup>	1.031	0.99
biomass; <i>Cecropia</i> >10cm dbh (wood bio.) <sup>3</sup>	= {exp (-3.78 + 0.95 ln (D <sup>2</sup> ) + 1.00 ln(H))/10 <sup>3</sup>	none	0.88
biomass; <i>Cecropia</i> >10cm dbh (leaf bio.) <sup>3</sup>	= {-0.56+0.02 (D <sup>2</sup> )+0.04 (H))/10 <sup>3</sup>	none	0.98
biomass; standing dead trees >10cm dbh <sup>1</sup>	=π((D/2) <sup>2</sup> )H(0.42)	none	
biomass; trees <10cm dbh <sup>1</sup>	= (exp (4.9375 + 1.0583 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.143	0.93
biomass; dead trees <10cm dbh <sup>1</sup>	= (exp (4.6014 + 1.1204 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.112	0.95
biomass; palms <sup>1</sup>	= (exp (3.6272 + 0.5768 ln (D <sup>2</sup> H ))) CF/10 <sup>6</sup>	1.022	0.73
biomass; palms <sup>1</sup>	=(EXP(5.7236 + 0.9285 ln (D <sup>2</sup> ))) CF/10 <sup>6</sup>	1.050	0.39
biomass; dead palms <sup>1</sup>	= (exp (-0.5285 + 0.9907 ln (D <sup>2</sup> H)))/10 <sup>6</sup>	none	0.98
biomass; lianas <sup>1</sup>	=(10 <sup>^(0.12 + 0.91 LOG10(BA))</sup> )/10 <sup>3</sup>	none	0.82
biomass; tree leaves <sup>5</sup>	=exp(-1.897+0.836 ln (D <sup>2</sup> H))/10 <sup>3</sup>	none	0.85
biomass; sapling wood <sup>1</sup>	= exp (4.7472 + 1.0915 ln (D <sup>2</sup> ))/10 <sup>6</sup>	1.132	0.93
biomass; sapling leaves <sup>1</sup>	= exp (3.0473 + .07778 ln (D <sup>2</sup> ))/10 <sup>6</sup>	1.450	0.71
biomass; liana leaves <sup>4</sup>	=((0.109 BA)-0.376)/10 <sup>3</sup>	none	none
biomass; wood debris 2.45-7.6 cm diam. <sup>6</sup>	= Sg x ((π <sup>2</sup> x N x S x Cs x d <sup>2</sup> )/8L) x 10 <sup>2</sup>	none	none
biomass; wood debris >7.6 cm diam. <sup>6</sup>	= Sg x ((π <sup>2</sup> x sumD <sup>2</sup> x S x Cs x d <sup>2</sup> )/8L) x 10 <sup>2</sup>	none	none
<b>Definitions for symbols used to represent the various components in the above equations:</b>			
D = diameter breast height (cm).		Cs = slope correction factor (square root of (1+(% slope/100) <sup>2</sup> )).	
H = height (m).		N = number of wood particles intersected per transect.	
Sg= wood density (g/cm <sup>3</sup> ).		S = secant of wood particle tilt.	
BA = basal area (cm <sup>2</sup> ).		d = quadratic mean diameter of wood particles (cm).	
CF = correction factor = exp(MSE/2).		sumD <sup>2</sup> = sum of wood particle diameters <sup>2</sup> (cm <sup>2</sup> ).	
Sg = specific gravity of wood (g cm <sup>-3</sup> ).		L = transect length (cm).	
Sources are indicated by superscript number following the description of each parameter: 1 = this study; 2 = Brown and Lugo 1989; 3 = Uhl et al. 1988; 4 = Putz 1983; 5 = Crow 1978; 6 = Van Wagner 1964.			

Table 3.3. Wood densities in woody debris of young and old secondary forests in the Los Tuxtlas Region, Mexico. Young secondary forests are those <15 years in age; old secondary forests are those >15 years in age. Sample size is denoted by "n".

characteristic and size/type of wood quadratic mean diameter (cm)	young secondary forests		old secondary forests	
	n	mean ± s.e.	n	mean ± s.e.
2.45-7.6 cm diameter	103	3.74 ± 0.11	105	3.96 ± 0.11
specific gravity (g/cm <sup>3</sup> )				
2.45-7.6 cm diameter	63	0.37 ± 0.01	62	0.32 ± 0.02
>7.6 cm diameter sound	21	0.34 ± 0.03	30	0.34 ± 0.02
>7.6 cm diameter rotten	15	0.22 ± 0.03	32	0.20 ± 0.02

Biomass of palms was calculated using a regression equation developed from dry weights of 15 *Astrocaryum mexicanum* individuals harvested from the study area, and biomass of dead palms was calculated from a regression based on stem biomass of each of the 15 harvested palms. Liana biomass was calculated from a regression model developed by Putz (1983) which used measures of basal area to predict biomass (Table 3.2).

Carbon and nutrient pools in aboveground vegetation were calculated by multiplying the mass of each component by its corresponding C or nutrient concentration. Concentrations of C, N, S, and P in trees >10 cm dbh were determined from samples of wood and sun leaves collected from randomly selected individuals at the majority of the secondary sites. Wood samples were collected from trees at 1.3 m in height using increment borers inserted to the center of each trunk to ensure that the entire bole was represented by each sample. Five composited samples, each consisting of wood subsamples taken from eight trees, were collected at each site. Five composited leaf samples consisting of subsamples taken from five trees, were collected at each site by climbing into the tree canopy. In cases in which samples were not collected from a given site, mean values derived from pooling values from all sampled sites were used. To partition leaf and wood pools, leaf biomass of each tree >10 cm dbh was determined using a regression equation developed by Crow (1978) (Table 3.2). Wood biomass of each tree was calculated by subtracting leaf biomass from the total tree biomass.

Carbon and nutrient concentrations in leaf and wood tissue of trees <10 cm dbh were determined from samples collected at eight of the secondary forest sites. Leaf and wood samples were obtained from 25 individuals selected at random at each site. Samples were composited to provide five leaf and five wood samples per site. Mean values derived from pooled values of sampled sites were used for trees at sites that were not directly sampled. Leaf and wood biomass of trees <10 cm dbh were calculated from regression models developed from a sample of 66 trees <10 cm dbh collected within the study area (Table 3.2).

Concentrations of C and nutrients in palms were determined from stem tissue of 15 *A. mexicanum* individuals selected at random within the study area. Because leaf and stem tissue of lianas were not sampled in this study, C and nutrient pools of lianas were calculated from leaf tissue of trees >10 cm dbh and stem tissue of trees <10 cm dbh, respectively.

Elemental concentrations of the three wood debris classes were determined from subsamples collected previously to determine the density of wood debris (Table 3.3); subsamples were composited to provide five samples for each wood debris class within each site age category (i.e. <15 years old and >15 years old). Elemental concentrations of surface layer pools were determined from the 15 samples previously collected to determine surface layer biomass; samples were composited to provide five samples for each site. In the case of the youngest secondary forest site (S-0.5), site specific nutrient concentrations were not obtained, and mean values from pooled samples of the other sites were used.

Mass of C and nutrients in soils was calculated by multiplying the mean elemental concentrations at each depth by the corresponding mean soil bulk density value determined for each depth at each site.

### Lab Analysis

All soil and vegetation samples were oven dried to a constant weight at a temperature of  $\approx 60^\circ \text{C}$ . Vegetation samples were ground to pass through a 40 mesh screen (0.5 mm) using a Udy Mill. Soil samples were sieved to remove roots >2 mm in diameter and ground to pass through a 60 mesh screen (250  $\mu\text{m}$  pore size). Total C, N, and S concentrations in vegetation and soils were determined by the induction furnace method using a Carlo-Erba NA Series 1500 NCS analyzer (Nelson and Sommers 1982). Total P concentrations were determined using a Kjeldahl digestion procedure followed by colorimetric analysis (Olson and Sommers 1982).

### Statistical Analysis

Single classification analysis of variance (ANOVA) and Tukey-Kramer post hoc tests were used to test differences among sites with regard to TAGB, C, N, S, and P pools. Regression analysis was used to evaluate the significance of the relationships between variables such as TAGB, C, N, S, and P pools and forest age and duration of land use (Sokal and Rohlf 1969).

A general logistic growth equation - the Richards function as described by Cooper (1983) - was used to predict rates of biomass accumulation over time based on the age and TAGB of the secondary forests sampled in the Los Tuxtlas Region. The form of this model is:  $TAGB_t = TAGB_{max} * (1 - \exp(-b1 * t))^{b2}$ . Where:  $TAGB_t$  = TAGB at a given time following site abandonment;  $TAGB_{max}$  = the potential maximum of TAGB;  $t$  = the period of secondary succession or the age of a given secondary forest;  $b1$  and  $b2$  are parameters controlling the rate of accumulation and the inflection point of the accumulation curve, respectively. In this model, we used 403 Mg/ha as the  $TAGB_{max}$  value. This value represents the average TAGB of primary forests sampled in the Los Tuxtlas region by Hughes (see chapter 1).

Throughout the presentation of results, two sets of values were provided for the S-4 site. The S-4\* site included biomass of remnant primary forest trees and large wood debris that originally occupied the site; in the S-4 site remnant primary forest trees and large wood debris were not included. In calculations such as biomass, C, N, S, and P accumulation, species richness, and in all statistical comparisons, values from the S-4 site were used. Furthermore, in our analysis of the effect of prior land-use history on TAGB accumulation, the S-50 site was excluded, because of its indeterminate land-use history.

### **Results**

TAGB was significantly correlated with secondary forest age, ranging from 4.8 Mg/ha in the 6-month-old forest to 286.7 Mg/ha in the 50-year-old forest ( $R^2 = 0.53$ ;  $P =$

0.007). In addition, TAGB of secondary forests >15 years in age was significantly higher than those <15 years in age ( $P = 0.001$ ; Table 3.4).

Annual accumulation rates of TAGB were also significantly correlated to the duration of prior land use (i.e., the amount of time that the site had been in active management as a pasture or cultivated site). As duration of land use increased, rates of annual TAGB accumulation during secondary succession decreased significantly ( $R^2 = 0.48$ ;  $P = 0.026$ ; Figure 3.2). This relationship cannot be explained by the relative ages of the secondary forests that were sampled; secondary forest age was not correlated with annual rates TAGB accumulation ( $R^2 = -0.115$ ;  $P = 0.799$ ).

Based on results obtained by fitting TAGB of secondary forest sites to the Richards function (Figure 3.3), secondary forests were predicted to reach TAGB levels of primary forests (i.e., 363 Mg/ha) after 73 years of secondary succession ( $R^2 = 0.65$ ). This TAGB value is 90%, and well within the standard error, of the mean value (403 Mg/ha) for TAGB of primary forests sampled in the Los Tuxtlas Region by Hughes (see chapter 1). In addition, fitting the Richards function to secondary forest sites with between one and seven years of land use prior to abandonment produced a rapid accumulation curve in which TAGB attained 90% of primary forest TAGB after only 31 years of secondary succession. In contrast, fitting the Richards function to sites with 13 to 30 years of land use prior to abandonment produced a slow accumulation curve in which TAGB of secondary forests attained the equivalent of 90% of primary forest TAGB after 79 years of secondary succession (Figure 3.3).

Species richness (number of species/.33 ha) of trees >10 cm dbh ranged from 0 in the 6-month-old site (S-0.5) to 50 in the 50-year-old site (S-50b) (Table 3.5) and was significantly higher in forests >15 years in age than in those <15 years in age ( $P = 0.008$ ). Species richness values in secondary forests with long land-use histories did not significantly differ from those of forests with short land-use histories.

Distributions of TAGB among the various biomass components varied between young and old secondary forests (Table 3.4). In young forests, combined pools of surface layer, wood debris, palms, lianas, and trees <10 cm dbh accounted for 60% of TAGB. In contrast, these combined components accounted for 15% of TAGB in old secondary forests.

Table 3.4. Aboveground biomass pools (Mg/ha) in secondary forests of the Los Tuxtlas Region, Mexico. Tree biomass is separated into diameter classes (dbh) measured in cm. Sites S-4\* and S-4 represent the same site; in S-4\* remnant primary forest trees and large wood debris are included, and in S-4 they are not. The surface layer component represents the combined biomass of litter and seedling pools. The average rate of annual biomass accumulation is expressed as  $\text{Mg ha}^{-1} \text{yr}^{-1}$ . Aboveground biomass values of primary forests are from Hughes (see chapter 1).

site and age (years)	litter	seedling	surface layer	wood debris	palm	liana	tree <10	tree 10-30	tree 30-70	tree >70	total	annual biomass accumulation
S-0.5	2.7	2.1	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8	9.6
S-4*	7.7	0.8	8.5	61.3	0.0	5.6	28.3	6.2	11.1	146.0	267.0	-
S-4	7.7	0.8	8.5	11.8	0.0	5.6	28.3	6.2	0.0	0.0	60.4	15.1
S-8a	2.1	3.1	5.2	12.6	0.0	0.9	7.4	10.2	0.0	0.0	36.3	4.5
S-8b	4.9	2.0	6.9	6.7	0.1	2.0	17.7	40.6	27.2	7.8	109.0	13.6
S-10	-	-	19.5	1.9	0.0	0.0	0.6	1.3	0.0	0.0	23.3	2.3
mean of sites <10 yrs.	4.2	2.0	9.0	6.6	0.0	1.7	10.8	11.7	5.4	1.6	46.8	9.0
S-16	7.0	0.8	7.9	13.4	0.0	5.8	11.5	35.4	176.8	41.7	292.5	18.3
S-20a	5.0	0.6	5.6	7.6	0.0	4.9	11.7	33.0	25.6	0.0	88.4	4.4
S-20b	6.2	1.4	7.6	10.5	0.1	7.5	24.9	163.0	56.2	0.0	269.8	13.5
S-26	5.4	1.3	6.7	13.5	1.5	3.5	9.1	74.6	92.3	16.2	217.4	8.4
S-30	5.7	0.7	6.4	7.1	0.0	4.5	11.7	86.9	137.2	0.0	253.9	8.5
S-50	6.8	0.8	7.6	5.5	0.1	3.4	15.1	45.6	156.0	53.4	286.7	5.7
mean of sites >10 yrs.	6.0	1.0	7.0	9.6	0.3	4.9	14.0	73.1	107.4	18.6	234.8	9.8
primary forests	6.1	1.1	7.3	14	5.2	3.2	6.0	46	144	177	403	-

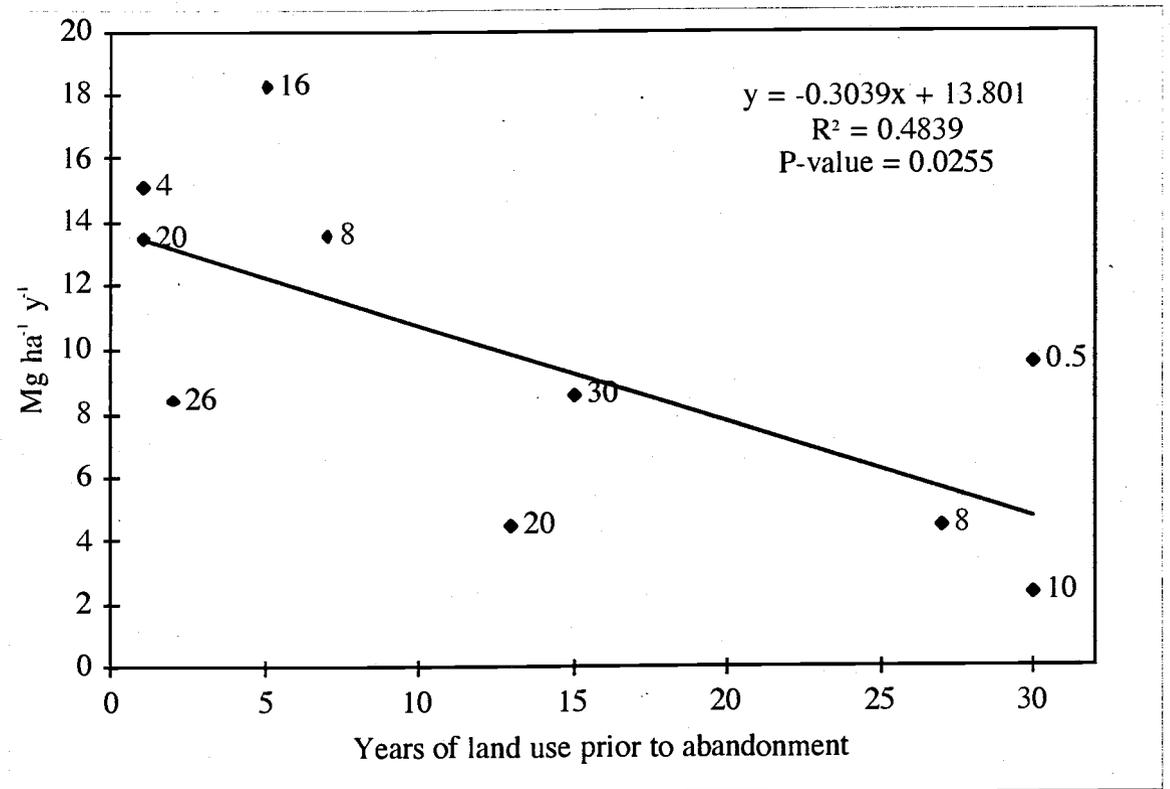


Figure 3.2. The relationship between annual rates of total aboveground biomass accumulation and duration of land use in secondary forests of the Los Tuxtlas Region, Mexico. Values next to each data point indicate the age of each secondary forest site (i.e., the number of years since abandonment)

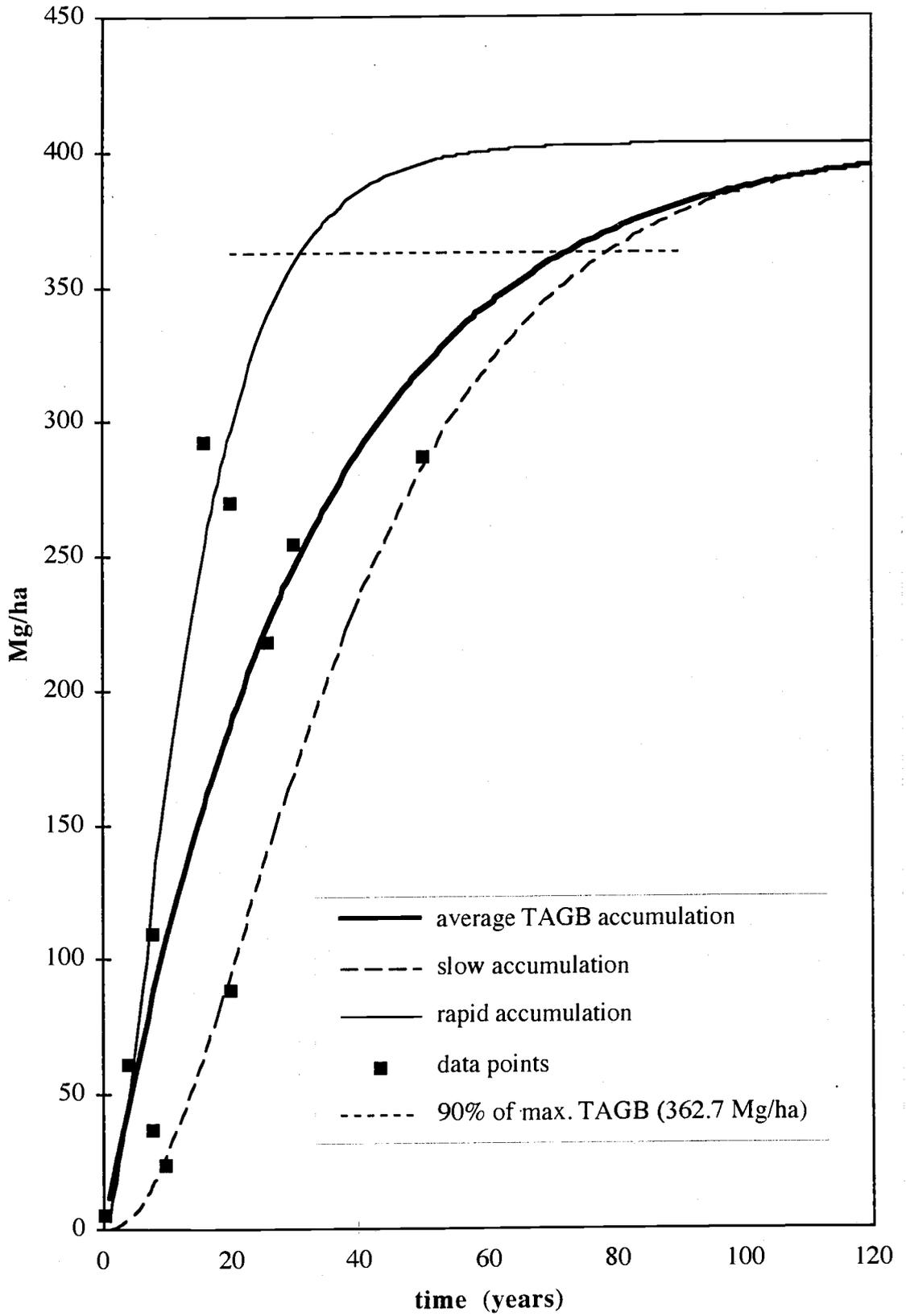


Figure 3.3. Estimates of total aboveground biomass (TAGB) accumulation during secondary succession in the Los Tuxtlas Region, Mexico. Accumulation rates are predicted using the Richards function. Maximum TAGB is defined as the average TAGB of primary forests sampled in the region and is 403 Mg/ha (Hughes, see chapter 1).

As the age of forests increased, both the biomass contribution and the structural importance of trees increased as well (Tables 3.4 and 3.5). Biomass of trees 10-30 cm and 30-70 cm dbh were significantly higher in old compared to young secondary forests ( $P = 0.014$  and  $P = 0.002$ ). Stem density was significantly higher in old compared to young secondary forests in both 10-30 cm dbh classes ( $P = 0.05$ ) and 30-70 cm dbh classes as well ( $P = 0.000$ ). Total basal area was also higher in old relative to young secondary forests in both the 10-30 cm dbh class ( $P = 0.032$ ) and the 30-70 cm dbh class ( $P = 0.002$ ).

Table 3.5. Stem density and basal area of woody species in secondary and primary forests of the Los Tuxtlas Region, Mexico. Groups are separated into diameter (dbh) classes measured in cm. Species richness was measured for all trees >10 cm dbh in 0.33 ha plots at each secondary forest site. Primary forest data are from Hughes (see chapter 1).

site and age (years)	density (stems/ha)					basal area (m <sup>2</sup> /ha)					Species Richness
	0-10	10-30	30-70	>70	total >10	0-10	10-30	30-70	>70	total	
S-0.5	0	0	0	0	0	0	0	0	0	0	0
S-4*	23,067	157	3	7	167	12	2	1	9	24	12
S-4	23,067	157	0	0	157	12	2	0	0	14	10
S-8a	18,200	510	20	3	533	8	10	3	1	22	28
S-8b	16,867	50	0	0	50	3	2	0	0	5	4
S-10	1,525	11	0	0	11	0	0	0	0	1	2
S-16	13,000	337	150	10	497	5	7	23	6	41	33
S-20a	26,200	300	37	0	337	5	7	5	0	17	14
S-20b	17,200	1,307	73	0	1,380	11	30	8	0	48	50
S-26	17,000	470	70	1	541	4	11	9	2	26	32
S-30	10,967	550	110	0	660	5	13	13	0	31	44
S-50	14,733	283	130	3	416	7	7	19	5	38	28
primary forest mean	6,602±399	294±61	90±9	22±3	406±53	4±1	7±1	15±1	15±3	42±3	n.a.

Concentrations of C, N, S, and P in biomass were variable between sites but did not show distinctive patterns with respect to age or land-use history of forests (Table 3.6).

Concentrations of C ranged from 41 to 51%, and were generally lower in litter, seedling, grass, and leaf tissue, and higher in wood tissue. In contrast, N concentrations were generally lower in wood tissue and higher in litter, seedling, grass, and leaf tissue; N concentrations ranged from 0.3% in wood tissue to 3.3% in leaf tissue of trees <10 cm dbh. Concentrations of S and P were distributed in a manner similar to N, with higher concentrations in herbaceous tissue and lower concentrations in wood tissue. Among aboveground components, S ranged from 0.02% to 0.4%, and P ranged from 0.02% to 0.3%.

There were also no discernible patterns in soil C, N, and S concentrations relating to land use or age (Table 3.7). Without exception, soil C and N concentrations decreased with increasing depth at each site. C concentrations ranged from 9.5% at the 0-2.5 depth in the S-20a site to 0.93% at the 50-100 cm depth of the S-16 site. N concentrations closely followed patterns of C concentrations, ranging from 0.1% in deep soils to 0.76% in shallow soils. Similarly, S concentrations tended to decrease with increasing depth, although changes in concentration from surface to deep soils were smaller than such changes for C and N; S ranged from 0.02% to 0.09%.

Like TAGB, total aboveground pools of C, N, S, and P increased with increasing forest age; pools of these elements were significantly higher in old secondary forests relative to young ones (Table 3.8). Total aboveground C increased from 2 Mg/ha in the youngest site to 136 Mg/ha in the oldest ( $R^2 = 0.53$ ;  $P = 0.007$ ). In young secondary forests the majority of C (59%) was concentrated in the combined biomass of the surface layer, wood debris, lianas, and trees <10 cm dbh. In old secondary forests, trees >10 cm dbh constituted  $\approx 85\%$  of aboveground C. Aboveground pools of N increased from 73 to 1167 kg/ha ( $R^2 = 0.54$ ;  $P = 0.006$ ). Pools of S increased from 9 to 147 kg/ha ( $R^2 = 0.46$ ;  $P = 0.013$ ), and P pools increased from 5 to 147 kg/ha ( $R^2 = 0.43$ ;  $P = 0.017$ ). In young secondary forests, 75% of N, 61% of S, and 71% of P pools were concentrated in

Table 3.6 Concentrations of N, C, S, and P in various components of vegetation in secondary forests of the Los Tuxtlas Region, Mexico. In the case of wood debris values, young 2nd and old 2nd represent secondary forests <15 years in age and secondary forests >15 years in age, respectively.

site	%N	%C	%S	%P
	<b>litter</b>			
S-4	1.7 ± 0.10	46.1 ± 0.6	0.16 ± 0.02	
S-8a	1.2 ± 0.05	42.3 ± 1.7	0.13 ± 0.01	0.08 ± 0.00
S-8b	1.5 ± 0.16	44.0 ± 0.4	0.28 ± 0.05	0.14 ± 0.01
S-16	1.4 ± 0.06	45.0 ± 0.9	0.20 ± 0.02	0.06 ± 0.00
S-20a	1.4 ± 0.06	45.8 ± 0.8	0.13 ± 0.02	0.09 ± 0.00
S-20b	1.4 ± 0.06	44.9 ± 2.2	0.16 ± 0.01	0.14 ± 0.02
S-26	1.7 ± 0.16	42.2 ± 1.3	0.14 ± 0.01	0.07 ± 0.00
S-30	1.4 ± 0.13	48.0 ± 0.3	0.20 ± 0.02	0.08 ± 0.01
S-50	1.8 ± 0.08	46.1 ± 0.2	0.24 ± 0.01	0.07 ± 0.00
mean of sites	1.5 ± 0.06	44.9 ± 0.6	0.18 ± 0.02	0.09 ± 0.01
<b>seedlings</b>				
S-4	1.4 ± 0.17	42.9 ± 1.1	0.19 ± 0.03	
S-8a	1.1 ± 0.05	42.6 ± 0.8	0.16 ± 0.02	0.16 ± 0.01
S-8b	1.5 ± 0.05	43.2 ± 0.2	0.25 ± 0.02	0.20 ± 0.02
S-10	1.1 ± 0.06	45.1 ± 0.2	0.16 ± 0.01	0.11 ± 0.01
S-16	1.8 ± 0.12	40.9 ± 0.9	0.21 ± 0.02	0.14 ± 0.01
S-20a	1.5 ± 0.09	42.0 ± 0.4	0.24 ± 0.03	0.19 ± 0.02
S-20b	1.3 ± 0.17	41.7 ± 0.7	0.20 ± 0.02	0.13 ± 0.04
S-26	1.9 ± 0.11	42.1 ± 0.8	0.22 ± 0.04	0.12 ± 0.01
S-30	1.2 ± 0.06	44.9 ± 0.6	0.20 ± 0.04	0.11 ± 0.01
S-50	1.8 ± 0.14	42.6 ± 0.6	0.22 ± 0.02	0.11 ± 0.00
mean of sites	1.5 ± 0.09	42.8 ± 0.4	0.20 ± 0.01	0.14 ± 0.01
<b>grass</b>				
S-4	1.0 ± 0.11	41.4 ± 1.8	0.26 ± 0.06	
<b>palm</b>				
	0.7 ± 0.13	47.3 ± 0.3	0.11 ± 0.02	0.10 ± 0.02
<b>downed wood debris</b>				
young 2nd 2.45-7.6 cm diam.	0.4 ± 0.02	49.2 ± 0.1	0.03 ± 0.00	0.05 ± 0.01
old 2nd 2.45-7.6 cm diam.	0.5 ± 0.02	49.4 ± 0.1	0.04 ± 0.01	0.02 ± 0.00
young 2nd sound >7.6 cm diam.	0.3 ± 0.03	50.8 ± 0.7	0.03 ± 0.01	0.03 ± 0.01
old 2nd sound >7.6 cm diam.	0.4 ± 0.05	49.8 ± 0.4	0.03 ± 0.01	0.02 ± 0.00
young 2nd rotten >7.6 cm diam.	0.7 ± 0.05	50.9 ± 0.8	0.05 ± 0.01	0.03 ± 0.00
old 2nd rotten >7.6 cm diam.	0.6 ± 0.09	50.4 ± 0.3	0.07 ± 0.01	0.02 ± 0.00

Table 3.6 continued. Concentrations of N, C, S, and P in various components of vegetation in secondary forests of the Los Tuxtlas Region, Mexico.

site	%N	%C	%S	%P
	leaves of trees <10 cm dbh			
S-4	2.6 ± 0.13	45.3 ± 1.1	0.31 ± 0.06	
S-8a	2.3 ± 0.04	46.5 ± 0.5	0.24 ± 0.02	0.19 ± 0.02
S-8b	2.4 ± 0.17	46.5 ± 3.0	0.39 ± 0.05	0.26 ± 0.04
S-16	2.8 ± 0.13	42.9 ± 0.7	0.29 ± 0.04	0.19 ± 0.03
S-20a	3.3 ± 0.22	42.5 ± 0.9	0.30 ± 0.03	0.19 ± 0.02
S-20b	2.5 ± 0.39	43.3 ± 5.5	0.29 ± 0.05	0.19 ± 0.04
S-26	2.8 ± 0.17	44.8 ± 0.9	0.32 ± 0.05	0.15 ± 0.00
S-30	2.4 ± 0.12	44.6 ± 0.4	0.31 ± 0.06	0.14 ± 0.02
mean of sites	2.6 ± 0.11	44.6 ± 0.54	0.31 ± 0.01	0.19 ± 0.01
	leaves of trees >10 cm dbh			
S-8a	2.5 ± 0.06	47.5 ± 0.2	0.29 ± 0.02	0.24 ± 0.02
S-8b	2.2 ± 0.10	45.9 ± 0.5	0.20 ± 0.01	0.26 ± 0.04
S-16	2.2 ± 0.05	47.0 ± 0.8	0.20 ± 0.01	0.14 ± 0.01
S-20a	2.9 ± 0.16	47.5 ± 0.4	0.27 ± 0.03	0.30 ± 0.04
S-20b	2.1 ± 0.14	44.8 ± 0.3	0.40 ± 0.06	0.16 ± 0.03
S-26	3.0 ± 0.10	46.7 ± 0.5	0.24 ± 0.01	0.13 ± 0.01
S-30	2.3 ± 0.13	46.3 ± 0.5	0.27 ± 0.02	0.16 ± 0.01
mean of sites	2.4 ± 0.16	46.4 ± 0.4	0.26 ± 0.03	0.19 ± 0.03
	wood of trees >10 cm dbh			
S-8a	0.3 ± 0.06	47.5 ± 0.2	0.08 ± 0.05	0.05 ± 0.01
S-16	0.3 ± 0.03	47.0 ± 0.3	0.04 ± 0.01	0.04 ± 0.00
S-20a	0.3 ± 0.02	47.5 ± 0.2	0.03 ± 0.00	0.09 ± 0.01
S-20b	0.3 ± 0.01	48.3 ± 0.2	0.03 ± 0.01	0.05 ± 0.01
S-26	0.4 ± 0.02	48.0 ± 0.1	0.02 ± 0.00	0.02 ± 0.00
S-30	0.3 ± 0.03	48.5 ± 0.1	0.04 ± 0.01	0.03 ± 0.00
mean of sites	0.3 ± 0.02	47.8 ± 0.2	0.04 ± 0.01	0.04 ± 0.01
	wood of trees <10 cm dbh			
S-4	0.4 ± 0.02	47.0 ± 0.2	0.05 ± 0.00	
S-8a	0.5 ± 0.02	46.6 ± 0.2	0.06 ± 0.00	0.10 ± 0.01
S-8b	0.3 ± 0.02	47.2 ± 0.2	0.06 ± 0.01	0.10 ± 0.02
S-16	0.7 ± 0.05	46.9 ± 0.1	0.09 ± 0.02	0.07 ± 0.01
S-20a	0.5 ± 0.03	45.7 ± 0.2	0.03 ± 0.00	0.14 ± 0.01
S-20b	0.5 ± 0.05	46.9 ± 0.2	0.06 ± 0.01	0.10 ± 0.01
S-26	0.8 ± 0.10	47.2 ± 0.3	0.08 ± 0.01	0.05 ± 0.01
S-30	0.6 ± 0.02	46.6 ± 0.2	0.08 ± 0.01	0.10 ± 0.02
mean of sites	0.5 ± 0.05	46.8 ± 0.17	0.06 ± 0.01	0.10 ± 0.01

Table 3.7. Concentrations of C, N, S, and P in soils of secondary forests of the Los Tuxtlas Region, Mexico. Categories represent soil depths. Mean  $\pm$  one standard error is presented.

carbon (%)					
site	0-2.5 cm	2.5-10 cm	10-30 cm	30-50 cm	50-100 cm
S-4	6.22 $\pm$ 0.35	5.68 $\pm$ 0.28	3.73 $\pm$ 0.42	2.17 $\pm$ 0.64	2.03 $\pm$ 0.41
S-8a	7.11 $\pm$ 0.54	5.72 $\pm$ 0.44	3.47 $\pm$ 0.31	2.09 $\pm$ 0.22	1.32 $\pm$ 0.16
S-8b	4.81 $\pm$ 0.07	3.95 $\pm$ 0.14	2.29 $\pm$ 0.30	1.31 $\pm$ 0.16	0.95 $\pm$ 0.14
S-16	6.49 $\pm$ 0.49	4.18 $\pm$ 0.25	2.96 $\pm$ 0.28	2.22 $\pm$ 0.17	1.51 $\pm$ 0.06
S-20a	6.02 $\pm$ 0.39	4.68 $\pm$ 0.15	3.34 $\pm$ 0.28	2.07 $\pm$ 0.26	1.64 $\pm$ 0.27
S-20b	6.88 $\pm$ 0.19	4.22 $\pm$ 0.12	2.61 $\pm$ 0.26	1.86 $\pm$ 0.14	1.10 $\pm$ 0.08
S-26	4.93 $\pm$ 0.25	3.32 $\pm$ 0.27	2.37 $\pm$ 0.34	1.52 $\pm$ 0.07	1.03 $\pm$ 0.12
S-30	7.41 $\pm$ 0.83	4.82 $\pm$ 0.55	3.13 $\pm$ 0.14	1.66 $\pm$ 0.15	0.93 $\pm$ 0.11
S-50	9.52 $\pm$ 1.16	6.58 $\pm$ 0.72			
mean	6.60 $\pm$ 0.11	4.80 $\pm$ 0.07	2.99 $\pm$ 0.03	1.86 $\pm$ 0.06	1.32 $\pm$ 0.04
nitrogen (%)					
site	0-2.5 cm	2.5-10 cm	10-30 cm	30-50 cm	50-100 cm
S-4	0.54 $\pm$ 0.03	0.51 $\pm$ 0.02	0.35 $\pm$ 0.03	0.19 $\pm$ 0.05	0.18 $\pm$ 0.03
S-8a	0.62 $\pm$ 0.04	0.52 $\pm$ 0.03	0.34 $\pm$ 0.03	0.18 $\pm$ 0.02	0.12 $\pm$ 0.01
S-8b	0.46 $\pm$ 0.01	0.41 $\pm$ 0.01	0.23 $\pm$ 0.03	0.13 $\pm$ 0.01	0.10 $\pm$ 0.01
S-16	0.55 $\pm$ 0.04	0.39 $\pm$ 0.03	0.28 $\pm$ 0.02	0.20 $\pm$ 0.01	0.13 $\pm$ 0.01
S-20a	0.53 $\pm$ 0.03	0.43 $\pm$ 0.01	0.32 $\pm$ 0.03	0.19 $\pm$ 0.03	0.15 $\pm$ 0.02
S-20b	0.65 $\pm$ 0.01	0.45 $\pm$ 0.01	0.28 $\pm$ 0.03	0.17 $\pm$ 0.02	0.10 $\pm$ 0.01
S-26	0.49 $\pm$ 0.03	0.35 $\pm$ 0.03	0.25 $\pm$ 0.04	0.16 $\pm$ 0.01	0.11 $\pm$ 0.01
S-30	0.65 $\pm$ 0.06	0.46 $\pm$ 0.04	0.31 $\pm$ 0.01	0.17 $\pm$ 0.01	0.10 $\pm$ 0.01
S-50	0.76 $\pm$ 0.10	0.54 $\pm$ 0.07			
mean	0.58 $\pm$ 0.01	0.45 $\pm$ 0.01	0.29 $\pm$ 0.00	0.17 $\pm$ 0.01	0.12 $\pm$ 0.00
sulfur (%)					
site	0-2.5 cm	2.5-10 cm	10-30 cm	30-50 cm	50-100 cm
S-4	0.06 $\pm$ 0.004	0.05 $\pm$ 0.005	0.04 $\pm$ 0.002	0.05 $\pm$ 0.026	0.02 $\pm$ 0.004
S-8a	0.08 $\pm$ 0.004	0.07 $\pm$ 0.003	0.05 $\pm$ 0.003	0.04 $\pm$ 0.002	0.03 $\pm$ 0.001
S-8b	0.06 $\pm$ 0.001	0.05 $\pm$ 0.001	0.03 $\pm$ 0.002	0.03 $\pm$ 0.004	0.02 $\pm$ 0.001
S-16	0.06 $\pm$ 0.005	0.05 $\pm$ 0.003	0.04 $\pm$ 0.001	0.03 $\pm$ 0.002	0.02 $\pm$ 0.001
S-20a	0.07 $\pm$ 0.002	0.06 $\pm$ 0.001	0.05 $\pm$ 0.003	0.03 $\pm$ 0.003	0.03 $\pm$ 0.003
S-20b	0.07 $\pm$ 0.001	0.05 $\pm$ 0.001	0.04 $\pm$ 0.003	0.03 $\pm$ 0.003	0.02 $\pm$ 0.002
S-26	0.06 $\pm$ 0.004	0.04 $\pm$ 0.004	0.04 $\pm$ 0.004	0.03 $\pm$ 0.001	0.03 $\pm$ 0.002
S-30	0.08 $\pm$ 0.003	0.06 $\pm$ 0.002	0.05 $\pm$ 0.001	0.04 $\pm$ 0.002	0.04 $\pm$ 0.002
S-50	0.09 $\pm$ 0.011	0.06 $\pm$ 0.008			
mean	0.07 $\pm$ 0.001	0.06 $\pm$ 0.001	0.04 $\pm$ 0.000	0.03 $\pm$ 0.003	0.03 $\pm$ 0.000
phosphorus (%)					
site	0-2.5 cm	2.5-10 cm	10-30 cm	30-50 cm	50-100 cm
S-16	0.136 $\pm$ 0.009	0.13 $\pm$ 0.011			
S-20a	0.148 $\pm$ 0.006	0.15 $\pm$ 0.004			
mean	0.14 $\pm$ 0.002	0.14 $\pm$ 0.004			

the surface layer, wood debris, lianas, and trees <10 cm dbh. In contrast, trees >10 cm dbh in old secondary forests constituted  $\approx 75\%$  of N, S, and P pools (Table 3.8).

The land-use history of secondary forests was significantly correlated to rates of accumulation of total aboveground C pools, but was not correlated with accumulations of total aboveground N, S, and P pools. Increases in the duration of land use resulted in decreased accumulation rates of C ( $R^2 = 0.45$ ;  $P = 0.02$ ).

Unlike aboveground pools, differences in soil pools of C, N, S, and P were few and did not differ consistently with regard to age or land-use history (Table 3.9). Total soil C to a 1 m depth ranged from 139 to 269 Mg/ha, but was not significantly correlated with forest age ( $R^2 = 0.00$ ;  $P = 0.44$ ) or duration of land use prior to abandonment ( $R^2 = 0.02$ ;  $P = 0.33$ ). Similarly, soil N ranged from  $\approx 14,000$  to  $\approx 24,000$  kg/ha but also was not correlated with forest age ( $R^2 = 0.00$ ;  $P = 0.69$ ) or duration of land use prior to abandonment ( $R^2 = 0.02$ ;  $P = 0.33$ ). Total soil S ranged from 2200 to 4500 kg/ha but was not correlated with forest age ( $R^2 = 0.00$ ;  $P = 0.46$ ) or duration of land use prior to abandonment ( $R^2 = 0.00$ ;  $P = 0.78$ ). Two forests, an 8 year old site (S-8b) and a 26 year old site (S-26), had significantly lower soil C and N pools than three of the other sites (i.e., S-8a, S-20a, and S-4). Soil S pools were also significantly lower in S-8b than in S-4, S-8a, S-20b, and S-30. Pools of soil S were also higher at the S-30 than at S-16, S-20b, and S-26. Finally, soil P pools to a 10 cm depth ranged from 1345 to 1480 kg/ha; pools did not differ between the 2 sites sampled (Table 3.9).

In general,  $\approx 20\%$  of C and N pools were present in the top 10 cm of the soil profile, and  $\approx 50\%$  of C and N pools were present in the top 30 cm. Soil S pools tended to be distributed somewhat lower in the soil profile;  $\approx 14\%$  of soil S was located in the top 10 cm and  $\approx 38\%$  was located in the top 30 cm of the soil profile.

Total ecosystem pools of C, N, and S (excluding roots) did not differ between young and old secondary forests. Total ecosystem C ranged from 156 to 331 Mg/ha, with soil pools accounting for between 58% and 91% of total pools. In addition, as forest age

increased, the ratio of aboveground to soil pools of C increased as well ( $R^2 = 0.47$ ;  $P = 0.036$ ). Ecosystem N ranged from  $\approx 14000$  to  $24000$  kg/ha, with 94% to 99% of the total N accounted for by soil pools. Ratios of aboveground N pools to soil N pools also

Table 3.8. Aboveground pools of C and N in secondary and primary forests of the Los Tuxtlas Region, Mexico. "Primary For." represents the mean values of primary forests sampled by Hughes (see chapter 1). "Mean <15 yrs." refers to the mean values of secondary forests <15 years in age. "Mean >15 yrs." refers to mean values of secondary forests >15 years in age. Sites S-4\* and S-4 refer to the same site; in S-4\* remnant trees and large wood debris are included, and in S-4 they are not included. Tree size classes refer to dbh measured in centimeters.

carbon (Mg/ha)											
site	litter	herb	surface layer	wood debris	palms	lianas	trees <10	trees 10-30	trees 30-70	trees >70	total
S-0.5	1.2	0.9	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1
S-4*	3.5	0.4	3.9	31.1	0.0	2.6	12.4	2.9	5.3	69.7	128.0
S-4	3.5	0.4	3.9	6.0	0.0	2.6	12.4	2.9	0.0	0.0	27.8
S-8a	2.1	0.8	2.9	3.3	0.0	0.9	7.7	19.3	12.9	3.7	50.8
S-8b	0.9	1.3	2.3	6.4	0.0	0.4	3.2	4.9	0.0	0.0	17.2
S-10	8.8	-	8.8	0.9	0.0	0.0	0.3	0.6	0.0	0.0	10.6
mean<15 yrs.	<b>3.3</b>	<b>0.9</b>	<b>4.0</b>	<b>3.3</b>	<b>0.0</b>	<b>0.8</b>	<b>4.7</b>	<b>5.6</b>	<b>2.6</b>	<b>0.7</b>	<b>21.7</b>
S-16	3.2	0.3	3.5	6.7	0.0	2.7	5.1	16.6	83.1	19.6	137.3
S-20a	2.3	0.3	2.6	3.8	0.0	2.3	5.0	15.7	12.1	0.0	41.4
S-20b	2.8	0.6	3.3	5.2	0.0	3.5	10.9	78.5	27.1	0.0	128.6
S-26	2.3	0.6	2.8	6.7	0.7	1.7	4.0	35.8	44.2	7.8	103.7
S-30	2.7	0.3	3.1	3.5	0.0	2.1	5.1	42.0	66.4	0.0	122.3
S-50	3.1	0.3	3.5	2.7	0.0	1.6	6.5	21.8	74.5	25.5	136.1
mean>15 yrs.	<b>2.7</b>	<b>0.4</b>	<b>3.1</b>	<b>4.8</b>	<b>0.1</b>	<b>2.3</b>	<b>6.1</b>	<b>35.0</b>	<b>51.2</b>	<b>8.8</b>	<b>111.5</b>
primary for.	<b>2.8</b>	<b>0.5</b>	<b>3.3</b>	<b>7.1</b>	<b>2.5</b>	<b>1.5</b>	<b>2.7</b>	<b>22.4</b>	<b>69.9</b>	<b>85.7</b>	<b>195.1</b>
nitrogen (kg/ha)											
site	litter	herb	surface layer	wood debris	palms	lianas	trees <10	trees 10-30	trees 30-70	trees >70	total
S-0.5	41	31	72	0	0	0	0	0	0	0	72
S-4*	133	11	144	232	0	28	125	27	37	461	1054
S-4	133	11	144	55	0	28	125	27	0	0	379
S-8a	59	23	82	24	0	10	87	153	90	28	474
S-8b	33	47	80	42	0	5	32	37	0	0	195
S-10	222	-	222	9	0	0	4	6	0	0	240
mean<15 yrs.	<b>98</b>	<b>28</b>	<b>120</b>	<b>26</b>	<b>0</b>	<b>9</b>	<b>50</b>	<b>45</b>	<b>18</b>	<b>6</b>	<b>272</b>
S-16	95	16	110	57	0	42	78	131	611	146	1177
S-20a	71	10	81	38	0	29	76	136	102	0	462
S-20b	88	18	105	44	1	43	127	574	187	0	1081
S-26	93	25	119	63	10	33	71	346	401	71	1113
S-30	80	9	88	33	0	28	64	309	454	0	976
S-50	119	15	134	24	0	20	83	168	558	180	1167
mean>15 yrs.	<b>91</b>	<b>15</b>	<b>106</b>	<b>43</b>	<b>2</b>	<b>33</b>	<b>83</b>	<b>277</b>	<b>385</b>	<b>66</b>	<b>996</b>
primary for.	<b>105</b>	<b>21</b>	<b>126</b>	<b>60</b>	<b>36</b>	<b>28</b>	<b>56</b>	<b>192</b>	<b>554</b>	<b>653</b>	<b>1705</b>

Table 3.8 continued. Aboveground pools of S and P in secondary and primary forests of the Los Tuxtlas Region, Mexico. "Primary For." represents the mean values of primary forests sampled by Hughes (see chapter 1). "Mean <15 yrs." refers to the mean values of secondary forests <15 years in age. "Mean >15 yrs." refers to mean values of secondary forests >15 years in age. Sites S-4\* and S-4 refer to the same site; in S-4\* remnant trees and large wood debris are included, and in S-4 they are not included. Tree size classes refer to dbh measured in centimeters.

sulfur (kg/ha)											
site	litter	herb	surface layer	wood debris	palms	lianas	trees <10	trees 10-30	trees 30-70	trees >70	total
S-0.5	5.0	4.3	9.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.3
S-4*	12.2	1.7	13.8	21.2	0.0	3.2	14.7	3.3	4.7	59.9	120.8
S-4	12.2	1.7	13.8	4.6	0.0	3.2	14.7	3.3	0.0	0.0	39.6
S-8a	6.5	3.2	9.7	2.0	0.1	1.3	10.6	38.1	24.3	7.2	93.1
S-8b	6.0	7.6	13.7	4.0	0.0	0.7	5.6	4.5	0.0	0.0	28.5
S-10	31.3	-	31.3	0.7	0.0	0.0	0.5	0.7	0.0	0.0	33.2
mean<15 yrs.	<b>12.2</b>	<b>4.2</b>	<b>15.6</b>	<b>2.3</b>	<b>0.0</b>	<b>1.0</b>	<b>6.3</b>	<b>9.3</b>	<b>4.9</b>	<b>1.4</b>	<b>40.8</b>
S-16	13.7	1.7	15.5	4.2	0.0	5.6	10.4	16.0	76.1	18.1	145.8
S-20a	6.5	1.6	8.1	3.4	0.0	2.0	5.4	13.8	10.4	0.0	43.1
S-20b	10.0	2.8	12.7	3.2	0.1	5.1	13.8	62.9	19.4	0.0	117.1
S-26	7.7	2.9	10.6	5.2	1.6	3.0	7.3	21.2	24.9	4.4	78.2
S-30	11.6	1.4	13.0	2.6	0.0	3.7	8.8	38.7	57.1	0.0	123.9
S-50	16.4	1.7	18.1	1.8	0.1	2.3	9.8	21.1	70.5	23.0	146.7
mean>15 yrs.	<b>11.0</b>	<b>2.0</b>	<b>13.0</b>	<b>3.4</b>	<b>0.3</b>	<b>3.6</b>	<b>9.2</b>	<b>28.9</b>	<b>43.1</b>	<b>7.6</b>	<b>109.1</b>
primary for.	<b>9.7</b>	<b>3.1</b>	<b>12.9</b>	<b>3.7</b>	<b>5.7</b>	<b>5.1</b>	<b>10.3</b>	<b>25.7</b>	<b>75.0</b>	<b>89.0</b>	<b>227.4</b>
phosphorus (kg/ha)											
site	litter	herb	surface layer	wood debris	palms	lianas	trees <10	trees 10-30	trees 30-70	trees >70	total
S-0.5	2.2	2.7	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9
S-4*	6.3	1.4	7.7	17.7	0.0	5.6	25.7	3.3	5.2	66.6	131.7
S-4	6.3	1.4	7.7	3.7	0.0	5.6	25.7	3.3	0.0	0.0	46.0
S-8a	4.0	3.2	7.1	3.0	0.1	2.1	17.2	22.8	14.1	4.3	70.6
S-8b	3.0	6.1	9.1	3.6	0.0	1.0	7.6	5.4	0.0	0.0	26.7
S-10	21.7	-	21.7	0.6	0.0	0.0	0.6	0.7	0.0	0.0	23.6
mean<15 yrs.	<b>7.4</b>	<b>3.3</b>	<b>10.1</b>	<b>2.2</b>	<b>0.0</b>	<b>1.7</b>	<b>10.2</b>	<b>6.4</b>	<b>2.8</b>	<b>0.9</b>	<b>34.4</b>
S-16	4.5	1.1	5.7	2.7	0.0	4.1	7.7	14.4	69.6	16.5	120.7
S-20a	4.7	1.2	5.9	1.6	0.0	7.2	15.8	33.1	25.4	0.0	89.0
S-20b	8.6	1.8	10.4	2.1	0.1	7.7	23.7	85.0	28.6	0.0	157.6
S-26	3.9	1.6	5.5	2.8	1.5	2.1	4.9	15.4	18.0	3.2	53.4
S-30	4.3	0.8	5.1	1.5	0.0	4.6	11.1	27.8	41.5	0.0	91.7
S-50	4.5	0.9	5.4	1.1	0.1	3.3	13.7	22.5	75.7	25.2	147.0
mean>15 yrs.	<b>5.1</b>	<b>1.2</b>	<b>6.3</b>	<b>2.0</b>	<b>0.3</b>	<b>4.8</b>	<b>12.8</b>	<b>33.0</b>	<b>43.1</b>	<b>7.5</b>	<b>109.9</b>
primary for.	<b>4.3</b>	<b>1.3</b>	<b>5.6</b>	<b>4.9</b>	<b>5.4</b>	<b>2.4</b>	<b>4.5</b>	<b>11.2</b>	<b>32.5</b>	<b>38.5</b>	<b>105.0</b>

Table 3.9. Soil pools of C, N, S, and P in secondary forests of the Los Tuxtlas Region, Mexico. Statistical comparisons use single classification analysis of variance and post-hoc Tukey-Kramer tests to detect differences between sites. Statistical comparisons pertain only to totals to 1 m.

carbon (Mg/ha)							
site	0-2.5 cm	2.5-10 cm	total to 10 cm	10-30 cm	30-50 cm	50-100 cm	total to 1 m
S-4	12.6	34.5	47.1	68.7	44.7	108.8	269.3
S-8a	14.4	34.8	49.1	70.8	47.3	75.4	242.6
S-8b	10.0	24.6	34.6	35.7	21.2	47.5	139.0
S-16	12.2	23.5	35.7	55.6	42.1	77.7	211.2
S-20a	12.2	28.4	40.6	62.1	48.4	97.4	248.5
S-20b	12.0	22.2	34.2	53.3	40.2	57.6	185.3
S-26	9.2	18.7	27.9	54.0	37.8	38.5	158.2
S-30	15.6	30.4	45.9	70.7	36.3	51.9	204.8
significant differences: S-8b and S-26 < S-4, S-8a, S-20a; S-20b < S-4.							
nitrogen (kg/ha)							
site	0-2.5 cm	2.5-10 cm	total to 10 cm	10-30 cm	30-50 cm	50-100 cm	total to 1 m
S-4	1096	3080	4176.5	6368	3879	9515	23939
S-8a	1249	3144	4392.4	6857	4163	6695	22107
S-8b	963	2530	3493.6	3515	2042	4910	13961
S-16	1039	2199	3238.4	5237	3829	6754	19058
S-20a	1076	2587	3662.6	5984	4555	8849	23051
S-20b	1135	2358	3492.4	5652	3657	5108	17910
S-26	915	1970	2885.2	5749	3911	4135	16679
S-30	1362	2877	4238.7	7030	3651	5540	20460
significant differences: S-8b < S-4, S-8a, S-26; S-26 < S-4.							
sulfur (kg/ha)							
site	0-2.5 cm	2.5-10 cm	total to 10 cm	10-30 cm	30-50 cm	50-100 cm	total to 1 m
S-4	114	333	446.7	736	1027	1241	3451
S-8a	154	422	576.3	1094	798	1551	4019
S-8b	118	310	427.4	512	421	879	2239
S-16	121	293	413.5	717	574	1279	2983
S-20a	133	335	468.7	903	788	1693	3853
S-20b	129	277	406.4	714	631	1150	2902
S-26	104	246	349.3	869	739	1003	2959
S-30	158	381	539.4	1080	808	2074	4502
significant differences: S-8b < S-4, S-8a, S-20a, S-30; S-30 > S-16, S-8b, S-20b, S-26.							
phosphorus (kg/ha)							
site	0-2.5 cm	2.5-10 cm	total to 10 cm	10-30 cm	30-50 cm	50-100 cm	total to 1 m
S-16	340	1005	1345.0				
S-20a	370	1110	1480.0				
significant differences: None							

increased with forest age ( $R^2 = 0.38$ ;  $P = 0.061$ ), but were not as strongly correlated to increasing forest age as ratios of aboveground C to soil C. Like ecosystem N pools, between 95 to 99% of total ecosystem S was present in soil pools. Ratios of aboveground to soil pools of S were not significantly correlated with site age.

## Discussion

Accumulations of aboveground biomass in secondary forests <15 years old in Los Tuxtlas were generally within the range of rates measured for secondary forests elsewhere in the tropics. By comparison, TAGB in 10-month-old and 7-year-old secondary forests of the Uxpanapa Region of Veracruz, Mexico were 5.3 and 52.7 Mg/ha, respectively (Williams-Linera 1983). Saldarriaga et al. (1988) reported a range of TAGB from 75 to 84 Mg/ha in 9- to 12-year-old secondary forests in northern Amazonia, and Ewel (1971) reported a range in TAGB from 13 to 43 Mg/ha in 2- to 6-year-old secondary forests of Costa Rica.

In contrast, pools of TAGB in secondary forests >15 years in age were high relative to values presented in other studies for secondary forests of comparable age located elsewhere in the tropics. Accumulations in secondary forests ranging from 16 to 20 years in age in the Los Tuxtlas Region were between 88.6 and 293 Mg/ha. In contrast, accumulations of TAGB in a series of 20-year-old secondary forests in northwestern Amazonia ranged from 63 to 98 Mg/ha (Saldarriaga 1988). Secondary forests in the Los Tuxtlas Region ranging from 25 to 50 years in age had TAGB pools that were between 217 and 302 Mg/ha, while TAGB in 30 to 80 year old secondary forests presented by Saldarriaga (1988) ranged from only 63 to 200 Mg/ha. In 16- to 50-year-old secondary forests located in various moist forest systems throughout the tropics, accumulations of total live aboveground biomass ranged from 63 to 205 Mg/ha (Brown and Lugo 1990).

Our estimate derived from the Richards function that secondary forests of the Los Tuxtlas region will reach the equivalent of primary forest biomass in 73 years is nearly double the successional period used by Riley et al. (1997) to model the effects of land use on C dynamics in the Los Tuxtlas Region. They estimated that C densities in secondary forests would reach the equivalent primary forest densities after 40 years. However, the successional period determined from our results is considerably shorter than estimates of the interval required to reach primary forest biomass densities in the Brazilian Amazon.

Fearnside (1996) reported a 100-year interval, and Saldarriaga et al. (1988) reported a 144- to 189-year interval using a linear model. Furthermore, if we use the Richards function to evaluate the relationship of secondary forest age to TAGB presented by Saldarriaga et al. (1988), we estimate that it will take 250 years of succession to reach TAGB levels that are within 90% of the mean value for mature forests of northwestern Amazonia ( $R^2 = 0.76$ ).

Duration of land use had a significant impact on rates of TAGB accumulation in secondary forests; as duration of land use increased, accumulation rates decreased. This relationship is made evident by the linear regression of the annual rate of TAGB accumulation and the duration of land use prior to abandonment (Figure 3.2). It is also made evident by the comparison of rapid and slow rates of TAGB accumulation in secondary forest sites (Figure 3.3).

The effect of land-use duration on rates of TAGB accumulation likely explains much of the variation seen in the relationship between site age and TAGB accumulations, and, by extension, the variation in our prediction of the interval necessary to attain the equivalent of primary forest biomass. For example, although the S-8a and S-8b secondary forest sites were both 8 years old, S-8b had a land-use history that was 20 years longer than S-8a and had a TAGB value that was one-third of the biomass of S-8a. Similarly, while the S-20a and S-20b sites were both 20 years old, the former site had experienced a land-use period that was 12 years longer than the latter site, and had one-third the aboveground biomass of the latter site. Furthermore, the site with the lowest rate of biomass accumulation (S-10) had been a pasture for 15 years prior to its abandonment, and the firmly established mat-forming exotic grasses (i.e. *Cynodon plectostachiys* and *Panicum maximum*) had limited the colonization and growth of early pioneer tree species (e.g., *Piper* spp., *Cecropia obtusifolia*, *Trema micranthra*) even after 10 years of secondary succession.

Other studies have demonstrated the impact of both the type and duration of prior land use on rates of TAGB accumulation in secondary forests. Forest recovery was

significantly delayed in abandoned pastures of Puerto Rico compared to forest recovery following other natural and human induced disturbances in the tropics (Aide et al. 1995). Uhl et al. (1988) reported similar results for secondary forests of eastern Amazonia where accumulation rates varied from  $\approx 1$  to  $10 \text{ Mg ha}^{-1} \text{ y}^{-1}$  and were highly dependent on the prior land use of each forest site. Fearnside and Guimaraes (1996) estimated that secondary forests that originated from degraded cattle pastures accumulated biomass and carbon at much lower rates than those that originated from shifting cultivation. Purata (1986), also found that floristic and structural development of secondary forests in the Los Tuxtlas Region were negatively related to duration of land use.

Overall, changes in TAGB in response to deforestation, land use, and abandonment in the Los Tuxtlas Region are substantial (Figure 3.4). Hughes (see chapter 1) found that approximately 95% of the TAGB in primary forests is lost as a result of the conversion to, and management of, pastures and cornfields. Results of this study have demonstrated that rapid accumulation of TAGB in secondary forest can occur following abandonment, with TAGB values approaching those of primary forests in 73 years. However, such accumulation rates are considerably constrained by the prior land-use history of the regenerating secondary forest.

As in secondary forests studied elsewhere (Brown and Lugo 1990, Gomez-Pompa and Vasquez-Yanes 1981), densities and basal area of stems, particularly of the small diameter classes, were higher overall in secondary forests relative to primary forests of the Los Tuxtlas Region. Our results document a shift in both stem density and basal area throughout secondary succession, with the relative contribution of larger diameter trees to both total stem density and basal area increasing with increasing secondary forest age. Our results also indicate an increase in the species richness of trees  $> 10 \text{ cm dbh}$  with increasing forest age.

Although secondary forests showed progress toward the structural and floristic characteristics of primary forests in the region, they remained distinctly different from

primary forests in that they contained few trees >70 cm dbh, and did not contain many of the species that constitute those large trees in primary forests. Trees >70 cm dbh accounted for 44% of TAGB in primary forests but accounted for only 8% of TAGB in secondary

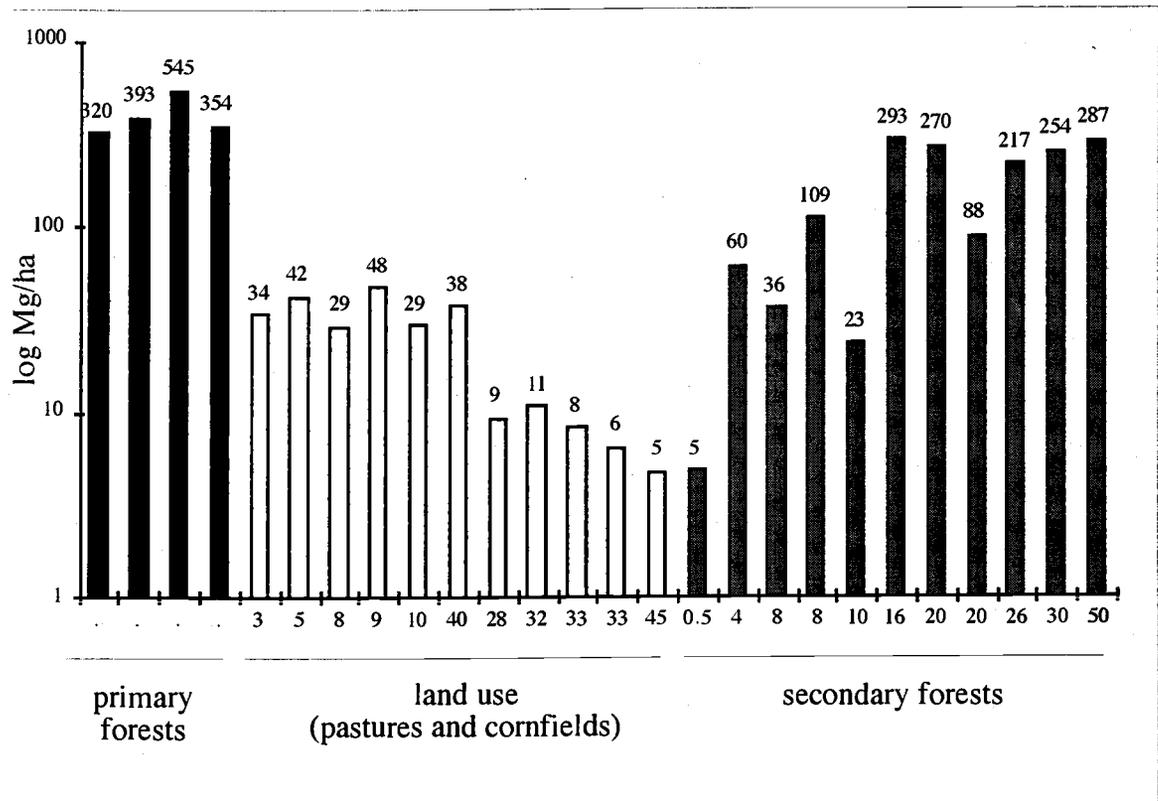


Figure 3.4. Dynamics of TAGB along a land-use gradient in the Los Tuxtlas Region, Mexico. Values are presented on a log scale. Values at the top of each bar are the non-log TAGB values of each site (Mg/ha). In the case of pastures and cornfields, values along the x-axis represent the number of years of land use following deforestation. In the case of secondary forest sites, values along the x-axis represent the number of years of secondary succession following abandonment. Values for primary forest, pasture, and cornfield sites are from Hughes (see chapter 1).

forests that were >15 years in age and supported >200 Mg/ha of TAGB. Furthermore, the group of dominant species that accounted for 50% of the biomass of trees >10 cm dbh in the four primary forest sites sampled by Hughes (see chapter 1) accounted for only 2% and 8% of the biomass of trees >10 cm in young and old secondary forests, respectively.

Thus, although the older secondary forests sampled in this study are relatively similar to

primary forests with regard to TAGB, they are strikingly different in terms of forest structure and community composition and will require a much longer successional interval to attain parity with primary forests with regard to these forest characteristics.

Like TAGB, aboveground pools of C, N, S, and P increased with increasing forest age. Pools of C, N, and S in vegetation of secondary forests ranged from <5% to  $\approx$ 70% of those in primary forests of Los Tuxtlas (Hughes see chapter 1). In contrast, aboveground P pools of secondary forests ranged from 5% to 140% of primary forest pools (Hughes see chapter 1). In addition, the average mass of P in secondary forests >15 years old (109.9 kg/ha) was equivalent to that in primary forests (105.0 kg/ha). These rapid rates of P accumulation are due to the high concentrations of P in vegetation of secondary forests compared to those in primary forest vegetation. Concentrations of P in litter, seedling, tree leaf, and tree wood biomass were significantly higher in vegetation of secondary forests than in vegetation of primary forests (paired t-test;  $P < 0.01$ ). In contrast, concentrations of C, N, and S in aboveground biomass components did not differ significantly between primary and secondary forests.

Contrary to the behavior of aboveground pools, soil pools of C, N, and S in secondary forests were not significantly different from those in primary forests, pastures and cornfields of the Los Tuxtlas Region (Single classification ANOVA;  $P$ -values  $> 0.65$ ; see chapter 1) and were not correlated to secondary forest age or duration of land use prior to abandonment. These results differ from the findings of Brown and Lugo (1990) who documented decreases in soil C and N pools in response to the conversion of forests to pastures and croplands, and accumulations of soil C and N during subsequent secondary succession. This lack of discernible change in soil pools can likely be attributed to the capacity of the young volcanic soils (i.e., Andosols) of the Los Tuxtlas to sequester large quantities soil organic matter (Sollins et al. 1988). Soil C content (to 1 m) averaged  $\approx$ 200 Mg/ha in secondary forests of Los Tuxtlas compared to a range of 77 to 147 Mg/ha in forest soils located elsewhere in the tropics (Brown et al. 1993). In addition, average

concentrations of C and N in the top 30 cm of soils in the Los Tuxtlas Region ranged from  $\approx 3$  to 6.6% and 0.29 to 0.58%, respectively. By comparison, C and N concentrations in soils to a 25 cm depth in moist forests of Puerto Rico ranged from 1.5 to 2.8% and 0.19 to 0.23%, respectively. Concentrations of C and N in secondary forest soils of the Los Tuxtlas Region were also more than double the mean values for tropical forests presented by Sanchez (1989). Soil P concentrations were approximately 10 times higher in secondary forest soils of Los Tuxtlas than in the highly weathered forest soils of southwestern Amazonia (Kauffman et al. 1995). The properties that allow for storage of large quantities of organic matter in soils of the Los Tuxtlas Region are likely the same properties that make those soil pools resistant to change in response to deforestation, land use, and secondary succession.

Consequently, differences in TAGB accumulation in response to prior land-use history of secondary forest sites clearly cannot be attributed to the status of soil pools of C, N, and S. In this region, the status of available nutrients in soil pools, soil seed-bank and seed rain status, plant competition at the early stages of secondary succession, or a combination of these factors are likely to be responsible for the effect of prior land-use history on rates of biomass accumulation. However, in tropical regions where total soil C and nutrient pools have been shown to be significantly reduced by land use (i.e. Brown and Lugo 1990, Sanchez 1983, and Detwiler 1986), we would expect the negative effects of land-use duration on aboveground biomass accumulation during secondary succession to be amplified beyond what we have seen in this study.

Dynamics of ecosystem pools of C, N, and S were largely determined by the relative distributions of each of those elements between aboveground biomass and soil pools. Soil pools constituted 91% of total ecosystem C (excluding roots) in the youngest secondary forest and 58% of total C in the oldest secondary forests; changes were due to the substantial accumulation of C in aboveground pools with increasing secondary forest age. This successional trend appears to be moving toward the distribution of C in primary

forests of the Los Tuxtlas Region in which C pools were approximately evenly distributed between soil and aboveground pools (Hughes see chapter 1). In contrast to C pools, the vast majority of ecosystem pools of N and S were located in soils of secondary forests. Soils accounted for 99% of total ecosystem N and S pools in young secondary forest and  $\approx 94\%$  in older forest sites. Consequently, despite the significant increases in aboveground pools of N and S with increasing forest age, aboveground accumulations during secondary succession had a relatively small impact on total ecosystem N and S pools of secondary forests.

Overall, these results, combined with the results of Hughes (see chapter 1), illustrate the distinct dynamics of soil versus aboveground pools of C and N in response to land-use change in the Los Tuxtlas Region (Figure 3.5). While aboveground pools of C, N, and S decreased dramatically in response to deforestation and land use and increased relatively rapidly to levels approaching those of primary forests during secondary succession, soil pools remained stable during the processes of deforestation, land use, and secondary succession.

The dynamics of C pools along the entire land-use gradient in the Los Tuxtlas Region differed greatly from those of N and S as a result of the respective distributions of those elements within the ecosystem. Loss of aboveground pools of C due to deforestation and land use resulted in a 50% decrease of total ecosystem pools, while accumulation of C during forest regeneration restored ecosystem C pools to levels approaching those of primary forest pools (Figure 3.5). In contrast, since the majority of N and S were concentrated in the relatively stable soil pools, ecosystem stocks of these elements at sites along the land-use gradient (i.e. pastures, cornfields, and secondary forests) never dropped below  $\approx 90\%$  of primary forest pools.

In conclusion, our results indicate that secondary forests of the Los Tuxtlas Region are capable of rapid accumulations of aboveground biomass and C, and that densities approach primary forest levels in relatively short periods of time (i.e., 73 years). In

contrast, soil pools of total C, N, and S remained relatively stable throughout both land-use and successional periods. Unfortunately, previous studies have noted that current land-use patterns in the region are creating a landscape dominated by semi-permanent and permanent

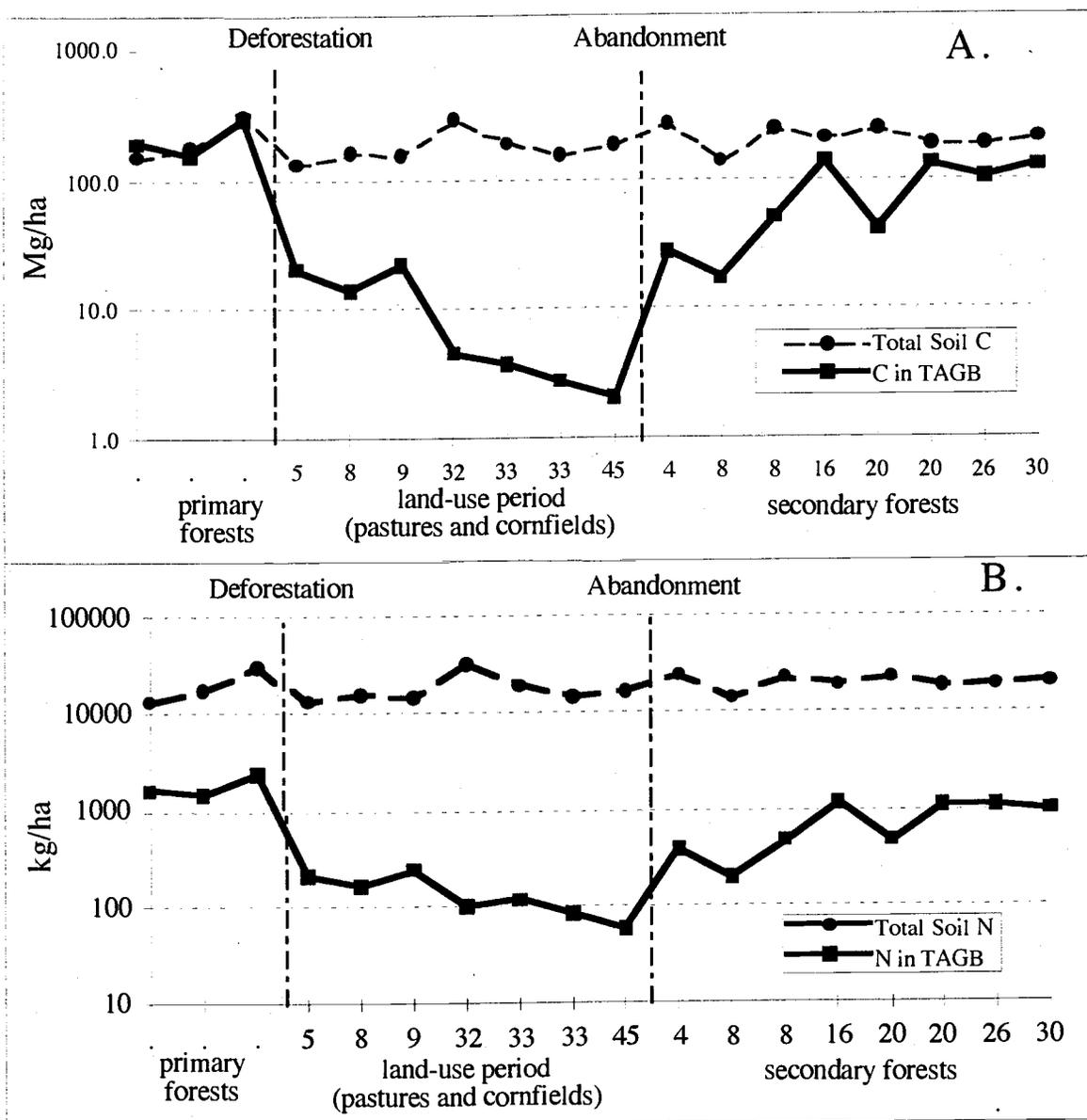


Figure 3.5. Dynamics of carbon (A) and nitrogen (B) in aboveground biomass and soil pools along a land-use gradient in the Los Tuxtlas Region, Mexico. Values are presented on log scales. In the case of pastures and cornfields, values along the x-axis represent the number of years of land use following deforestation. In the case of secondary forests, values along the x-axis represent the number of years of secondary succession following abandonment. Data for primary forests, pastures, and cornfields are from Hughes (see chapter 1).

pastures in which the areal and temporal extent of secondary forests is relatively small (Guevara et al. 1997). If such trends continue, and secondary forests are not allowed to establish and grow, their capacity to act as sinks to sequester C and other elemental pools lost due to deforestation and land-use will remain untapped. As Lugo and Brown (1992) assert, and as results of this study have demonstrated, secondary forests represent potentially large sinks for atmospheric C, but only if they are allowed to establish, persist, and attain maturity in regions such as Los Tuxtlas and elsewhere in the tropics. Our results also indicate that with ever increasing periods of land use following deforestation in the Los Tuxtlas Region, we can expect to see ever slower rates of aboveground biomass, carbon and nutrient accumulation by secondary forests following the abandonment.

## **CHAPTER 4**

### **Dynamics of Available Soil Nitrogen in Response to Land-Use Change in Tropical Evergreen Forest Ecosystems of the Los Tuxtlas Region, Mexico.**

**R. Flint Hughes**

**Keywords:** Soil N availability, net N mineralization, net nitrification, deforestation, land use, Los Tuxtlas, tropical forested ecosystems, pastures, cornfields, secondary forests.

## Abstract

Previous studies indicate that total C, N, and S pools in soils of the Los Tuxtlas Region, Mexico remain relatively stable in response to land-use change. However, the dynamics of such pools are not necessarily indicative of the dynamics of soil nutrients available for plant uptake. To evaluate the impacts of deforestation and land use on dynamics of available N in soils of the Los Tuxtlas Region, Mexico, pools of nitrate and ammonium-N and rates of nitrification and N mineralization were quantified during the wet season in soils of primary forests, pastures, cornfields, recently abandoned sites, and secondary forests greater than 15 years in age. Concentrations of the combined pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  to a soil depth of 10 cm ranged from 6 to 15 mg/kg, and bulk soil measures of these combined pools to a soil depth of 10 cm ranged from 5 to 11 kg/ha. Rates of nitrification and N-mineralization were determined by 14 day aerobic incubations. Nitrification and N mineralization rates to a soil depth of 10 cm ranged from 0.7 to 1.8  $\text{mg kg}^{-1} \text{d}^{-1}$  and from 0.7 to 1.7  $\text{mg kg}^{-1} \text{d}^{-1}$ , respectively. As a group, soils of primary and old secondary forest sites had significantly larger pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  and significantly higher rates of nitrification and N mineralization than the combined group of pastures, cornfields, and recently abandoned sites. Our results indicate that availability of soil N is significantly altered by land-use change in the Los Tuxtlas Region. Sizes of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  pools and transformation rates of N were relatively high in primary forests, declined during land-use periods, and returned to levels seen in primary forests, but only after at least 8 years of secondary succession.

## Introduction

Determining the response of N availability to deforestation and land use is important in understanding the overall impacts of land-use change in the tropics. Nitrogen availability has been shown to limit productivity in the majority of the world's ecosystems (Schlesinger 1997, Vitousek and Howarth 1991). Changes in the cycling of N as a result of land-use change may lead to significant declines in available N in ecosystems and cause subsequent

declines in site productivity. Such losses may be caused by volatilization of N during biomass burning, leaching of  $\text{NO}_3\text{-N}$  during periods of depressed plant and microbial uptake of N, and increased emissions of  $\text{N}_2$ ,  $\text{NO}$ , and  $\text{N}_2\text{O}$  due to altered rates of denitrification (Neill et al. 1997, Davidson et al. 1993). Land-use/land-cover change has been shown to result in alterations of N cycles in tropical evergreen forest ecosystems through each of the above pathways (Kauffman et al. 1995, Robertson and Tiedje 1988, Keller et al. 1993, McClain et al. 1994, Montagnini and Buschbacher 1989).

Deforestation and land use have the potential to affect N cycling in a variety of ways. Significant declines in forest canopy cover and biomass stocks resulting from deforestation and conversion to pastures or croplands typically leads to increases in soil temperature due to reduced shading and decreases in rates of evapotranspiration due to reduced plant uptake of water. These factors consequently lead to increased rates of nitrification and increase the potential for nitrate loss due to leaching, particularly when post-disturbance plant establishment is slow or patchy in nature (Vitousek 1983). In addition, deforestation may also lead to declines in the C inputs necessary to fuel soil microbial populations. Rates of N-mineralization immediately following deforestation may be two to three times greater than rates measured prior to disturbance, returning to pre-disturbance rates within approximately 6 months (Matson et al. 1987, Palm et al. 1996). However, Matson et al. (1987) also found that losses of N through denitrification or leaching following deforestation may be reduced by anion exchange of  $\text{NO}_3\text{-N}$  at depth within the soil profile. Such anion absorption is likely to be substantial in variable-charge clays of volcanic ash-derived soils elsewhere in the tropics (Sollins et al. 1988).

Following the relatively short-lived pulse of available N immediately after deforestation, prolonged periods of land use have been shown to lead to decreased rates of net N-mineralization and nitrification, with increasing duration of land use resulting in decreasing rates (Reiners et al. 1994, Neill et al. 1995). Site abandonment and the initiation of secondary succession generally results in increased rates of N-mineralization in

secondary forests relative to pastures and, in some cases, relative to primary forests (Robertson 1984, Reiners et al. 1994, Matson et al. 1987).

In the heavily deforested Region of Los Tuxtlas, Mexico, Hughes (see chapters 1 and 2) documented significant declines in the pools of aboveground biomass, C, N, S, and P following deforestation and throughout periods of prolonged land use. Following abandonment, aboveground pools accumulated at relatively rapid rates in secondary forest vegetation. In contrast, no significant changes were detected in pools of total soil C, N, or S to a 1 m depth between any of the land cover types throughout the land-use gradient. However, this does not necessarily mean that availability of N was unaltered by land-use change in the Los Tuxtlas Region. Indeed, the status of large, relatively stable total N pools in soils are generally poorly correlated with the much smaller, more dynamic pools of biologically available N in soils (Vitousek and Sanford 1986). This is likely to be particularly true for relatively young volcanic soils (Andosols) such as those found in the Los Tuxtlas Region (Nelson and Gonzalez-Caver 1990).

The objective of this study was to determine the impact of land-use change on pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  and rates of net N-mineralization and nitrification in soils of the Los Tuxtlas Region, Mexico. To accomplish this, we measured available N pools and used aerobic laboratory incubations to obtain an index of net N-mineralization and nitrification rates in soils from a series of primary forest, pasture, cornfield, and secondary forest sites that represent a land-use gradient in this deforested region of tropical Mexico.

### Study Area

All study sites were located within or very near the Los Tuxtlas Biological Station (LTBS) administered by the Universidad Nacional Autonoma de Mexico (UNAM) ( $18^{\circ}35'\text{N}$ ,  $95^{\circ}05'\text{W}$ ). The LTBS is located in the northeastern portion of the Los Tuxtlas Region in the state of Veracruz, Mexico. This region is defined by the Sierra de Los Tuxtlas - a series of volcanoes constituting the easternmost portion of the Trans-Mexican Volcanic Belt (Nelson and Gonzalez-Caver 1992). All secondary forest sites were located

on the lower, southeastern slopes of the San Martin volcano between 100 and 300 m in elevation. Parent material originating from San Martin are classified as basanite and alkali basalt. Volcanism in the Los Tuxtlas Region began approximately 7 million years ago and has continued up to the recent past with extensive activity during the last several thousand years; historical eruptions occurred as recently as 1664 and 1793 (Nelson and Gonzalez-Caver 1992). The topography of the region is characteristic of recent volcanism with undulating hills grading to steep slopes; cinder cones of various sizes are numerous, and maars (i.e. water filled craters) are common.

Soils have been classified as well-drained, coarse textured, vitric Andosols mixed with volcanic ash (FAO/UNESCO 1975). Forest soils are poorly developed, contain high concentrations of total C, N, P, and K, and are weakly acid (pH range 6.1-6.5) (Hughes see chapter 1, Bongers et al. 1988, Chizon 1984).

The climate is classified as hot and humid (Holdridge et al. 1971, Garcia 1970); the mean annual temperature is 27°C and mean annual precipitation is ≈4500 mm (Soto and Gama 1997). Precipitation is highest between June and February and is interrupted by a dry season between March and May during which time monthly rainfall does not exceed 150 mm. Monthly temperatures range from a minimum of 16°C during December and January to and maximum of 32 °C during July and August (Ibarra-Manriquez and Sinaca-Colin 1987).

The potential vegetation throughout the study area has been classified as tall evergreen forest (Miranda and Hernandez-X 1963) and is characterized by an overstory tree canopy 30 to 35 m in height with occasional emergent trees exceeding 40 m. Due to deforestation and land use, primary forest vegetation now comprises only a small fraction of the landscape, and large, intact portions are limited to the forest reserve of the LTBS. Land-use change (i.e. conversion of forests to pastures and croplands) in the Los Tuxtlas Region has been both rapid and extensive; Dirzo and Garcia (1992) reported annual deforestation rates of over 4% in the Los Tuxtlas Region during the period between 1967

and 1986, and estimated that  $\approx 84\%$  of the area had been deforested by the end of that period. As a result, the overall study area appears as a matrix of land-cover types in which pasture and agricultural lands dominate, with scattered fragments of primary and secondary forests present but limited in extent.

Soil nitrogen availability was assessed at a total of twelve sites in the Los Tuxtlas Region. The characteristics, land-use histories, and duration of secondary succession following abandonment of these sites have been presented in Hughes (see chapters 1 and 2). Of the 4 primary forests sampled previously, soil N availability was measured in Selva Bongers (SB) and Selva Plana (SP) sites. Two pasture sites (P-8 and P-33b) and two cornfield sites (C-5 and C-45) were also sampled. In addition, we sampled N availability in three recently abandoned sites ( $<10$  years since abandonment) labeled S-4, S-8a, and S-8b, and in three old secondary forests ( $>15$  years since abandonment) labeled S-16, S-20a, and S-26.

### Methods

All soil samples were collected in September 1995 during the middle of the rainy season. At each of the 12 sites, pools of available N ( $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$ ) and rates of net nitrification and N-mineralization in mineral soil were determined from eight samples collected at 10 m intervals along two 30 m transects placed in the central portion of each sample plot established by Hughes (see chapters 1 and 2). Samples were collected from 0-2.5 cm and 2.5-10 cm depths in the following manner: at each of the eight sample points, four subsamples were collected 1 m from the sample point center in each cardinal direction and composited into a single sample.

Bulk density of soils was determined at each site from collections using sample cores of known volume sampled at five points located within each site. Samples were collected from the 0-10 cm depth.

Composite soil samples were transported to the laboratory and processed within 8 hours following their collection from the field. All rocks and roots  $>2$  mm in diameter

were removed by hand from each sample. A subsample  $\approx 30$  g fresh weight was removed from each soil sample, weighed, and dried at  $\approx 100^\circ\text{C}$  to a constant weight in order to determine water content. Two, 10 g (fresh weight) subsamples were then removed from each composite sample; the first of these was extracted immediately by shaking initially with 50 ml of 2 N KCl and equilibrating for  $\approx 24$  hours. After this period,  $\approx 10$  ml of the supernatant was pipetted into sample vials and frozen pending analysis.

Each of the second set of 10 g soil subsamples were placed in plastic sample cups covered with perforated caps to allow for gas exchange. Samples were then incubated under aerobic conditions at a temperature of  $\approx 26^\circ\text{C}$  for 14 days. Samples were maintained at field water holding capacity throughout the incubation period by daily monitoring and addition of small amounts of distilled water when necessary. Following the incubation period,  $\approx 10$  ml of supernatant was extracted from each sample as described above and kept frozen pending transport to Oregon State University for analysis.

Concentrations of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in soil extracts were determined colorimetrically using an ALPCHEM 300 Series rapid flow analyzer. Available soil concentrations of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were represented by the concentration in initial extracts. Potential net nitrification was calculated as final (incubated)  $\text{NO}_3\text{-N}$  concentrations minus initial  $\text{NO}_3\text{-N}$  concentrations. Potential net N-mineralization was calculated as final  $\text{NH}_4\text{-N}$  plus final  $\text{NO}_3\text{-N}$  minus initial  $\text{NH}_4\text{-N}$  plus  $\text{NO}_3\text{-N}$ . Concentrations were multiplied by soil bulk density values to determine bulk soil pools of available N (kg/ha) and potential rates of nitrification and net N-mineralization ( $\text{kg ha}^{-1} \text{d}^{-1}$ ). Concentrations and pools of available N for the 0-10 cm depth were calculated by combining values for the 0-2.5 cm and 2.5-10 cm depths in proportion to their relative contribution to the 0-10 cm depth (i.e., the 0-2.5 cm value multiplied by 0.25, plus the 2.5-10 cm value multiplied by 0.75).

Single classification analysis of variance was used to determine differences between land cover type groups for the various components of N availability (Sokal and Rohlf 1969).

## Results

Pool sizes of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  were generally higher in primary forests and old secondary forest sites than in cornfields, pastures, and recently abandoned sites (Table 4.1). Concentrations of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  at the 0-10 depth ranged from 5.7 mg/kg at one of the recently abandoned sites (S-8a) to 15 mg/kg at one of the older secondary forest sites (S-26). Although combined concentrations of available N ( $\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$ ) were relatively low in recently abandoned sites, concentrations of  $\text{NH}_4\text{-N}$  were high in these sites relative to the other land cover types (Table 4.1).

Rates of both net  $\text{NO}_3\text{-N}$  production and net N mineralization, on a concentration basis, were also higher in primary and old secondary forests than pastures, cornfields, and recently abandoned sites (Table 4.2). Nitrification rates at the 0-10 cm depth varied from  $0.7 \text{ mg kg}^{-1} \text{ d}^{-1}$  in a recently abandoned site (S-8b) to  $1.8 \text{ mg kg}^{-1} \text{ d}^{-1}$  in an old secondary forest site (S-20a).

Bulk soil pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  as well as rates of N transformation were similar in pattern to concentration values (Table 4.3). Combined pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  to a 0-10 cm depth ranged from 4.6 to 10.9 kg/ha. Rates of net nitrification and N mineralization to a 0-10 cm depth ranged from 0.61 to  $1.45 \text{ kg ha}^{-1} \text{ d}^{-1}$  and from 0.57 to  $1.41 \text{ kg ha}^{-1} \text{ d}^{-1}$ , respectively.

Based on the above results, available N pools and rates of net N transformation values were separated into two groups based on land-cover type. The first group contained primary forest and old secondary forest sites. The second group contained pasture, cornfield, and recently abandoned sites. The latter group represented the middle portion of the land-use gradient and is subsequently referred to as the land-use group. The former

Table 4.1. Concentrations (mg/kg) of available N in soils of primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites of the Los Tuxtlas Region, Mexico. Samples are to a 10 cm soil depth and are means  $\pm$  one standard error.

land cover type and site name	NH <sub>4</sub> -N			NO <sub>3</sub> -N			total mineral N NH <sub>4</sub> -N+NO <sub>3</sub> -N 0-10 cm
	0-2.5 cm	2.5-10 cm	0-10 cm	0-2.5 cm	2.5-10 cm	0-10 cm	
<b>Forest Sites</b>							
primary forests							
SB	8.7 $\pm$ 1.7	3.6 $\pm$ 0.7	4.9	8.2 $\pm$ 1.0	5.1 $\pm$ 0.7	5.9	10.8 $\pm$ 1.6
SP	17.1 $\pm$ 1.8	3.6 $\pm$ 0.4	7.0	11.7 $\pm$ 1.1	4.0 $\pm$ 0.3	5.9	12.9 $\pm$ 0.9
Old Secondary forests							
S-16	8.6 $\pm$ 1.1	2.9 $\pm$ 0.5	4.3	8.1 $\pm$ 0.8	4.7 $\pm$ 0.4	5.5	9.9 $\pm$ 0.8
S-20a	8.9 $\pm$ 1.1	4.0 $\pm$ 0.4	5.2	9.3 $\pm$ 1.3	4.6 $\pm$ 0.4	5.7	11.0 $\pm$ 1.1
S-26	14.9 $\pm$ 1.8	4.0 $\pm$ 0.4	6.7	15.2 $\pm$ 1.9	5.4 $\pm$ 0.6	7.9	14.5 $\pm$ 1.4
<b>Land Use Sites</b>							
Pastures							
P-8	4.5 $\pm$ 0.2	2.4 $\pm$ 0.1	2.9	4.1 $\pm$ 0.5	2.4 $\pm$ 0.3	2.9	5.8 $\pm$ 0.3
P-33b	7.8 $\pm$ 0.4	4.1 $\pm$ 0.2	5.0	6.0 $\pm$ 0.5	3.8 $\pm$ 0.3	4.4	9.4 $\pm$ 0.4
Cornfields							
C-5	4.1 $\pm$ 0.7	2.2 $\pm$ 0.2	2.7	5.4 $\pm$ 0.7	3.7 $\pm$ 0.5	4.1	6.8 $\pm$ 0.7
C-45	2.1 $\pm$ 0.2	1.9 $\pm$ 0.1	1.9	5.0 $\pm$ 0.4	3.9 $\pm$ 0.3	4.2	6.1 $\pm$ 0.4
Recently Abandoned							
S-4	9.5 $\pm$ 0.9	3.4 $\pm$ 0.5	4.9	4.2 $\pm$ 0.6	3.8 $\pm$ 0.4	3.9	8.8 $\pm$ 0.8
S-8a	7.3 $\pm$ 0.5	3.1 $\pm$ 0.4	4.2	2.0 $\pm$ 0.3	1.3 $\pm$ 0.2	1.5	5.7 $\pm$ 0.2
S-8b	8.9 $\pm$ 1.3	3.3 $\pm$ 0.4	4.7	3.1 $\pm$ 0.5	1.4 $\pm$ 0.1	1.8	6.5 $\pm$ 0.7

Table 4.2. Rates of nitrification and N mineralization in soils to a 10 cm depth of primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites in the Los Tuxtlas Region, Mexico. Means  $\pm$  one standard error are reported.

land cover type and site name	net NO <sub>3</sub> -N production (mg kg <sup>-1</sup> day <sup>-1</sup> )			net N mineralization (mg kg <sup>-1</sup> day <sup>-1</sup> )		
	0-2.5 cm	2.5-10 cm	0-10 cm	0-2.5 cm	2.5-10 cm	0-10 cm
<b>Forest Sites</b>						
primary forests						
SB	1.9 $\pm$ 0.4	1.1 $\pm$ 0.1	1.3 $\pm$ 0.1	2.0 $\pm$ 0.4	1.1 $\pm$ 0.1	1.3 $\pm$ 0.1
SP	1.5 $\pm$ 0.5	1.6 $\pm$ 0.1	1.6 $\pm$ 0.1	1.3 $\pm$ 0.5	1.6 $\pm$ 0.1	1.5 $\pm$ 0.1
old secondary forests						
S-16	0.4 $\pm$ 0.3	1.4 $\pm$ 0.1	1.2 $\pm$ 0.1	0.4 $\pm$ 0.3	1.4 $\pm$ 0.1	1.2 $\pm$ 0.1
S-20a	2.6 $\pm$ 1.4	1.5 $\pm$ 0.2	1.8 $\pm$ 0.4	2.6 $\pm$ 1.6	1.5 $\pm$ 0.2	1.7 $\pm$ 0.4
S-26	1.9 $\pm$ 0.9	1.4 $\pm$ 0.2	1.5 $\pm$ 0.3	1.7 $\pm$ 0.9	1.4 $\pm$ 0.2	1.5 $\pm$ 0.3
<b>Land Use Sites</b>						
pastures						
P-8	0.8 $\pm$ 0.2	1.1 $\pm$ 0.1	1.0 $\pm$ 0.1	0.8 $\pm$ 0.2	1.0 $\pm$ 0.1	1.0 $\pm$ 0.1
P-33b	0.7 $\pm$ 0.3	1.0 $\pm$ 0.1	0.9 $\pm$ 0.1	0.7 $\pm$ 0.3	1.0 $\pm$ 0.1	1.0 $\pm$ 0.1
cornfields						
C-5	1.8 $\pm$ 0.1	0.9 $\pm$ 0.2	1.1 $\pm$ 0.1	1.7 $\pm$ 0.1	0.9 $\pm$ 0.2	1.1 $\pm$ 0.1
C-45	1.7 $\pm$ 0.1	1.1 $\pm$ 0.1	1.3 $\pm$ 0.1	1.7 $\pm$ 0.1	1.1 $\pm$ 0.1	1.3 $\pm$ 0.1
recently abandoned						
S-4	0.8 $\pm$ 0.2	1.1 $\pm$ 0.1	1.0 $\pm$ 0.1	0.6 $\pm$ 0.2	1.0 $\pm$ 0.1	0.9 $\pm$ 0.1
S-8a	0.4 $\pm$ 0.1	0.9 $\pm$ 0.2	0.8 $\pm$ 0.2	0.5 $\pm$ 0.1	0.9 $\pm$ 0.2	0.8 $\pm$ 0.2
S-8b	0.5 $\pm$ 0.2	0.8 $\pm$ 0.1	0.7 $\pm$ 0.1	0.4 $\pm$ 0.2	0.8 $\pm$ 0.1	0.7 $\pm$ 0.1

Table 4.3. Soil bulk densities, soil pools of available N, and rates of transformation of available N in soils to a 10 cm depth in primary forests, old secondary forests, pastures, cornfields, and recently abandoned sites in the Los Tuxtlas Region, Mexico.

land cover type and site name	soil bulk density (g/cm <sup>3</sup> )	pools (kg/ha)			rates (kg ha <sup>-1</sup> day <sup>-1</sup> )	
		NH <sub>4</sub> -N	NO <sub>3</sub> -N	(NH <sub>4</sub> -N)+(NO <sub>3</sub> -N)	net NO <sub>3</sub> -N production	net N mineralization
<b>Forest Sites</b>						
primary forests						
SB	0.89	4.4	5.3	9.6	1.19	1.19
SP	0.60	4.2	3.6	7.8	0.93	0.91
old secondary forests						
S-16	0.75	3.3	4.1	7.4	0.87	0.87
S-20a	0.81	4.2	4.6	8.9	1.45	1.41
S-26	0.75	5.0	5.9	10.9	1.13	1.11
<b>Land Use Sites</b>						
pastures						
P-8	0.89	2.6	2.5	5.2	0.90	0.88
P-33b	0.89	4.5	3.9	8.3	0.84	0.86
cornfields						
C-5	0.84	2.3	3.5	5.7	0.95	0.91
C-45	0.83	1.6	3.5	5.0	1.06	1.04
recently abandoned sites						
S-4	0.81	4.0	3.2	7.1	0.82	0.74
S-8a	0.83	3.4	1.2	4.6	0.61	0.64
S-8b	0.81	3.9	1.5	5.4	0.61	0.57

group contained the primary forest sites that preceded land use and the secondary forest sites that followed land-use periods and had at least 16 years of secondary succession following abandonment; this group of sites is subsequently referred to as the forest group.

In nearly all of the N availability parameters measured, the group consisting of forest sites had significantly higher values than the land-use group. Concentrations of NH<sub>4</sub>-N and NO<sub>3</sub>-N in soils to a 0-10 cm depth were 50% and 90% higher, respectively, in forest sites compared to land-use sites; combined pools of NH<sub>4</sub>-N and NO<sub>3</sub>-N were nearly 70% higher in forest sites relative to land-use sites (Figure 4.1). Rates of net nitrification and N mineralization were also 42 to 51% higher in forest sites compared to land-use sites at 2.5-10 cm and 0-10 cm depths. At the 0-2.5 cm depth, large within-group variation resulted in no significant difference in net nitrification and N mineralization rates between groups (Figure 4.2).

Bulk soil pools of available N and potential rates of net nitrification and N mineralization were also higher in forest sites relative to land-use sites. Pools of  $\text{NO}_3\text{-N}$  and combined pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  to a 10 cm soil depth were 71% and 51% higher in forest sites than in land-use sites (Figure 4.3). Potential rates of net nitrification and N mineralization were  $\approx 35\%$  higher in forest sites relative to land-use sites (Figure 4.4). Differences in bulk soil N values between the two groups were somewhat less than the differences in concentration values. Reduced differences are due to differences in soil bulk density values used to calculate soil bulk N values; soil bulk densities were somewhat higher in land-use sites relative to forest sites (Table 4.3).

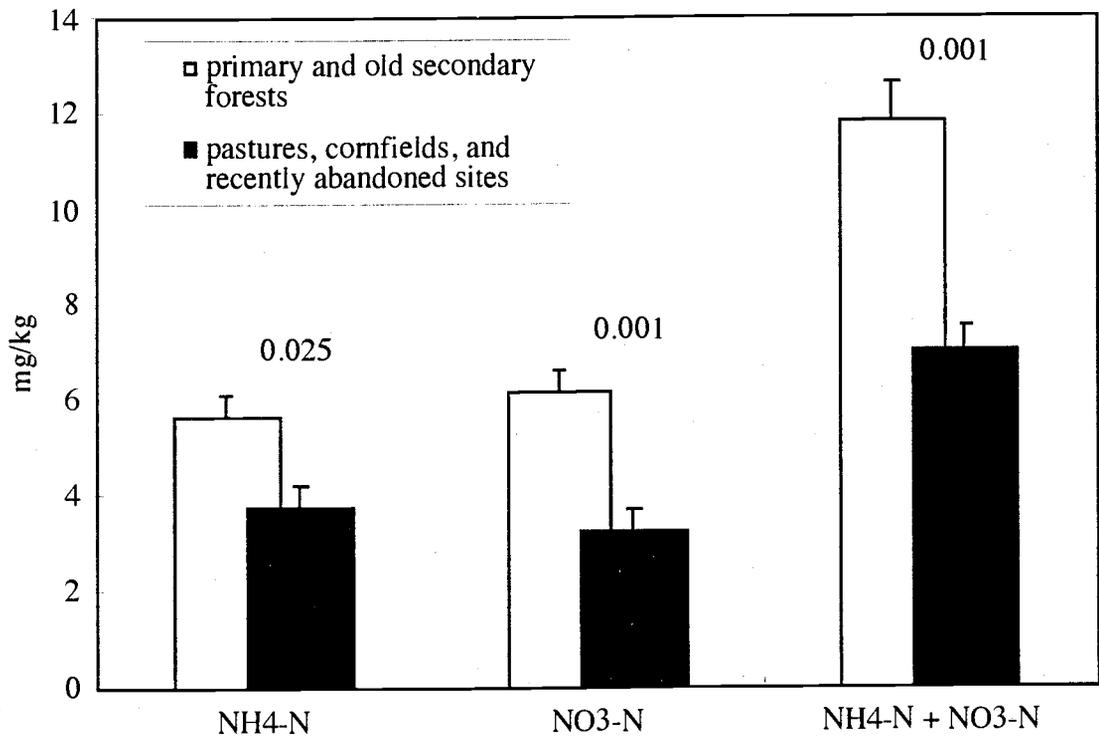


Figure 4.1. Concentrations of available N to a 10 cm depth in soils at sites along a land-use gradient in the Los Tuxtlas Region, Mexico. Mean and standard error are presented for each cover type group. Numbers above each cover type pair are P-values of the difference between the two means of each pair.

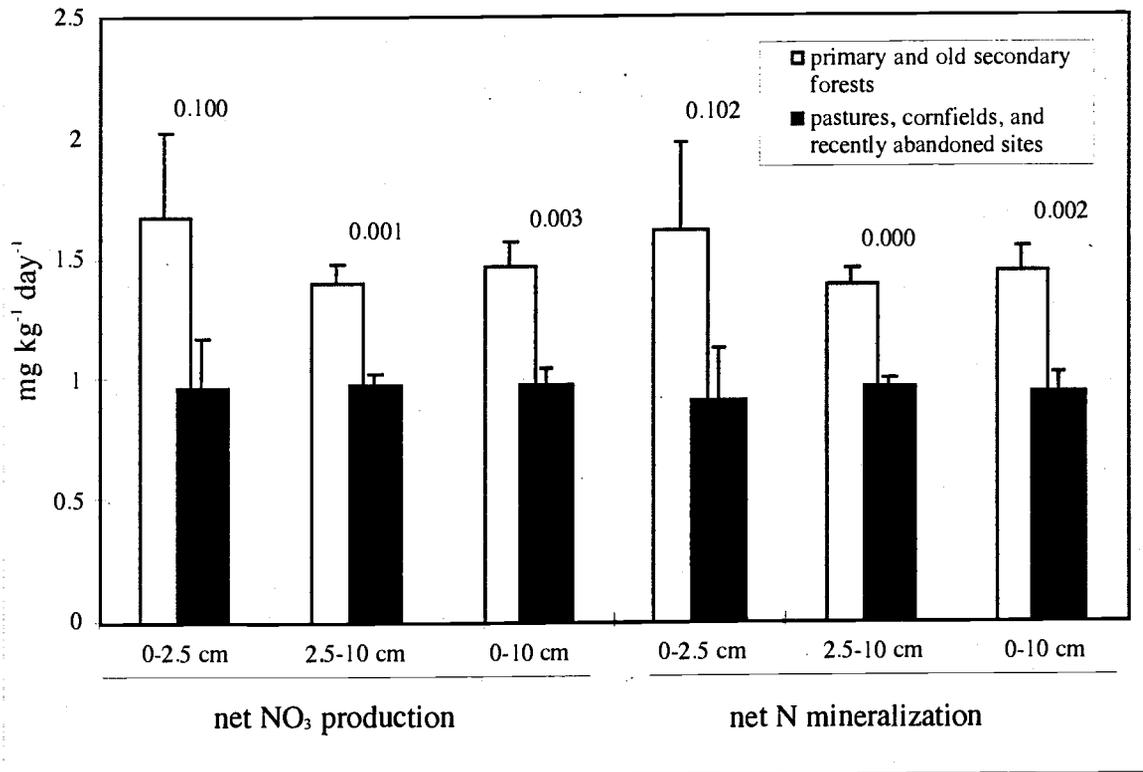


Figure 4.2. Potential rates of net nitrification and N mineralization in soils to a 10 cm depth at sites along a land-use gradient in the Los Tuxtlas Region, Mexico. Mean and standard error are presented for each cover type group. Numbers above each cover type pair are P-values of the difference between the two means of each pair.

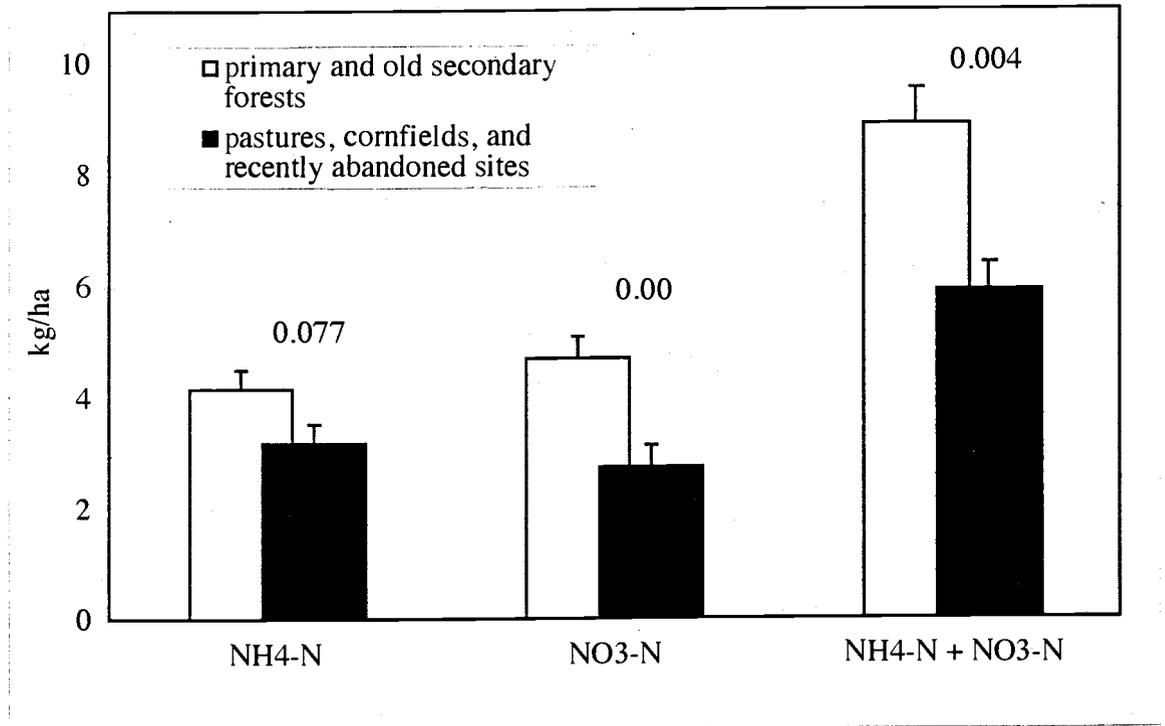


Figure 4.3. Bulk soil pools of ammonium and nitrate to a 10 cm depth at sites along a land-use gradient in the Los Tuxtlas Region, Mexico. Mean and standard error are presented for each cover type group. Numbers above each cover type pair are P-values of the difference between the two means of each pair.

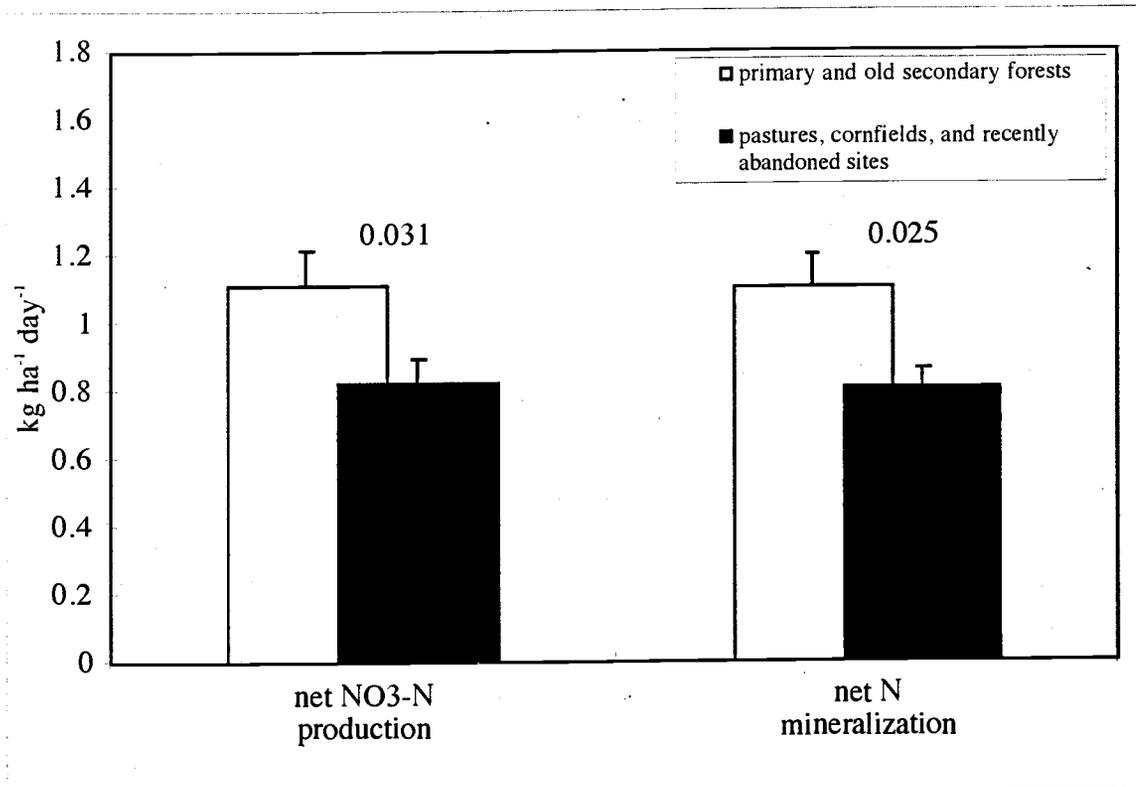


Figure 4.4. Potential rates of net nitrification and N mineralization in soils to a 10 cm depth along a land-use gradient in the Los Tuxtlas Region, Mexico. Mean and standard error are presented for each cover type group. Numbers above each cover type pair are P-values of the difference between the two means of each pair.

## Discussion

In general, the above results indicate a decline in pool sizes of available N and rates of N transformations as a result of conversion of primary forest to pasture and cornfields in the Los Tuxtlas Region, Mexico. However, these results must be cautiously interpreted as they represent a set of one-time measurements during the wet season for each site. In addition, because rates of net NO<sub>3</sub>-N production and net N mineralization were measured via laboratory incubations rather than in situ measurements, they should be interpreted as reflecting potential rates rather than actual field estimates (Binkley and Hart 1989).

Pools of NO<sub>3</sub>-N and NH<sub>4</sub>-N in soils of forest sites in Los Tuxtlas were similar to values presented elsewhere. Vitousek and Matson (1988) reported a range of 0.07 to 8.5

mg/kg for  $\text{NH}_4\text{-N}$  and range of 0.0 to 11.7 mg/kg for  $\text{NO}_3\text{-N}$  in a series of forest sites throughout Tropical America and Hawai'i. Reiners et al. (1994) reported mean values of 2.1 and 4.3 mg/kg for pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  in forest soils of Costa Rica; these values are somewhat lower than those of forest soils in Los Tuxtlas (Table 4.1).

Rates of potential net nitrification and N mineralization in forest soils of the Los Tuxtlas Region (Tables 4.2 and 4.3) were generally lower than rates of N transformation measured in other tropical forest ecosystems. Rates of net nitrification and N mineralization ranged from 0.08 to 3.1  $\text{mg kg}^{-1} \text{d}^{-1}$  and from 0.0 to 4.1  $\text{mg kg}^{-1} \text{d}^{-1}$ , respectively, in tropical forest soils sampled by Vitousek and Matson (1988), and Reiners et al. (1994).

The findings of this study that deforestation and land use resulted in decreased pool sizes of available N and rates of N transformation generally agree with results reported elsewhere. Conversion of primary forests to pastures in Costa Rica led to decreased rates in potential net nitrification and net N mineralization (Reiners et al. 1994, Robertson 1984). Neill et al. (1997) also reported decreased rates of N transformation as a result of forest conversion to pasture along a wide geographic range in the southwestern Amazon Basin.

The increases in pool sizes of available N and rates of N transformations in old secondary forests were also consistent with trends in N cycling during secondary succession reported in other studies. Reiners et al. (1994) reported higher rates of net nitrification and net N mineralization in secondary forests compared to pastures; rates in secondary forests were approximately equivalent to rates of primary forests. Maars et al. (1988) found N transformation rates to be higher in secondary forests compared to primary forests. In secondary forests of Los Tuxtlas and elsewhere, increased rates of net nitrification and N mineralization are likely due to the production of litter that is more easily decomposed than in primary forests (Reiners et al. 1994, Brown and Lugo 1990).

Following site abandonment, pools of available N and rates of net nitrification and N mineralization remained relatively low throughout the initial stages of secondary

succession in the Los Tuxtlas Region. Indeed, at  $\approx 0.75 \text{ mg kg}^{-1} \text{ day}^{-1}$ , rates of both net nitrification and N mineralization were lower in the two eight-year-old forests than in any of the other sites that were sampled (Tables 4.1 and 4.2). In contrast, pools sizes of available  $\text{NH}_4\text{-N}$  at these site were among the highest values of the sites sampled in this study. Taken together, these results suggest that nitrifying bacteria are either being limited in numbers or metabolism or are immobilizing large quantities of  $\text{NH}_4\text{-N}$  in these recently abandoned sites. Our results suggest that such limitations may persist for up to nearly 10 years of secondary succession following abandonment.

Overall, conversion of forests to managed systems in the Los Tuxtlas Region results in significant reductions in both pools sizes and rates of transformation of available N, and these levels remain low far into the initial stages of secondary succession. Results of this study and that of Hughes (see chapters 1 and 2) indicate that the dramatic changes in aboveground pools of C and N that result from land-use change in the Los Tuxtlas Region are associated with significant changes in pools and transformation rates of available N. These findings, and the findings of other recent studies (e.g., Kauffman et al. 1995, Kauffman et al. in press, Neill et al. 1997, Reiners et al. 1994) indicate that proper evaluation of the local, regional, and global impacts of land-use change in tropical forested ecosystems should include measures of both C and N dynamics and the manner in which these dynamics interact with one another through space and time.

## CHAPTER 5 CONCLUSIONS

The efforts of this study to quantify the response of aboveground biomass, C, N, S, and P pools to land-use change in the Los Tuxtlas Region, Mexico led to the following results:

- Conversion of primary forests to pastures and cornfields in the Los Tuxtlas Region resulted in declines in total aboveground biomass (TAGB) of  $\approx 380$  Mg/ha. TAGB of primary forests in the Los Tuxtlas Region averaged 403 Mg/ha; pasture and cornfield sites averaged 24 and 23 Mg/ha, respectively.
- In addition to declines in TAGB, results indicate that conversion of forest sites to pasture or cornfield sites resulted in declines of  $\approx 95\%$  of aboveground C pools,  $\approx 91\%$  of aboveground N pools,  $\approx 83\%$  of aboveground P pools, and between 89% and 95% of aboveground S pools.
- Soil pools of C, N, and S remained relatively stable in response to deforestation and land use; soil pools of these elements did not significantly differ among primary forest, pasture, and cornfield sites. In addition, neither duration nor type (i.e. pasture vs. cornfield) of land use had a significant impact on soil pools of C, N, and S. Average C mass in soils of forest, pasture, and cornfield sites ranged from 166-210 Mg/ha; mass of N and S in soils ranged from  $\approx 16,000$ -20,000 kg/ha and  $\approx 3400$  and 3800 kg/ha, respectively. Changes in aboveground biomass pools of C and nutrients dominated those of soil pools along the land-use gradient.
- Approximately 50% of the total ecosystem pool of C was lost as a result of deforestation and land use; all of this decline can be attributed to the decline in aboveground pools. In contrast, because the vast majority of N and S pools were present in the relatively stable pools of the young volcanic soils in the Los Tuxtlas Region, less than 10% of total ecosystem pools of N and S were lost due to land-use change.

- Total aboveground biomass (TAGB) of secondary forest sites in the Los Tuxtlas Region increased with increasing site age; accumulations ranged from 4.8 Mg/ha in a recently abandoned site to 287 Mg/ha in a 50 year old secondary forest site.
- Results indicate that secondary forests will reach the TAGB of primary forests of the Los Tuxtlas Region in approximately 73 years. In addition, rates of TAGB accumulation were negatively correlated to the prior land-use history of each secondary forest; as the duration of land use prior to abandonment increased, rates of TAGB accumulation decreased.
- Soil pools remained relatively unchanged throughout the successional chronosequence; they did not differ with respect to forest age or prior land-use history, and did not differ from soil pools of primary forest, pasture, and cornfield sites in the Los Tuxtlas Region.
- Dynamics of total ecosystem C following abandonment were characterized by increasing contributions from aboveground pools with increasing secondary forest age. In contrast, changes in total ecosystem pools of N and S during secondary succession were relatively small because the vast majority (>90%) of N and S was located in the stable soil pools.
- As a group, soils of primary and old secondary forest sites had significantly larger pools of  $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$  and significantly higher rates of nitrification and N mineralization than the combined group of pastures, cornfields, and recently abandoned sites. These results indicate that availability of soil N is significantly altered by land-use change in the Los Tuxtlas Region.
- Values of both pool sizes and transformation rates of N were relatively high in primary forests, declined during land-use periods, and returned to levels seen in primary forests, but only after at least eight years of secondary succession.

Overall, the above results attest to the dramatic impacts of deforestation and land use on biomass, C, and nutrient distributions in both aboveground vegetation and soil pools of tropical evergreen forests of the Los Tuxtlas Region, Mexico. It is hoped that these results will promote proper quantification of the regional-scale impacts of land-use change in this part of Mexico, and will contribute to a better understanding of the

greenhouse gas emissions produced during conversion of Mexico's tropical evergreen forest systems to pastures or croplands. Under present land use patterns, our results indicate that the Los Tuxtlas Region is functioning as a source of greenhouse gases to the atmosphere. Although regenerating secondary forests hold the promise of sequestering biomass, C, N, S, and P pools at relatively rapid rates, the Los Tuxtlas Region will not realize its role as a potential sink for greenhouse gas emissions until rates of deforestation are reduced, significant areas currently maintained as pastures or croplands are abandoned, and secondary forests are allowed to establish and persist over substantial portions of the landscape.

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