

## BIOMASS, CARBON, AND NUTRIENT DYNAMICS OF SECONDARY FORESTS IN A HUMID TROPICAL REGION OF MÉXICO

R. FLINT HUGHES,<sup>1,4</sup> J. BOONE KAUFFMAN,<sup>2</sup> AND VÍCTOR J. JARAMILLO<sup>3</sup>

<sup>1</sup>Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

<sup>2</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA

<sup>3</sup>Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, Universidad Nacional Autónoma de México, Campus Morelia, Morelia, Michoacán 58089, México

**Abstract.** Tropical secondary forests have the capacity to function as large carbon and nutrient sinks and may offset losses resulting from deforestation and land use. In the heavily deforested Los Tuxtlas Region of México, aboveground biomass as well as aboveground and mineral soil C, N, S, and P pools were quantified in 11 secondary forest sites. These sites ranged in age from 6 mo to 50 yr following abandonment and had experienced between 1 and 30 yr of land use prior to abandonment. Total aboveground biomass (TAGB) increased with increasing site age and ranged from 4.8 Mg/ha in a recently abandoned site to 287 Mg/ha in the 50-yr-old secondary forest site. Results indicate that secondary forests would reach TAGB levels equivalent to those of primary forests in the Los Tuxtlas Region after 73 yr. Furthermore, mean annual aboveground biomass accumulation (ABA) of secondary forests was strongly and inversely related to the duration of prior land use.

Aboveground pools of C, N, S, and P were also positively correlated with secondary forest age. For forests between 6 mo and 50 yr of age, C pools increased from 2 to 136 Mg/ha, N increased from 72 to 1167 kg/ha, S increased from 9 to 147 kg/ha, and P increased from 5 to 147 kg/ha. In contrast, C, N, and S pools in mineral soil to a 1-m depth remained relatively stable throughout the successional chronosequence and averaged 207, 20, and 3.4 Mg/ha, respectively. Mineral soil pools did not differ with respect to forest age or prior land use history and did not differ from soil pools of primary forest, cornfield, and pasture sites in the Los Tuxtlas Region.

Dynamics of the combined aboveground and mineral soil C pools (i.e., excluding C in root biomass) were characterized by increasing contributions from aboveground pools with increasing forest age; aboveground C pools accounted for 9% and 42% of the combined pool in the youngest and oldest forests, respectively. In contrast, changes in combined aboveground and mineral soil pools of N and S during secondary succession were relatively small because >90% of N and S mass was located in mineral soil pools.

**Key words:** aboveground biomass; carbon sequestration; greenhouse gas flux; land use; Los Tuxtlas, México; México; nutrient dynamics; secondary forests; tropical ecosystems.

### INTRODUCTION

Secondary forests are rapidly becoming a common land cover type in tropical regions of the world. It has been estimated that  $\sim 9 \times 10^6$  ha of secondary forests are formed annually within these regions (Brown and Lugo 1990a). While secondary succession has always been an integral process in tropical forest ecosystems following natural disturbances (e.g., hurricanes and tree falls due to senescence), current increases in secondary forest cover are primarily the result of anthropogenic disturbances such as logging and conversion of forests to pasture and agricultural lands (Brown and Lugo 1990a, Skole and Tucker 1993).

In general, secondary forests have rapid rates of

aboveground production, particularly during the initial stages of succession. Previous studies have documented rates of biomass accumulation of up to 100 Mg/ha after the first 15 yr of succession (Ewel 1980, Brown and Lugo 1990a, Lugo 1992, 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. 1998, Hughes et al., *in press*). Lugo and Brown (1992) estimated that forest fallows (i.e., secondary forests) may sequester between 0.6 and 1.4 Pg of C each year in tropical regions, or 40–90% of the estimated annual C emissions resulting from biomass burning in those regions. In this way, secondary forests in tropical regions have the capacity to play an integral role in ameliorating increasing levels of atmospheric CO<sub>2</sub> by assimilating and storing C in the terrestrial biosphere (Brown et al. 1996). However, Vitousek (1991) cautioned that while tree regeneration on de-

Manuscript received 20 April 1998; revised 17 August 1998; accepted 18 August 1998.

<sup>4</sup> Present address: Cooperative Institute for Research in Environmental Sciences, Campus Box 216, University of Colorado, Boulder, Colorado 80309-0216 USA. E-mail: hughesf@hypatia.colorado.edu

forested land results in potentially rapid carbon and nutrient accumulation, this storage is likely to be an ephemeral effect due to the shifting nature of land use in the tropics, which ultimately determines the long-term fate of stored C and nutrients. Given the growing prevalence of secondary forests in tropical regions and their potential importance to global carbon and nutrient cycles, a greater understanding of their development and functioning has been needed. Indeed, a body of knowledge regarding tropical secondary forest succession and function is accumulating in response to this need, and a number of developmental and functional patterns, as well as the potential controls on the variation of such patterns, have emerged from this growing database (Ewel 1980, Brown and Lugo 1990a, Lugo 1992, Zarin and Johnson 1995, Johnson et al. 2000).

While it is true that numerous studies have documented biomass and elemental pool dynamics and functional changes of tropical secondary forests through successional time (e.g., Ewel 1971, Toky and Ramakrishnan 1983, Uhl and Jordan 1984, Saldarriaga et al. 1988), less attention has been focused on the influence of prior land use on secondary forest succession. Since the majority of secondary forests in tropical regions establish and develop on lands that have experienced periods of management (e.g., as croplands or pastures), an increased understanding of how prior land use might constrain tropical secondary forest development, and thus constrain the potential rates of terrestrial C storage in tropical regions, is called for. Consequently, one of the primary objectives of this study was to determine the degree to which duration of prior land use affects accumulation rates of biomass, C, and nutrients in tropical secondary forests of the Los Tuxtlas Region of México.

Additionally, accurate calculation of carbon budgets at both regional and national scales in the tropics depends on our capacity to quantify the accumulation of C by secondary forests now present in the regions and/or nations that have experienced high rates of deforestation. In México, rates of deforestation in tropical evergreen forest systems have been exceedingly high. During the 1980s, ~5000 km<sup>2</sup> of tropical forests were deforested annually (Masera et al. 1997). Hughes et al. (*in press*) showed that conversion of primary forests to pastures and cornfields in the Los Tuxtlas Region of México resulted in dramatic reductions in total aboveground biomass as well as C, N, S, and P pools; declines ranged from 85 to 95% of the biomass and elemental pools contained in primary forest vegetation. Such losses of C, N, and S via combustion (i.e., anthropogenic biomass burning) and decomposition are of particular importance as these elements represent the major constituents of numerous radiatively active gas species currently accumulating in the earth's atmosphere (Levine 1990, Taylor and Penner 1994). While tropical secondary forests have been identified as a potential terrestrial C sink in México (Masera et

al. 1997), relatively little is currently known regarding potential rates of biomass and elemental accumulation by that nation's tropical secondary forests. To date only one study has quantified aboveground biomass and nutrient dynamics in secondary forests of the Mexican tropics (Williams-Linera 1983).

As a result, regional and national estimates of C accumulation by tropical secondary forests are left to be calculated using generalized data sets from regions located elsewhere in the tropics. Such generalized information is not likely to be capable of providing accurate estimates of biomass accumulation, given the strong control of site-specific biotic, climatic, and edaphic characteristics on secondary succession (Johnson et al. 2000). In their effort to estimate regional C dynamics resulting from land cover change in the Los Tuxtlas Region in the southern state of Veracruz, México, Riley et al. (1997) modeled C dynamics of both above- and belowground pools in secondary forests under the assumption that it would take secondary forests 40 yr to accumulate the C pools equivalent to those of intact forest sites. However, these estimates were derived from average values for C accumulation by secondary forests from tropical regions outside of México. Clearly, regional-scale C budgets that attempt to include rates of C sequestration by secondary forests in tropical México would be enhanced by direct measures of such rates in secondary forests now occupying the previously deforested tropical regions of that nation.

The objectives of this study were to quantify the dual effects of successional time (i.e., time since abandonment) and duration of prior land use (years of land use prior to abandonment) on accumulations of aboveground biomass and elements in secondary forests of the Los Tuxtlas Region, and, in the process, to quantify the degree to which secondary forests may act as C and nutrient sinks in moist tropical regions of México. To do this, we quantified total aboveground biomass as well as C, N, S, and P pools in both aboveground vegetation and mineral soil pools at secondary forest sites that varied with regard to age (i.e., from 0.5 to 50 yr) and duration of prior land use (i.e., from 1 to 30 yr). For comparison, aboveground biomass as well as C and nutrients in aboveground and mineral soil pools of primary forest sites previously measured in the Los Tuxtlas Region were used to represent the potential maximum for each of the aforementioned pools measured at each secondary forest site (Hughes et al., *in press*). We then used this secondary forest chronosequence to quantify potential rates of aboveground biomass and mineral soil pool accumulation, to document changes in partitioning of aboveground biomass and elemental pools between structural components through time, and to evaluate the influence of site age and prior land use history on accumulation rates.

## METHODS

*Study area*

All study sites were located within or near the Los Tuxtlas Biological Station (LTBS) administered by the Universidad Nacional Autónoma de México (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, México. This region is defined by the Sierra de Los Tuxtlas which constitute 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 Martín Tuxtla volcano between 100 and 300 m in elevation. Lava flows from San Martín Tuxtla are classified as basanite and alkali basalt. Volcanism in the Los Tuxtlas Region began  $\sim 7 \times 10^6$  yr 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 (Mooser 1958). The topography of the region is characteristic of recent volcanism, with undulating hills grading to steep slopes.

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, and are weakly acidic (pH range 6.1–6.5) (Chizon 1984, Bongers et al. 1988). The climate is classified as hot and humid (García 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, when monthly rainfall does not exceed 150 mm. Mean monthly temperatures range from a minimum of 16°C during December and January to a maximum of 32°C during July and August (Ibarra-Manríquez and Sinaca-Colín 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 30–35 m in height with occasional emergent trees exceeding 40 m. Common canopy tree species include *Nectandra ambigens*, *Pseudolmedia loxyphyllaria*, *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 region, and large, intact portions are limited to the forest reserve of the LTBS. Dirzo and García (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 region 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 plectostachyis*, 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 landholders (Guevara et al. 1997, Hughes et al., *in press*).

Following abandonment of pasture and cultivated sites, early successional tree species colonize the sites. Young secondary forests (i.e., <15 yr 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 schiedeana*, *Rollinia* spp., *Myriocarpa longipes*, and *Omphalea oleifera* become characteristic species of the overstory canopy community (Ibarra-Manríquez et al. 1997).

*Plot design*

We sampled 11 secondary forest sites ranging in age from 6 mo to 50 yr since abandonment (Table 1). The land use history and time since abandonment of each site were determined from interviews with the local landholders 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 mineral soil to a 1-m depth at 8 of the 11 sites, and P in mineral soil to a depth of 10 cm at 2 sites.

TAGB as well as C and nutrient pools of secondary forest sites were quantified using a nested plot design. A 60 × 50 m plot was established at each site in which the diameter at breast height (dbh, 1.3 m) was measured for all trees and dead snags >10 cm dbh. The genus and species of each tree >10 cm dbh was recorded as well. Woody debris was sampled at five transects placed at 15-m intervals along three 60-m transects that were located on the edges and down the center of the plot ( $n = 15$ ). Each 15-m transect was placed in a randomly selected direction from its point of origin. To avoid instances in which a randomly selected direction caused one transect to overlap another transect, the former transect was placed in a direction that was 180° from the selected random direction. 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. Downed wood pieces 2.54–

TABLE 1. Land use histories of secondary forest sites sampled in the Los Tuxtlas Region, México.

Site	Land use history (years prior to abandonment)	Land use period (yr)	Abandonment period (yr)
S-0.5	20 yr as a cornfield, 8 yr as a pasture, 2 yr as a cornfield	30	0.5
S-4	1 yr as a cornfield	1	4
S-8a	15 yr as a cornfield, 10 yr as a pasture, 2 yr as a cornfield	27	8
S-8b	5 yr as a cornfield, 2 yr as a pasture	7	8
S-10	15 yr as a cornfield, 15 yr as a pasture	30	10
S-16	5 yr as a cornfield	5	16
S-20a	13 yr as a cornfield	13	20
S-20b	1 yr as a cornfield	1	20
S-26	2 yr as a cornfield	2	26
S-30	15 yr as a cornfield	15	30
S-50	site was a cornfield for an indeterminate period	...	50

Notes: Land use period denotes the duration of land use following deforestation but prior to abandonment. Abandonment period refers to the time following cessation of land use and prior to sampling. Where sites experienced a series of land use periods, the chronology of initial to subsequent land use reads from left to right. Values in site labels indicate the period of secondary succession experienced by sites. Sites that experienced the same period of succession are distinguished from each other by a lowercase letter following values.

7.6 cm in diameter were counted along a 10-m section of each 15-m transect. Biomass of downed woody debris was measured along each 15-m transect using the planar intersect technique (Van Wagner 1968, Brown and Roussopoulous 1974). The quadratic mean diameter of woody debris 2.45–7.6 cm diameter and specific gravity values for each particle class (i.e., 2.45–7.6 cm diameter, >7.6 cm diameter sound, and >7.6 cm diameter rotten) were determined by collecting wood debris samples at random within a subset of the 11 forest sites, and mean values of each parameter were used in models to calculate biomass (Table 2). Bias due to slope was corrected for at all sites (Van Wagner 1968, Brown and Roussopoulous 1974). Percent slope was measured along each woody 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.

Trees, lianas, and palms at least 1.3 m in height but <10 cm dbh were measured within 2 × 10 m belt transects located adjacent to each of the 15 woody debris transects. 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 diameter) were destructively sampled in 50 × 50 cm microplots placed at the 5 m point along each woody 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 et al. (*in press*) were used at this site. Briefly,

all trees, lianas, and palms >1.3 m in height were measured in a 60 × 90 m plot established at the site. Woody debris was sampled along 15-m transects placed at 10-m intervals along three parallel transects 90 m in length established within the plot ( $n = 30$ ). The surface layer (i.e., the combined biomass of litter, graminoids, and other vegetation <1.3 m in height) was destructively sampled in 25 × 25 cm microplots located at the 2-m point along each woody debris transect ( $n = 30$ ).

Pools of C, N, S, and P in mineral soils were determined from five samples collected at 10-m intervals along a 40-m transect established in the center of each 60 × 50 m plot. Samples were collected at 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 along the 40-m transect, samples were obtained by compositing four subsamples collected 1 m from the sampling point in each cardinal direction ( $n = 5$  per site). Mineral soils at depths of 10–30 cm, 30–50 cm, and 50–100 cm were collected by randomly selecting one of the four holes from which surface soils had been collected ( $n = 5$  per site) for sampling. Bulk density of mineral 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).

TABLE 2. Quadratic mean diameter and specific gravity of downed woody debris components in secondary forests of the Los Tuxtlas Region, México.

Decomposition class	Size (cm)	Quadratic mean diameter (cm)		Specific gravity (g/cm <sup>3</sup> )	
		Mean ± 1 SE	$n$	Mean ± 1 SE	$n$
Wood	2.45–7.6	3.86 ± 0.08	208	0.35 ± 0.01	125
Sound wood	>7.6	...	...	0.34 ± 0.02	51
Rotten wood	>7.6	...	...	0.21 ± 0.01	47

TABLE 3. Equations to determine components of aboveground biomass of secondary forest sites in the Los Tuxtlas Region, México. All biomass values are expressed as dry mass (Mg).

Parameter	Equation	CF	R <sup>2</sup>
Height of trees >10 cm dbh†	= 4.722 ln(D <sup>2</sup> ) - 13.323	none	0.70
Biomass; trees >10 cm dbh‡	= (exp(-2.409 + 0.9522 ln(D <sup>2</sup> H Sg)))CF/10 <sup>3</sup>	1.03	0.99
Biomass; <i>Cecropia</i> >10 cm dbh (wood)§	= (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> >10 cm dbh (leaf)§	= (-0.56 + 0.02(D <sup>2</sup> ) + 0.04(H))/10 <sup>3</sup>	none	0.98
Biomass; standing dead trees >10 cm dbh†	= π((D/2) <sup>2</sup> )H(0.42)	none	none
Biomass; trees <10 cm dbh†	= (exp(4.9375 + 1.0583 ln(D <sup>2</sup> )))CF/10 <sup>6</sup>	1.14	0.93
Biomass; dead trees <10 cm dbh†	= (exp(4.6014 + 1.1204 ln(D <sup>2</sup> )))CF/10 <sup>6</sup>	1.11	0.95
Biomass; palms†	= (exp(3.6272 + 0.5768 ln(D <sup>2</sup> H)))CF/10 <sup>6</sup>	1.02	0.73
Biomass; dead palms†	= (exp(-0.5285 + 0.9907 ln(D <sup>2</sup> H)))/10 <sup>6</sup>	none	0.98
Biomass; lianas	= (10 <sup>(0.12 + 0.91 log<sub>10</sub>(BA))</sup> )/10 <sup>3</sup>	none	0.82
Biomass; tree leaves¶	= exp(-1.897 + 0.836 ln(D <sup>2</sup> H))/10 <sup>3</sup>	none	0.85
Biomass; sapling wood†	= exp(4.7472 + 1.0915 ln(D <sup>2</sup> ))/10 <sup>6</sup>	1.13	0.93
Biomass; sapling leaves†	= exp(3.0473 + 0.07778 ln(D <sup>2</sup> ))/10 <sup>6</sup>	1.45	0.706
Biomass; liana leaves	= ((0.109 BA) - 0.376)/10 <sup>3</sup>	none	none
Biomass; wood debris 2.45–7.6 cm diameter††	= Sg((π <sup>2</sup> NCSd <sup>2</sup> )/8L) × 10 <sup>2</sup>	none	none
Biomass; wood debris >7.6 cm diameter††	= Sg((π <sup>2</sup> sum D <sup>2</sup> SCs <sup>2</sup> )/8L) × 10 <sup>2</sup>	none	none

Notes: Definitions for symbols used in the above equations: D = diameter breast height (cm); Cs = slope correction factor, square root of [1 + (% slope/100)<sup>2</sup>]; Sg = specific gravity of wood (g/cm<sup>3</sup>); N = number of pieces of wood debris intersected per transect; BA = basal area (cm<sup>2</sup>); H = height (m); S = secant of wood debris tilt; d = quadratic mean diameter of wood debris (cm); L = transect length (cm); CF = correction factor = exp(MSE/2); sum D<sup>2</sup> = sum of (wood debris diameters)<sup>2</sup> (cm<sup>2</sup>); Symbols following each parameter term indicate source: † = this study; ‡ = Brown and Lugo (1989); § = Uhl et al. (1988); || = Putz (1983); ¶ = Crow (1978); †† = Van Wagner (1964).

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 to predict biomass (Table 3). Tree height was determined via a regression model developed from a sample of 553 trees of varying species sampled for this study and from data collected by Bongers et al. (1988). Species-specific wood density values were obtained for each tree species from Barajas-Morales (1987), Brown (1997), and T. Carmona-Valdovinos (unpublished data). 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 g/cm<sup>3</sup> for tree species of the Los Tuxtlas Region determined by Barajas-Morales (1987). Correction factors (CF) were used in several of the predictive models to account for bias introduced during conversion from logarithmic to arithmetic units (Baskerville 1972, Newman 1993). In certain cases correction factors were not employed because they were either not available from cited sources, or they failed to improve the predictability of the respective models, based on the difference between expected and observed values (Table 3).

Biomass of *Cecropia obtusifolia* was calculated from genus-specific models developed by Uhl et al. (1988). 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 0.34 g/cm<sup>3</sup> derived from samples of sound wood debris (Table 2) was used to convert volume of standing dead trees to biomass.

Biomass of trees >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). Biomass of dead trees >1.3 m in height but <10 cm dbh was calculated using a regression model of dbh vs. main stem biomass of those 66 trees.

Biomass of palms was calculated using a regression equation developed from dry masses of 15 *Astrocaryum mexicanum* individuals harvested from the study area. Biomass of dead palms was calculated from a regression based on the stem biomass of each of these 15 individuals. Liana biomass was calculated from a regression model developed by Putz (1983) which used stem basal area to predict biomass (Table 3).

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 each site. Wood samples were collected from trees 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 subsamples taken from eight trees, were collected at each site. Five composited leaf samples, each 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). 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 of all 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).

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 using leaf tissue of trees >10 cm dbh and wood tissue of trees <10 cm dbh, respectively.

Elemental concentrations of woody debris were determined from five composited samples for each woody debris class. Elemental concentrations of surface layer pools (i.e., litter and seedling pools) were determined from 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 mineral 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.

#### Laboratory and statistical analysis

All soil and vegetation samples were oven dried to a constant mass at a temperature of approximately 65°C. Vegetation samples were ground to pass through a 40-mesh screen (0.5 mm) using a cyclotec sample mill (Tecator Inc., Herndon, Virginia). Soil samples were sieved to remove roots >2 mm in diameter and ground to pass through a 60-mesh screen (250- $\mu$ m pore size). Total C, N, and S concentrations in biomass and mineral soils were determined by the induction furnace method using a Carlo-Erba NA Series 1500 NCS analyzer (Fisons Instruments, Danvers, Massachusetts); (Nelson and Sommers 1982). Total P concentrations were determined using a Kjeldahl digestion procedure followed by colorimetric analysis (Olson and Sommers 1982).

Regression analysis was used to evaluate the significance of the relationships between variables such as TAGB; C, N, S, and P pools; forest age; and duration of land use (Sokal and Rohlf 1969). In addition, a general logistic growth equation, the Richards function as described by Cooper (1983), was used to predict mean annual aboveground biomass accumulation (ABA) based on the age and TAGB of the secondary forests sampled in the Los Tuxtlas Region. The form of this model is

$$\text{TAGB}_t = \text{TAGB}_{\text{max}}(1 - \exp(-b1 \times t))^{b2}$$

where TAGB<sub>t</sub> = TAGB at a given time following site abandonment; TAGB<sub>max</sub> = the potential maximum of TAGB; *t* = the period of secondary succession or the age of a given secondary forest; *b*<sub>1</sub> and *b*<sub>2</sub> are parameters controlling the rate of mean annual ABA and the inflection point of the accumulation curve, respectively. In this model, we used 403 Mg/ha as the TAGB<sub>max</sub> value. This value represents the average TAGB of primary forests sampled in the Los Tuxtlas region by Hughes et al. (*in press*). In addition, we assumed that secondary forests were equivalent to primary forests regarding TAGB, when they reached 90%, or 363 Mg/ha, of the TAGB<sub>max</sub> value.

In tables and figures, mean and standard error values are presented for components that were subsampled within each plot (e.g., litter and trees <10 cm in diameter). In cases where values consist of or include whole-plot measures (e.g., trees >10 cm in diameter and TAGB), mean and standard error values were not available and not included. In addition, site S-50 was excluded from our analysis of the effect of prior land use history on mean annual ABA, because of the indeterminate land use history of that site.

## RESULTS

### Dynamics of aboveground biomass during secondary succession

TAGB was significantly correlated with secondary forest age, ranging from 4.8 Mg/ha in the 6-mo-old forest to 287 Mg/ha in the 50-yr-old forest ( $R^2 = 0.53$ ;  $P < 0.01$ ; Table 4). Mean annual ABA was inversely related to the duration of prior land use of each site (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, mean annual ABA decreased significantly ( $R^2 = 0.50$ ;  $P = 0.02$ ; Fig. 1). This relationship cannot be explained by differences in the ages of the secondary forests that were sampled; secondary forest age was not correlated with mean annual ABA ( $R^2 = 0.01$ ;  $P = 0.799$ ). Thus, while the total aboveground biomass of each site was strongly related to forest age, forest age was not a good predictor of a forest's mean annual aboveground biomass accumulation. Mean annual ABA was best predicted by each forest's prior land use history.

Based on results obtained by fitting TAGB of secondary forest sites to the Richards function (Fig. 2), secondary forests were predicted to reach TAGB levels that were at least 90% of primary forests (i.e., 363 Mg/ha) after 73 yr of secondary succession ( $R^2 = 0.65$ ). A rapid accumulation curve was produced by fitting the Richards function to secondary forest sites with between 1 and 7 yr of land use prior to abandonment; this curve predicted that TAGB would attain 90% of primary forest TAGB after 31 yr of secondary succession. In contrast, fitting the Richards function to sites with 13–30 yr of land use prior to abandonment pro-

TABLE 4. Aboveground biomass (Mg/ha) in secondary forest sites of the Los Tuxtlas Region.

Site	Wood debris	Litter	Seedling	Surface layer	Palms	Lianas
S-0.5	0.0	2.7 ± 0.6	2.1 ± 0.3	4.8 ± 0.7	0 ± 0	0 ± 0
S-4	11.8	7.7 ± 1.3	0.8 ± 0.2	8.5 ± 1.3	0 ± 0	5.6 ± 1.9
S-8a	12.6	2.1 ± 0.4	3.1 ± 0.6	5.2 ± 0.7	0 ± 0	0.9 ± 0.2
S-8b	6.7	4.9 ± 0.5	2.0 ± 0.4	6.9 ± 0.7	0.1 ± 0.1	2.0 ± 0.7
S-10	1.9	...	...	19.5 ± 1.2	0.0	0.0
S-16	13.4	7.0 ± 0.9	0.8 ± 0.2	7.9 ± 0.9	0 ± 0	5.8 ± 1.1
S-20a	7.6	5.0 ± 0.8	0.6 ± 0.2	5.6 ± 0.8	0 ± 0	4.9 ± 1.3
S-20b	10.5	6.2 ± 0.9	1.4 ± 0.3	7.6 ± 0.9	0.1 ± 0.1	7.5 ± 1.5
S-26	13.5	5.4 ± 0.5	1.3 ± 0.4	6.7 ± 0.7	1.5 ± 0.5	3.5 ± 0.8
S-30	7.1	5.7 ± 0.8	0.7 ± 0.2	6.4 ± 0.9	0 ± 0	4.5 ± 1.0
S-50	5.5	6.8 ± 0.6	0.8 ± 0.3	7.6 ± 0.6	0.1 ± 0.04	3.4 ± 1.1
Primary forests	14 ± 5	6 ± 0.4	1 ± 0.4	7 ± 1	5 ± 1	3 ± 1

Notes: Mean ± 1 SE is given for components subsampled within each 50 × 60 m plot, but not for components that include whole plot measures. Tree biomass is divided into diameter (dbh) classes (cm). The "surface layer" category is the sum of litter and seedling biomass. Litter and seedling components of S-10 were not separated during sampling; their combined biomass is listed in the "surface layer" category. "TAGB" is the sum of all aboveground biomass components. "Total dead" includes litter and woody debris; "total live" includes all other categories. "Mean ABA" represents mean aboveground biomass accumulation and is defined as the TAGB of each site divided by its age (i.e., years since abandonment). See Table 1 for the age and land use history of each site. Biomass values of primary forests are from Hughes et al. (*in press*).

duced a slow accumulation curve in which TAGB of secondary forests attained the equivalent of 90% of primary forest TAGB after 79 yr of secondary succession (Fig. 2).

Distribution of TAGB among the various biomass components varied with secondary forest age. Relative contributions of the combined pools of surface layer, woody debris, palms, lianas, and trees <10 cm dbh to TAGB, decreased significantly as the age of secondary forests increased ( $R^2 = 0.55$ ,  $P < 0.01$ ). In contrast, both the absolute value and relative contribution of trees >10 cm dbh to TAGB increased significantly with increasing forest age ( $R^2 = 0.60$  and  $0.55$ ,  $P < 0.01$ ).

#### Concentrations of elements in aboveground biomass and mineral soil pools

Concentrations of C, N, S, and P in biomass were not highly variable between sites, and did not show distinctive patterns with respect to age or land use his-

tory of forests. Mean concentrations of C in vegetation components ranged from 41 to 51%, and were highest in wood (Table 5). In contrast, N concentrations were generally low in wood and high in litter, seedlings, grasses, and leaves; N concentrations ranged from 0.3% in wood tissue to 2.6% in leaf tissue of trees <10 cm dbh. Sulfur and P concentrations were distributed similarly to N, with higher concentrations in herbaceous tissue and lower concentrations in wood tissue. Among aboveground components, S ranged from 0.03 to 0.31%, and P ranged from 0.02 to 0.2%.

There were also no discernible patterns in mineral soil C, N, and S concentrations relating to land use or age. Without exception, mineral soil C and N concentrations decreased with increasing depth at each site. Mean carbon concentrations for all sites ranged from 1.3 to 6.2% for 50–100 cm and 0–2.5 cm depths, respectively (Table 5). Mineral soil N concentrations ranged from 0.1% in deep soils to 0.6% in upper soil

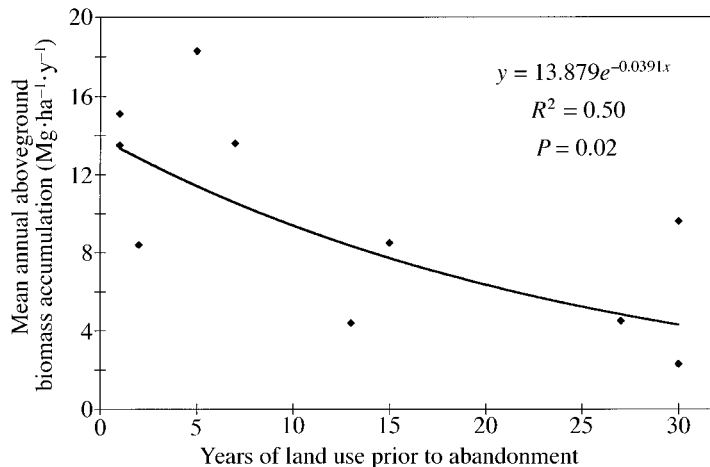


FIG. 1. The negative exponential relationship between mean annual aboveground biomass accumulation and duration of land use in secondary forests of the Los Tuxtlas Region, Mexico.

TABLE 4. Extended.

Trees				Total live	Total dead	TAGB	Mean ABA (Mg·ha <sup>-1</sup> ·yr <sup>-1</sup> )
dbh < 10 cm dbh	10–30 cm dbh	30–70 cm dbh	dbh > 70 cm				
0 ± 0	0.0	0.0	0.0	2.1	2.7	4.8	9.6
28.3 ± 4.7	6.2	0.0	0.0	40.9	19.4	60.4	15.1
7.4 ± 1.3	10.2	0.0	0.0	21.6	14.7	36.3	4.5
17.7 ± 2.5	40.6	27.2	7.8	97.4	11.6	109.0	13.6
0.6	1.3	0.0	0.0	...	...	23.3	2.3
11.5 ± 2.0	35.4	176.8	41.7	272.1	20.4	292.5	18.3
11.7 ± 1.7	33.0	25.6	0.0	75.8	12.6	88.4	4.4
24.9 ± 4.9	163.0	56.2	0.0	253.1	16.7	269.8	13.5
9.1 ± 1.9	74.6	92.3	16.2	198.5	18.8	217.4	8.4
11.7 ± 2.2	86.9	137.2	0.0	241.1	12.8	253.9	8.5
15.1 ± 3.5	45.6	156.0	53.4	274.1	12.3	286.7	5.7
6 ± 3	46 ± 7	144 ± 9	177 ± 39	382 ± 47	20 ± 5	403 ± 50	...

horizons, and were positively correlated with soil C concentrations ( $R^2 = 0.98$ ,  $P < 0.0001$ ). Mineral soil C/N ratios averaged 10.6/1 for all depths at all sites. Soil S concentrations also decreased with increasing depth, although changes in concentration from surface to deep soils were smaller than for C and N; S ranged from 0.03 to 0.07%.

#### *Elemental pools in aboveground biomass and mineral soils*

Like TAGB, total aboveground pools of C, N, S, and P increased with increasing forest age. Aboveground C pools were positively correlated to site age ( $R^2 = 0.53$ ;  $P < 0.01$ ) and increased from 2 Mg/ha in the youngest to 136 Mg/ha in the oldest site (Table 6). In young secondary forests (i.e., <15 yr old), the majority of aboveground C (59%) was concentrated in the combined biomass of the surface layer, woody debris, lianas, and trees <10 cm dbh. In old secondary forests (i.e., >15 yr old), trees >10 cm dbh constituted ~85% of aboveground C. Aboveground pools of N also increased with increasing site age ( $R^2 = 0.54$ ;  $P < 0.01$ ), as did pools of S ( $R^2 = 0.46$ ;  $P = 0.01$ ) and P ( $R^2 = 0.43$ ;  $P = 0.017$ ). In young secondary forests, 75% of N, 61% of S, and 71% of P pools were concentrated

in the surface layer, woody debris, lianas, and trees <10 cm dbh. In contrast, trees >10 cm dbh in old secondary forests constituted ~75% of N, S, and P pools (Table 6).

Accumulation of total aboveground C pools was inversely correlated to the duration of land use prior to abandonment ( $R^2 = 0.45$ ;  $P = 0.02$ ). Accumulations of aboveground N, S, and P pools, however, were not correlated to duration of land use.

Unlike aboveground pools, differences in mineral soil pools of C, N, S, and P were few and were not consistent with regard to age or land use history. Total mineral soil C to a 1-m depth ranged from 139 to 269 Mg/ha, but was not significantly correlated with forest age ( $R^2 = 0.10$ ;  $P = 0.44$ ) or duration of land use prior to abandonment ( $R^2 = 0.16$ ;  $P = 0.32$ ; Table 7). Similarly, mineral soil N to a 1-m depth ranged from ~14 000 to 24 000 kg/ha and was not correlated with age ( $R^2 = 0.03$ ;  $P = 0.69$ ) or duration of land use ( $R^2 = 0.13$ ;  $P = 0.39$ ). Total S in mineral soil to a 1-m depth ranged from 2200 to 4500 kg/ha and also was not correlated with age ( $R^2 = 0.10$ ;  $P = 0.45$ ) or duration of land use ( $R^2 = 0.01$ ;  $P = 0.78$ ). Surface mineral soil pools (0–10 cm depth) of C, N, S, and P also were not correlated to age or duration of prior land use.

FIG. 2. Estimates of mean annual aboveground biomass accumulation during secondary succession in the Los Tuxtlas Region, Mexico. Accumulation rates are predicted using the Richards function. Maximum total aboveground biomass (TAGB) is defined as the average TAGB of primary forests sampled in the region and is 403 Mg/ha (Hughes et al., *in press*).

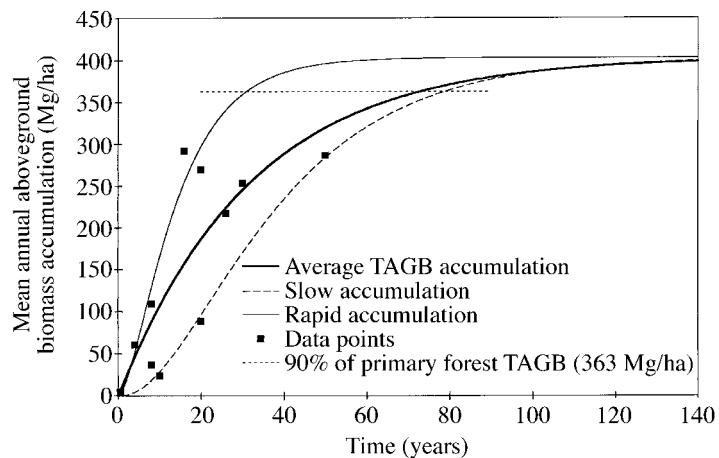




TABLE 5. Concentrations (mean  $\pm$  1 SE of samples for all sites) of N, C, S, and P in components of aboveground vegetation and mineral soils in secondary forests of the Los Tuxtlas Region, México.

Vegetation/soil component	%C	%N	%S	%P
Litter	45 $\pm$ 0.6	1.5 $\pm$ 0.06	0.18 $\pm$ 0.02	0.09 $\pm$ 0.01
Seedlings	43 $\pm$ 0.4	1.5 $\pm$ 0.09	0.20 $\pm$ 0.01	0.14 $\pm$ 0.01
Grass	41 $\pm$ 1.8	1.0 $\pm$ 0.11	0.26 $\pm$ 0.06	n.a.
Palm	47 $\pm$ 0.3	0.7 $\pm$ 0.13	0.11 $\pm$ 0.02	0.10 $\pm$ 0.02
Leaves of trees <10 cm dbh	45 $\pm$ 0.5	2.6 $\pm$ 0.11	0.31 $\pm$ 0.01	0.19 $\pm$ 0.01
Leaves of trees >10 cm dbh	47 $\pm$ 0.4	2.5 $\pm$ 0.14	0.27 $\pm$ 0.03	0.20 $\pm$ 0.03
Wood of trees >10 cm dbh	48 $\pm$ 0.2	0.3 $\pm$ 0.02	0.04 $\pm$ 0.01	0.04 $\pm$ 0.01
Wood of trees <10 cm dbh	47 $\pm$ 0.2	0.5 $\pm$ 0.05	0.06 $\pm$ 0.01	0.10 $\pm$ 0.01
Woody debris				
2.45–7.6 cm diameter	49 $\pm$ 0.1	0.4 $\pm$ 0.02	0.04 $\pm$ 0.004	0.04 $\pm$ 0.008
Sound, >7.6 cm diameter	50 $\pm$ 0.4	0.4 $\pm$ 0.03	0.03 $\pm$ 0.006	0.02 $\pm$ 0.003
Rotten, >7.6 cm diameter	51 $\pm$ 0.4	0.7 $\pm$ 0.05	0.06 $\pm$ 0.006	0.03 $\pm$ 0.002
Soil depth				
0–2.5 cm	6.2 $\pm$ 0.08	0.6 $\pm$ 0.006	0.07 $\pm$ 0.0005	0.14 $\pm$ 0.002
2.5–10 cm	4.6 $\pm$ 0.05	0.4 $\pm$ 0.004	0.05 $\pm$ 0.0005	0.14 $\pm$ 0.004
10–30 cm	3.0 $\pm$ 0.03	0.3 $\pm$ 0.003	0.04 $\pm$ 0.0004	n.a.
30–50 cm	1.9 $\pm$ 0.06	0.2 $\pm$ 0.005	0.03 $\pm$ 0.0030	n.a.
50–100 cm	1.3 $\pm$ 0.04	0.1 $\pm$ 0.003	0.03 $\pm$ 0.0004	n.a.

Note: The term "n.a." indicates that samples were not analyzed for %P in this study.

#### Combined aboveground and mineral soil pools of C, N, and S

The combined pools of aboveground and mineral soil C ranged from 156 to 331 Mg/ha, with mineral soil pools accounting for between 58 and 91% of total pools. In addition, as forest age increased, the ratio of aboveground C to mineral soil C increased as well ( $R^2 = 0.47$ ;  $P < 0.05$ ). Combined aboveground and mineral soil N ranged from ~14 000 to 24 000 kg/ha, with 94–99% of the total N accounted for by mineral soil pools. Ratios of aboveground to mineral soil N pools also increased with forest age ( $R^2 = 0.38$ ;  $P = 0.061$ ), but were not as strongly correlated to increasing forest age as analogous ratios of aboveground and soil C. Like combined pools of N, between 95 and 99% of combined S pools were located in mineral soils. Ratios of aboveground to mineral soil pools of S were not significantly correlated with site age.

#### DISCUSSION

##### Biomass accumulation in secondary forests

Aboveground biomass in secondary forests <15 yr old in Los Tuxtlas ranged from ~5 to 100 Mg/ha. This was generally within the spectrum of aboveground biomass pools of secondary forests of similar age measured elsewhere in the tropics. Aboveground biomass in 10-mo-old and 7-yr-old secondary forests in the Uxpanapa Region of Veracruz, México 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 9–12 yr old secondary forests in northern Amazonia, and Ewel (1971) reported that TAGB ranged from 13 to 43 Mg/ha in 2–6 yr old secondary forests in Costa Rica. At a 4-yr old tropical plantation site in Puerto Rico, by comparison, aboveground biomass was 40 Mg/ha (Lugo 1992).

In contrast, pools of TAGB in secondary forests >15 yr in age were large relative to those of secondary forests of comparable age located elsewhere in the tropics. TAGB pools were between 88 and 293 Mg/ha in secondary forests that ranged from 16 to 20 yr in age in the Los Tuxtlas Region. By comparison, TAGB in a series of 20-yr-old secondary forests in northwestern Amazonia ranged from 63 to 98 Mg/ha (Saldarriaga et al. 1988). Secondary forests in the Los Tuxtlas Region ranging from 25 to 50 yr in age had TAGB pools that were between 217 and 302 Mg/ha, while TAGB in 30 to 80 yr old secondary forests presented by Saldarriaga et al. (1988) ranged from only 63 to 200 Mg/ha. In 16–50 yr old secondary forests located throughout the tropics, total live aboveground biomass ranged from 63 to 205 Mg/ha (Brown and Lugo 1990a). Furthermore, at 17-, 18.5-, and 49-yr-old plantations located in Puerto Rico, Lugo (1992) reported total aboveground biomass values of 102, 171, and 125 Mg/ha, respectively. These comparisons indicate that, in contrast to secondary forests located elsewhere in the tropics that tend to show declining rates of biomass accumulation through successional time, secondary forests of the Los Tuxtlas Region appear capable of maintaining relatively high rates of aboveground biomass accumulation even into the latter stages of succession (i.e., >30 yr).

Our estimate that secondary forests of the Los Tuxtlas region will require 73 yr to reach the equivalent of primary forest biomass 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 pools in secondary forests would reach those of primary forests after 40 yr of secondary succession. However, our estimate for the Los Tuxtlas Region is considerably shorter than accumulation periods for secondary forests in the Ama-

zon Basin. Using linear models, Fearnside and Guimarães (1996) estimated that it would take 100 yr for secondary forests to reach levels of TAGB in primary forests of the Brazilian Amazon, and Saldarriaga et al. (1988) reported a 144–189 yr interval. Furthermore, use of a nonlinear model (i.e., the Richards function) to estimate TAGB accumulation in secondary forest sites of Amazonia (Saldarriaga et al. 1988) resulted in an estimate of 250 yr to reach TAGB levels that are within 90% of the mean value for mature forests ( $R^2 = 0.76$ ).

Mean annual ABA was inversely correlated with duration of land use prior to abandonment in the Los Tuxtlas Region (Fig. 1). Comparison of rapid vs. slow accumulation rates (Fig. 2) provides further evidence of the influence of prior land use on mean annual ABA. The rapid accumulation curve was developed from sites that had experienced short periods of land use prior to abandonment, while the slow accumulation curve was developed from sites that had experienced relatively long periods of land use. These curves indicate that prolonged periods of land use may more than double the length of time required for secondary forests to accumulate biomass approximating those of primary forests in the region.

The effects of increasing periods of land use prior to abandonment on mean annual ABA likely contribute to the variation in the relationship between site age and TAGB, and, by extension, to the variation in our prediction of the interval necessary to attain the equivalent of primary forest biomass. For example, we sampled two secondary forests that had each experienced 8 yr of secondary succession since abandonment. However, land use prior to abandonment had been 20 yr longer at one of the sites, and its TAGB was approximately one-third of the other (Tables 1 and 4, Fig. 1). Similarly, of the two 20-yr-old forests sampled in this study, the site with a prior land use period of 13 yr had a TAGB pool that was one-third that of the site that had experienced only 1 yr of land use. Furthermore, the site with the lowest mean annual ABA had been a pasture for 15 yr prior to its abandonment. At this site, firmly established mat-forming exotic grasses (i.e., *Cynodon plectostachyis* and *Panicum maximum*) had apparently limited colonization and growth of early pioneer tree species (e.g., *Piper* spp., *Cecropia obtusifolia*, *Trema micranthra*) even after 10 yr of secondary succession.

Previous studies in other tropical regions have also demonstrated the impacts of both the type and duration of prior land use on mean annual ABA 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 (Aide et al. 1995). Uhl et al. (1988) reported similar results for secondary forests of eastern Amazonia where mean annual ABAs varied from 1 to 10  $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$  and were highly dependent on the prior land use of each site. Fearnside and Guimarães (1996)

estimated that secondary forests originating from degraded cattle pastures accumulated biomass and carbon at much lower rates than those originating 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.

Although secondary forests approach the biomass of primary forests in the Los Tuxtlas Region relatively rapidly, they remain distinctly different with regard to the structure and distribution of total aboveground biomass. Trees >70 cm dbh accounted for 44% of TAGB in primary forests (Hughes et al., *in press*), but accounted for only 8% of TAGB in secondary forests that were >15 yr in age and supported >200  $\text{Mg}/\text{ha}$  of TAGB. Thus, while older secondary forests sampled in this study were relatively similar to primary forests with regard to TAGB, they will likely require a longer successional period to attain parity with primary forests regarding the structure and distribution of total aboveground biomass.

An additional ecosystem level pool not reported in this study is root biomass. R. Ahedo (*unpublished data*) found that belowground biomass of both large structural roots and fine roots constituted between only 6 and 8% of the combined above- and belowground biomass pools for three secondary forest sites measured during this study. The oldest of these sites (S-30) had the largest root biomass pool (22.5  $\text{Mg}/\text{ha}$ ) and was very similar to the root biomass of primary forest sites. In addition, the site with the longest period of land use prior to abandonment (S-20a) had the smallest root biomass (5.5  $\text{Mg}/\text{ha}$ ). While these findings suggest that belowground biomass of secondary forests varies in response to the duration of both prior land use and secondary succession in a manner similar to aboveground pools, the differences in absolute values of root biomass among these three secondary forest sites were very small compared to the differences in aboveground biomass among those sites. At the three sites where it was measured, C mass of roots accounted for between 1 and 3% of the total combined C mass of biomass and mineral soil pools. Consequently, belowground biomass does not appear to play a substantial role in the storage of biomass and C in secondary forests of the Los Tuxtlas Region.

#### *Dynamics of elemental pools in aboveground biomass and mineral soils of secondary forests*

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 70% of those in primary forests of Los Tuxtlas. In contrast, aboveground P pools ranged from 5 to 140% of primary forest pools (Hughes et al., *in press*), and average P mass in secondary forests >15 yr old (110  $\text{kg}/\text{ha}$ ) was equivalent to that in primary forests (105  $\text{kg}/\text{ha}$ ). The rapid rate of P accumulation in sec-

TABLE 6. Aboveground pools of nutrients in secondary and primary forests of the Los Tuxtlas Region.

Site	Woody debris	Litter	Seedling	Surface layer	Palms	Lianas
Carbon (Mg/ha)						
S-0.5	0.0	1.2	0.9	2.1	0.0	0.0
S-4	6.0	3.5	0.4	3.9	0.0	2.6
S-8a	6.4	0.9	1.3	2.3	0.0	0.4
S-8b	3.3	2.1	0.8	2.9	0.0	0.9
S-10	0.9	...	...	9.0	0.0	0.0
S-16	6.7	3.2	0.3	3.5	0.0	2.7
S-20a	3.8	2.3	0.3	2.6	0.0	2.3
S-20b	5.2	2.8	0.6	3.3	0.0	3.5
S-26	6.7	2.3	0.6	2.8	0.7	1.7
S-30	3.5	2.7	0.3	3.1	0.0	2.1
S-50	2.7	3.1	0.3	3.5	0.0	1.6
Primary forest	7.1 ± 2.5	2.8 ± 0.2	0.5 ± 0.2	3.3 ± 0.4	2.5 ± 0.5	1.5 ± 0.6
Nitrogen (kg/ha)						
S-0.5	0	41	31	72	0	0
S-4	55	133	11	144	0	28
S-8a	42	33	47	80	0	5
S-8b	24	59	23	82	0	10
S-10	9	...	...	222	0	0
S-16	57	95	16	110	0	42
S-20a	38	71	10	81	0	29
S-20b	44	88	18	105	1	43
S-26	63	93	25	119	10	33
S-30	33	80	9	88	0	28
S-50	24	119	15	134	0	20
Primary forest	60 ± 20	105 ± 5	21 ± 8	126 ± 10	36 ± 8	28 ± 11
Sulfur (kg/ha)						
S-0.5	0.0	5.0	4.3	9.3	0.0	0.0
S-4	4.6	12.2	1.7	13.8	0.0	3.2
S-8a	4.0	6.0	7.6	13.7	0.0	0.7
S-8b	2.0	6.5	3.2	9.7	0.1	1.3
S-10	0.7	...	...	31.3	0.0	0.0
S-16	4.2	13.7	1.7	15.5	0.0	5.6
S-20a	3.4	6.5	1.6	8.1	0.0	2.0
S-20b	3.2	10.0	2.8	12.7	0.1	5.1
S-26	5.2	7.7	2.9	10.6	1.6	3.0
S-30	2.6	11.6	1.4	13.0	0.0	3.7
S-50	1.8	16.4	1.7	18.1	0.1	2.3
Primary forest	3.7 ± 1.2	9.7 ± 0.8	3.1 ± 1.3	13 ± 1.6	5.7 ± 1.3	5.1 ± 2
Phosphorus (kg/ha)						
S-0.5	0.0	2.2	2.7	4.9	0.0	0.0
S-4	3.7	6.3	1.4	7.7	0.0	5.6
S-8a	3.6	3.0	6.1	9.1	0.0	1.0
S-8b	3.0	4.0	3.2	7.1	0.1	2.1
S-10	0.6	...	...	21.7	0.0	0.0
S-16	2.7	4.5	1.1	5.7	0.0	4.1
S-20a	1.6	4.7	1.2	5.9	0.0	7.2
S-20b	2.1	8.6	1.8	10.4	0.1	7.7
S-26	2.8	3.9	1.6	5.5	1.5	2.1
S-30	1.5	4.3	0.8	5.1	0.0	4.6
S-50	1.1	4.5	0.9	5.4	0.1	3.3
Primary forest	4.9 ± 1.8	4.3 ± 0.5	1.3 ± 0.5	5.6 ± 0.8	5.4 ± 1.2	2.4 ± 0.9

Notes: Tree size classes refer to diameter measured at a 1.3 m height (dbh). "Surface layer" represents the sum of litter and seedling pools. At the S-10 site, litter and seedling components were not separated during sampling; their combined biomass is listed in the "surface layer" category. "Total" indicates the sum of all aboveground components. "Total dead" is the sum of litter and woody debris; "total live" is the sum of all other categories. Primary forest values (mean ± 1 SE) are indicated by "primary forest" and are from Hughes et al. (*in press*).

secondary forests was the result of their higher P concentrations in litter, seedling, tree leaf, and tree wood biomass, compared to those in primary forest vegetation (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, pools of C, N, and S in mineral soils of secondary forests were not significantly different from those of primary forests, pastures, and cornfields of the Los Tuxtlas Region ( $P$  values  $>0.65$ ; Hughes et al., *in press*) and were not correlated to secondary-forest age or duration of land use prior to abandonment. These

TABLE 6. Extended.

Trees				Total live	Total dead	Total
dbh < 10 cm	dbh 10–30 cm	dbh 30–70 cm	dbh > 70 cm			
0.0	0.0	0.0	0.0	0.9	1.2	2.1
12.4	2.9	0.0	0.0	18.3	9.5	27.8
3.2	4.9	0.0	0.0	9.9	7.3	17.2
7.7	19.3	12.9	3.7	45.4	5.4	50.8
0.3	0.6	0.0	0.0	...	...	10.8
5.1	16.6	83.1	19.6	127.5	9.8	137.3
5.0	15.7	12.1	0.0	35.3	6.1	41.4
10.9	78.5	27.1	0.0	120.6	8.0	128.6
4.0	35.8	44.2	7.8	94.7	9.0	103.7
5.1	42.0	66.4	0.0	116.0	6.3	122.3
6.5	21.8	74.5	25.5	130.2	5.9	136.1
2.7 ± 1	22 ± 3	70 ± 5	86 ± 19	185 ± 23	9.9 ± 2.7	195 ± 24
0	0	0	0	31.5	41.0	72.5
125	27	0	0	191.4	187.5	378.9
32	37	0	0	120.1	75.0	195.0
87	153	90	28	391.1	83.0	474.1
4	6	0	0	...	...	240.5
78	131	611	146	1024.5	152.3	1176.8
76	136	102	0	352.3	109.5	461.9
127	574	187	0	949.3	132.0	1081.3
71	346	401	71	956.6	156.2	1112.8
64	309	454	0	863.7	112.5	976.1
83	168	558	180	1024.0	143.2	1167.2
56 ± 24	192 ± 28	554 ± 37	653 ± 140	1540 ± 162	165 ± 18	1705 ± 165
0.0	0.0	0.0	0.0	4.3	5.0	9.3
14.7	3.3	0.0	0.0	22.8	16.8	39.6
5.6	4.5	0.0	0.0	18.5	10.0	28.5
10.6	38.1	24.3	7.2	84.6	8.5	93.1
0.5	0.7	0.0	0.0	...	...	33.2
10.4	16.0	76.1	18.1	127.8	17.9	145.8
5.4	13.8	10.4	0.0	33.1	10.0	43.1
13.8	62.9	19.4	0.0	104.0	13.1	117.1
7.3	21.2	24.9	4.4	65.3	12.8	78.2
8.8	38.7	57.1	0.0	109.7	14.2	123.9
9.8	21.1	70.5	23.0	128.5	18.2	146.7
10 ± 4	26 ± 4	75 ± 5	89 ± 19	214 ± 22	13 ± 1.9	227 ± 23
0.0	0.0	0.0	0.0	2.7	2.2	4.9
25.7	3.3	0.0	0.0	36.0	10.0	46.0
7.6	5.4	0.0	0.0	20.1	6.6	26.7
17.2	22.8	14.1	4.3	63.7	6.9	70.6
0.6	0.7	0.0	0.0	...	...	23.6
7.7	14.4	69.6	16.5	113.5	7.2	120.7
15.8	33.1	25.4	0.0	82.6	6.3	89.0
23.7	85.0	28.6	0.0	146.8	10.7	157.6
4.9	15.4	18.0	3.2	46.6	6.8	53.4
11.1	27.8	41.5	0.0	85.9	5.8	91.7
13.7	22.5	75.7	25.2	141.4	5.7	147.0
4.5 ± 2.0	11 ± 1.6	33 ± 2.1	39 ± 8.3	96 ± 8.7	9.1 ± 1.6	105 ± 9.2

results differ from other studies that document 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 in other tropical regions (Brown and Lugo 1990*b*). Zarin and Johnson (1995) also documented significant accumulations of total C and N pools in soils during succession following landslides in tropical forest systems of Puerto Rico. The lack of discernible change in mineral soil pools of sites in the Los Tuxtlas Region is likely related to the capacity of the young volcanic

soils (i.e., Andosols) of this region to sequester large quantities of soil organic matter (Sollins et al. 1988). Mineral soil C content to 1 m averaged 200 Mg/ha in secondary forests of Los Tuxtlas compared to a range of 77–147 Mg/ha in forest soils located elsewhere in the tropics (Brown et al. 1993). In addition, average C and N concentrations in the top 30 cm of mineral soils in the Los Tuxtlas Region ranged from 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

TABLE 7. Mass of nutrients in mineral soils of secondary forests in the Los Tuxtlas Region.

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
<b>Carbon (Mg/ha)</b>							
S-4	13 ± 0.9	34 ± 2.3	47	69 ± 8.4	45 ± 14	109 ± 24	269
S-8a	10 ± 0.4	25 ± 1.2	35	36 ± 4.8	21 ± 2.6	48 ± 7.3	139
S-8b	14 ± 1.2	35 ± 2.9	49	71 ± 6.5	47 ± 5.1	75 ± 9.8	243
S-16	12 ± 1.1	23 ± 1.8	36	56 ± 6.9	42 ± 5.3	78 ± 5.3	211
S-20a	12 ± 0.9	28 ± 1.5	41	62 ± 5.9	48 ± 7.4	97 ± 16	249
S-20b	12 ± 0.9	22 ± 1.7	34	53 ± 6.0	40 ± 3.1	58 ± 4.6	185
S-26	9.2 ± 0.6	19 ± 1.7	28	54 ± 8.9	38 ± 2.5	38 ± 10	158
S-30	16 ± 1.8	30 ± 3.6	46	71 ± 3.2	36 ± 3.5	52 ± 6.4	205
Mean ± 1 SE	12 ± 0.7	27 ± 2.1	39 ± 2.7	59 ± 4.2	40 ± 3.1	69 ± 8.8	207 ± 16
<b>Nitrogen (Mg/ha)</b>							
S-4	1.1 ± 0.01	3.1 ± 0.2	4.2	6.4 ± 0.6	3.9 ± 1.2	9.5 ± 2.0	23.9
S-8a	1.0 ± 0.04	2.5 ± 0.1	3.5	3.5 ± 0.5	2.0 ± 0.2	4.9 ± 0.5	14.0
S-8b	1.2 ± 0.09	3.1 ± 0.2	4.4	6.9 ± 0.7	4.2 ± 0.5	6.7 ± 0.8	22.1
S-16	1.0 ± 0.1	2.2 ± 0.2	3.2	5.2 ± 0.6	3.8 ± 0.5	6.8 ± 0.5	19.1
S-20a	1.0 ± 0.07	2.6 ± 0.1	3.7	6.0 ± 0.6	4.6 ± 0.7	8.8 ± 1.4	23.1
S-20b	1.1 ± 0.08	2.4 ± 0.2	3.5	5.7 ± 0.6	3.7 ± 0.3	5.1 ± 0.5	17.9
S-26	0.9 ± 0.06	2.0 ± 0.2	2.9	5.7 ± 1.0	3.9 ± 0.3	4.1 ± 1.1	16.6
S-30	1.4 ± 0.1	2.9 ± 0.3	4.2	7.0 ± 0.2	3.7 ± 0.3	5.5 ± 0.5	20.5
Mean ± 1 SE	1.1 ± 0.05	2.6 ± 0.15	3.7 ± 0.2	5.8 ± 0.4	3.7 ± 0.3	6.4 ± 0.7	19.6 ± 1.2
<b>Sulfur (kg/ha)</b>							
S-4	114 ± 8.9	333 ± 33	447	736 ± 56	1027 ± 551	1241 ± 240	3451
S-8a	118 ± 4.4	310 ± 12	427	512 ± 35	421 ± 68	879 ± 62	2239
S-8b	154 ± 10	422 ± 21	576	1094 ± 69	798 ± 52	1551 ± 95	4019
S-16	121 ± 11	293 ± 22	414	717 ± 61	574 ± 66	1279 ± 81	2983
S-20a	133 ± 7.2	335 ± 15	469	903 ± 72	788 ± 105	1693 ± 198	3853
S-20b	129 ± 9.3	277 ± 21	406	714 ± 65	631 ± 59	1150 ± 91	2902
S-26	104 ± 8.6	246 ± 25	349	869 ± 109	739 ± 38	999 ± 207	2956
S-30	158 ± 8.2	381 ± 16	539	1080 ± 33	808 ± 46	2074 ± 132	4502
Mean ± 1 SE	129 ± 7	325 ± 20	453 ± 26	828 ± 70	723 ± 64	1358 ± 139	3363 ± 359
<b>Phosphorus (kg/ha)</b>							
S-16	253 ± 22	749 ± 71	1002	...	...	...	...
S-20a	300 ± 17	901 ± 42	1201	...	...	...	...
Mean ± 1 SE	277 ± 23.5	825 ± 76	1102 ± 100				

0.23%, respectively (Brown and Lugo 1990b). 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 Sánchez (1989). In addition, while our measures of mineral soil P were restricted to a 0–10 cm depth at just two sites and should be interpreted with caution, mineral 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). In general, the properties that allow the storage of large quantities of organic matter in mineral soils of the Los Tuxtlas Region are likely the same properties that make total elemental pools of those mineral soils resistant to change in response to deforestation, land use, and secondary succession. These properties include weakly acidic to neutral pH values, relatively high clay and allophane content, and relatively high cation exchange capacity (FAO/UNESCO 1975, Chizon 1984, Bongers et al. 1988, Sollins et al. 1988).

Consequently, differences in mean annual ABA in response to duration of succession or prior land use history of secondary forest sites cannot be attributed to the size of total C, N, and S pools in mineral soils. Previous studies have shown that the majority of nu-

trient pools in young volcanic soils are tightly bound within the soil matrix and not readily available for plant uptake (Vitousek and Sanford 1986, Sollins et al. 1988, Crews et al. 1995). Thus, the status of available nutrients (e.g.,  $\text{PO}_4^{3-}\text{-P}$ ,  $\text{NH}_4^+\text{-N}$ , and  $\text{NO}_3^-\text{-N}$ ) in soil pools, the soil seed bank and seed rain, plant competition during the early stages of secondary succession, or a combination of these factors, are more likely to be the parameters through which prior land use history affects rates of aboveground biomass accumulation in secondary forests of the Los Tuxtlas Region. However, in tropical regions where total C and nutrient pools in mineral soils have been shown to be significantly reduced by land use (e.g., Sánchez et al. 1983, Detwiler 1986, Brown and Lugo 1990b), 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 pools of C, N, and S were largely determined by their distribution between aboveground biomass and mineral soil pools. Mineral soil pools constituted 91% of combined aboveground/mineral soil C pools in the youngest secondary forest and 58% of combined C pools in the oldest secondary forests; changes were due to the substantial accumulation of C in aboveground pools with increasing secondary forest

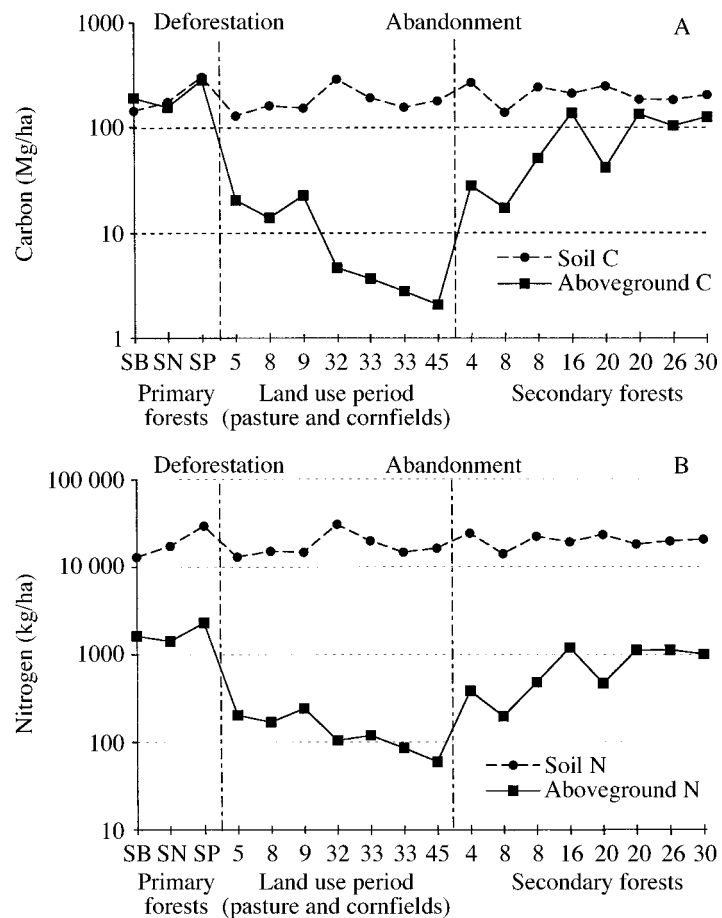


FIG. 3. Dynamics of carbon (A) and nitrogen (B) in aboveground biomass and mineral soil pools along a land use gradient in the Los Tuxtlas Region, Mexico. Values are presented using log scales. In the case of pastures and cornfields, values along the x-axis represent the number of years of land use following 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 et al. (*in press*). Site labels for each of the three primary forest sites (i.e., SB, SN, and SP) follow labels presented in Hughes et al. (*in press*).

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 mineral soil and aboveground pools (Hughes et al., *in press*). In contrast to C pools, the vast majority of pools of N and S were located in mineral soils of secondary forests. Mineral soils accounted for 99% of combined aboveground/mineral soil N and S pools in young secondary forests, and 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 combined aboveground/soil pools of N and S of secondary forests.

Overall, these results, combined with the results of Hughes et al. (*in press*), illustrate the differing responses of mineral soil and aboveground pools of C and N in response to land use change (Fig. 3). While aboveground pools of C and N are subject to extreme variations (i.e., rapid losses due to deforestation, and rapid gains during secondary succession), soil pools remained relatively stable along the land use gradient. Loss of aboveground C mass following deforestation

and land use resulted in a 50% reduction in total combined aboveground/mineral soil pools. Accumulation of C during forest regeneration restored total combined C pools to levels approaching those of primary forest pools (Fig. 3). In contrast, since the majority of N was concentrated in relatively stable mineral soil pools, combined aboveground/mineral soil pools of N never dropped below ~90% of those in primary forests.

In conclusion, our results demonstrate that secondary forests of the Los Tuxtlas Region are capable of high mean annual aboveground biomass accumulation rates and concurrent rapid accumulations of aboveground pools of C, N, S, and P. However, previous studies have noted that current land use patterns in the region are creating a landscape dominated by semipermanent and permanent pastures in which the spatial and temporal extent of secondary forests is extremely limited (Guevara et al. 1997). If current land use trends continue, and secondary forests remain a minor component in the landscape of the Los Tuxtlas Region, 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) have asserted, and as results of this study demonstrate, secondary forests

represent potentially rapid accumulators of, and large sinks for, atmospheric C, but only if they are allowed to establish, persist, and attain maturity in tropical regions such as Los Tuxtlas.

Our results further indicate that even when secondary forests are allowed to reestablish, their ability to accumulate biomass will be constrained by prior land use. As periods of land use increase, we expect that secondary forests will have diminished rates of biomass accumulation. Secondary forests that had experienced prolonged periods of land use in the Los Tuxtlas Region required 79 yr to reach primary forest TAGB levels. This rate of accumulation is, on average, approximately 2.5 times slower than accumulation rates of secondary forests regenerating on sites that have experienced relatively brief periods of land use prior to abandonment. Such prior land use constraints may have a significant impact on C sequestration at the global scale as well. As part of the Intergovernmental Panel on Climate Change, Brown et al. (1996) presented global estimates of the potential amount of C that could be sequestered by regeneration of tropical forests during the 55-yr period between 1995 and 2050. These estimates ranged from 11.5 to 28.7 Pg for the entire period, and the latter, higher global estimate is 2.5 times greater than the lower estimate. This difference in global-scale sequestration rates of tropical secondary forests is virtually identical to the difference between sequestration rates of regenerating forests following long and short periods of land use in the Los Tuxtlas Region. Consequently, just as our results concerning secondary forest regeneration in this region of México demonstrate, the constraints posed by duration of prior land use may explain and account for much of the variability in potential rates of global-scale C sequestration by regenerating tropical secondary forests.

#### ACKNOWLEDGMENTS

We thank Annalee Hughes and numerous members of the Sinaca family of Ejido Laguna Escondida, Veracruz, México for their assistance during all stages of the fieldwork. Tomas Carmona-Valdovinos, Franz Bongers, and Raul Ahedo provided previously unpublished data for the benefit of this project, and Lisa Ellingson and Dian Cummings conducted much of the laboratory analysis. We also thank Chris Heider for his help in developing palm biomass models, and Jack Hartman, Danna Lytjen, and Nick Otting for additional assistance with efforts in the field. Sandra Brown, Mark Harmon, Marc Abrams, and two anonymous reviewers provided thoughtful and helpful reviews of previous drafts of this manuscript. We also thank Rodolfo Dirzo for his invaluable assistance in facilitating the initial stages of fieldwork. This research was supported by the United States Environmental Protection Agency and the National Aeronautics and Space Administration's Global Change Fellowship Program.

#### LITERATURE CITED

- Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management* **77**:77–86.
- Barajas-Morales, J. 1987. Wood specific gravity in species from two tropical forests in México. *International Association of Wood Anatomists Bulletin* **8**:143–148.
- Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forestry* **2**:49–53.
- Bongers, F., J. Popma, J. Meave del Castillo, and J. Carabias. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, México. *Vegetatio* **74**:55–80.
- Brown, J. K., and P. J. Roussopoulos. 1974. Eliminating biases in the planar intersect method for estimating volumes of small fuels. *Forest Science* **20**:350–356.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: a primer. FAO Forestry Paper. Food and Agriculture Organization, Rome, Italy.
- Brown, S., A. J. R. Gillespie, and A. E. Lugo. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* **35**:881–902.
- Brown, S., L. R. Iverson, A. Prasad, and D. Liu. 1993. Geographical distributions of carbon in biomass and soils of tropical Asian forests. *Geocarto International* **4**:45–59.
- Brown, S., and A. E. Lugo. 1990a. Tropical secondary forests. *Journal of Tropical Ecology* **6**:1–32.
- Brown, S., and A. E. Lugo. 1990b. Effects of forest clearing and succession on the carbon and nitrogen content of soil in Puerto Rico and US Virgin Islands. *Plant and Soil* **124**:53–64.
- Brown, S., J. Sathaye, M. Cannell, and P. Kauppi. 1996. Management of forests for mitigation of greenhouse gas emissions. Pages 773–797 in R. T. Watson, M. C. Zinyowera, R. H. Moss, and D. J. Dokken, editors. *Climate change 1995*. Cambridge University Press, Cambridge, UK.
- Chizon, S. E. 1984. Relación suelo-vegetación en la Estación de Biología Los Tuxtlas, Ver. (Un análisis de la distribución de los diferentes tipos de suelo en relación con la cubierta vegetal que soporta). Thesis. ENEP-Zaragoza, Universidad Nacional Autónoma de México, México.
- Cooper, C. F. 1983. Carbon storage in managed forests. *Canadian Journal of Forest Research* **13**:155–166.
- Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Mueller-Dombois, and P. M. Vitousek. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* **76**:1407–1424.
- Crow, T. R. 1978. Common regressions to estimate tree biomass in tropical stands. *Forest Science* **24**:110–114.
- Detwiler, R. P. 1986. Land use change and the global carbon cycle: the role of tropical soils. *Biogeochemistry* **2**:67–93.
- Dirzo, R., and M. C. García. 1992. Rates of deforestation in Los Tuxtlas, a neotropical area in southeast México. *Conservation Biology* **6**:84–90.
- Ewel, J. 1980. Tropical succession: manifold routes to maturity. *Biotropica* **12**:1–95.
- Ewel, J. J. 1971. Biomass changes in early tropical succession. *Turrialba* **21**:110–112.
- Fearnside, P. M., and W. M. Guimarães. 1996. Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management* **80**:35–46.
- Food and Agriculture Organization/UNESCO. 1975. Soil maps of the world Vol. III México and Central America Food and Agriculture Organization/UNESCO, Paris, France.
- García, E. 1970. Los Climas del estado de Veracruz (según el sistema de clasificación climático de Köppen, modificado por la autora). *Anales del Instituto de Biología Universidad Nacional Autónoma de México Serie Botanica* **41**:3–42.
- Guevara, S., J. Laborde, D. Liesenfeld, and O. Barrera. 1997. Potrerros y ganadería. Pages 43–58 in E. Gonzalez-Soriano, R. Dirzo, and R. C. Vogt, editors. *Historia natural de Los Tuxtlas*. Universidad Nacional Autónoma de México, México.

- Hughes, R. F., J. B. Kauffman, and V. J. Jaramillo. *In press*. Deforestation and land use in tropical evergreen forests of the Los Tuxtlas Region, México: consequences for biomass, carbon, and nutrient pools. *Ecological Applications*.
- Ibarra-Manríquez, G., M. Martínez-Ramos, R. Dirzo, y J. Nunez-Farfán. 1997. La vegetación. Pages 61–181 in E. González-Soriano, R. Dirzo, and R. C. Vogt, editors. *Historia natural de Los Tuxtlas*, Universidad Nacional Autónoma de México, México.
- Ibarra-Manríquez, G., and S. Sinaca-Colín. 1987. Listados florísticos de México VII. Estación de biología tropical Los Tuxtlas, Veracruz. Universidad Nacional Autónoma de México, México.
- Johnson, C. M., D. J. Zarin, and A. H. Johnson. 2000. Post-disturbance aboveground biomass accumulation in global secondary forests: climate, soil texture, and forest type effects. *Ecology*, *in press*.
- Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1998. Fire in the Brazilian Amazon: 2. Biomass, nutrient pools and losses in cattle pastures. *Oecologia* **113**:415–427.
- Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests. *Oecologia* **104**:397–408.
- Levine, J. S. 1990. Global biomass burning: atmospheric, climatic, and biospheric implications. *Eos* **71**:1075–1077.
- Lugo, A. E., 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs* **62**:1–41.
- Lugo, A. E., and S. Brown. 1992. Tropical forests as sinks of atmospheric carbon. *Forest Ecology and Management* **54**:239–255.
- Masera, O. R., M. J. Ordóñez, and R. Dirzo. 1997. Carbon emissions from Mexican forests: the current situation and long-term scenarios. *Climatic Change* **35**:265–295.
- Miranda, F., y E. Hernández-X. 1963. Los tipos de vegetación de México y su descripción. *Boletín. Sociedad Botánica de México* **28**:29–178.
- Mooser, F. 1958. Volcán de San Martín. Pages 32–36 in *Catalogue of the active volcanoes of the world*. International Volcanological Association, Napoli, Italy.
- Nelson, D. W., and L. E. Sommers. 1982. Total carbon, organic carbon, and organic matter. Pages 539–579 in A. L. Page, editor. *Methods of soil analysis: Part 2, Chemical and microbiological properties*. Second edition. Soil Science Society of America Incorporated. Madison, Wisconsin, USA.
- Nelson, S. A., and E. Gonzalez-Caver. 1992. Geology and K-Ar dating of the Tuxtla volcanic field, Veracruz, México. *Bulletin of Volcanology* **55**:85–96.
- Newman, M. C. 1993. Regression analysis of log-transformed data: statistical bias and its correction. *Environmental Toxicology and Chemistry* **12**:1129–1133.
- Olson, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403–427 in A. L. Page, editor. *Methods of soil analysis: Part 2, Chemical and microbiological properties*. Second edition. Soil Science Society of America Incorporated. Madison, Wisconsin, USA.
- Purata, S. E. 1986. Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. *Journal of Tropical Ecology* **2**:257–276.
- Putz, F. E. 1983. Liana biomass and leaf area of a “tierra firme” forest in the Rio Negro Basin, Venezuela. *Biotropica* **15**:185–189.
- Riley, R. H., D. L. Phillips, M. J. Schuft, and M. C. García. 1997. Resolution and error in measuring land-cover change: effects on estimating net carbon release from Mexican terrestrial ecosystems. *International Journal of Remote Sensing* **18**:121–137.
- Saldarriaga, J. G., D. C. West, M. L. Tharp, and C. Uhl. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* **76**:938–958.
- Sánchez, P. A. 1989. Soils. Pages 73–87 in H. Lieth and M. J. A. Werger, editors. *Ecosystems of the world; Volume 14B, Tropical rain forest ecosystems*. Elsevier, New York, New York, USA.
- Sánchez, P. A., J. H. Villachica, and D. E. Bandy. 1983. Soil fertility dynamics after clearing a tropical rainforest in Peru. *Soil Science Society of America Journal* **47**:1171–1178.
- Skole, D. L., and C. J. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* **260**:1905–1910.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry: the principles and practices of statistics in biological research*. Second edition. W. H. Freeman and Company, New York, New York, USA.
- Sollins, P., G. P. Robertson, and G. Uehara. 1988. Nutrient mobility in variable- and permanent-charge soils. *Biogeochemistry* **6**:181–199.
- Soto, M., and L. Gama. 1997. Climas. Pages 7–23 in E. González-Soriano, R. Dirzo, and R. C. Vogt, editors. *Historia natural de Los Tuxtlas*. Universidad Nacional Autónoma de México, México.
- Taylor, K. E., and J. E. Penner. 1994. Responses of the climate system to atmospheric aerosols and greenhouse gases. *Nature* **369**:734–739.
- Toky, O. P., and P. S. Ramakrishnan. 1983. Secondary succession following slash and burn agriculture in north-eastern India: I. Biomass, litterfall, and productivity. *Journal of Ecology* **71**:735–745.
- Uhl, C., R. Buschbacher, and E. A. S. Serrao. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* **76**:663–681.
- Uhl, C., and C. F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology* **65**:1476–1490.
- Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science* **14**:20–26.
- Vitousek, P. M. 1991. Can planted forests counteract increasing atmospheric carbon dioxide? *Journal of Environmental Quality* **20**:348–354.
- Vitousek, P. M., and R. L. Stanford, Jr. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**:137–167.
- Williams-Linera, G. 1983. Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, México. *Biotropica* **15**:275–284.
- Zarin, D. J., and A. H. Johnson. 1995. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal* **59**:1444–1452.