Ecological Applications, 10(2), 2000, pp. 515–527

ECOSYSTEM-SCALE IMPACTS OF DEFORESTATION AND LAND USE IN A HUMID TROPICAL REGION OF MEXICO

R. Flint Hughes,[1,4] J. Boone Kauffman,[2] and Víctor J. Jaramillo[3]

[1]*Department of Forest Science, Oregon State University, Corvallis, Oregon, 97331, USA*
[2]*Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon, 97331, USA*
[3]*Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, Universidad Nacional Autónoma de México, Campus Morelia, Morelia, Michoacán 58089, México*

Abstract. Deforestation of tropical evergreen forests is 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. Elemental losses associated with land conversion in the heavily deforested Los Tuxtlas Region of Mexico were quantified. Total aboveground biomass (TAGB) as well as carbon and nutrient pools in aboveground vegetation and soils were measured along a land-use gradient that included primary forests as well as pastures and cornfields, which represent the dominant land-use types in the region. 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 forests was composed of trees >30 cm in diameter at breast height (dbh), while trees >70 cm dbh accounted for 44% of TAGB. Conversion of forests to pastures or cornfields resulted in declines of 95% of aboveground C pools, 91% of aboveground N pools, 83% of aboveground P pools, and 89–95% of aboveground S pools in sites ranging in age from 3 to 45 years since deforestation. In contrast to aboveground pools, soil pools of C, N, and S to a 1 m depth were highly variable and did not show detectable declines in pasture and cornfield sites compared to forest sites, nor did they decline with increasing periods of land use. Average C mass in soils of forest, pasture, and cornfield sites ranged between 166 and 210 Mg/ha; mass of N and S in soils ranged from 16 to 20 and from ~3 to 4 Mg/ha, respectively. Approximately 50% of the combined aboveground and soil pools of C were 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 these young volcanic soils, less than 10% of combined aboveground and soil N and S pools were lost due to land-use change in the Los Tuxtlas Region.

Key words: aboveground biomass; carbon and nutrient pools; deforestation and land use; forest conversion; greenhouse gas flux; Los Tuxtlas, Mexico; mature forests, pastures, and cornfields; N, S, and P dynamics, aboveground vs. soils; tropical evergreen forests.

Introduction

Deforestation of tropical evergreen forests (TEFs) is occurring at unprecedented rates and is altering biogeochemical cycles at local, regional, and global scales. While TEFs comprise only 11% of the earth's land area, they account for ~60% of the carbon in aboveground pools of the world's forests and 37% of the total terrestrial net primary productivity of the earth (Potter et al. 1993, Dixon et al. 1994, Dixon and Wisniewski 1995). The conversion of TEFs to pastures or croplands has resulted in increased emissions of CO_2 (Kauffman and Uhl 1990, Levine 1990, Ward et al. 1992), and decreased terrestrial storage of C, N, S, and P. During the 1980s the estimated rate of deforestation in tropical forest ecosystems was 15.4×10^6 ha/yr, and associated C emissions were 1.6 ± 1.0 Pg/yr (Dixon et al. 1994, Schimel et al. 1995). Similarly, N volatilization arising from the combustion of slashed TEFs has accounted for an annual loss of between 10 and 20 Tg N from tropical ecosystems; this loss is equivalent to 6–20% of the total amount of N fixed annually by the earth's terrestrial systems (Crutzen and Andreae 1990).

Although 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 TEFs, the losses of such pools during the conversion of TEFs to pasture and agricultural lands, and the size of those pools sustained by converted lands during periods of management.

In Mexico, deforestation and forest burning during the 1980s accounted for 40% of that nation's total C emissions, with ~75% of deforestation occurring in

Manuscript received 20 April 1998; revised 1 April 1999; accepted 6 April 1999; final version received 27 May 1999.
[4] Present address: Cooperative Institute for Research in Environmental Sciences, Campus Box 216, University of Colorado, Boulder, Colorado 80309-0216 USA.
E-mail: hughesf@terra.colorado.edu.

tropical forests (Masera et al. 1997). Masera et al. (1997) estimated that deforestation of TEFs averaged ~2% per year during the 1980s, with substantially higher rates in certain areas (e.g., 4, 5, and 12% 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 TEFs 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 activities.

The Los Tuxtlas Region of Mexico represents 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 one of the most heavily deforested areas in Mexico. By the mid-1980s, 84% of the Los Tuxtlas Region had been deforested, with the majority of the deforestation occurring during the past 30 years (Dirzo and García 1992). Establishment of cattle pastures is currently the primary land use in the region, although conversion of forested land to cropland is also common (Guevara et al. 1997, Masera et al. 1997). Riley et al. (1997) estimated that, between 1986 and 1990, $\sim 2 \times 10^4$ ha were deforested and converted to agricultural uses with an associated carbon loss of 1.5×10^6 Mg. If current deforestation rates continue, <9% of the forests in the Los Tuxtlas Region will remain by the year 2000 (Dirzo and García 1992).

Few site-specific studies have estimated total aboveground biomass (TAGB) or the size of elemental pools in intact TEFs (see reviews by Kauffman and Uhl 1990, Hao et al. 1990, Golley 1983, and Brown et al. 1989). Estimates of TAGB in tropical evergreen forests range widely from 143 to 1174 Mg/ha (Golley 1983, Fearnside 1992). Less information is available on biomass, C, and nutrient pools in pastures and cultivated systems of the tropics. TAGB of pastures converted from TEFs in the Brazilian Amazon ranged from 53 to 119 Mg/ha. Total aboveground C pools of these pastures ranged between 26 and 59 Mg/ha, and aboveground N pools ranged between 271 and 661 kg/ha (Guild et al. 1998, Kauffman et al. 1998, R. F. Hughes and J. B. Kauffman, *unpublished manuscript*).

The objectives of this study were to quantify changes in TAGB, C, N, S, and P pools associated with conversion of TEFs to pastures and cropland in the Los Tuxtlas Region, Mexico. Biomass, C, N, S, and P pools were determined via measurements of aboveground vegetation and soils in forest, pasture, and cornfield sites located within the 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 Tuxtla in the Sierra de Los Tuxtlas, a series of 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 (García 1970); mean annual temperature is 27°C, and mean annual rainfall is 4700 mm (Soto and Gama 1997). Precipitation varies seasonally with ~60% of annual precipitation occurring between June and October. A relatively dry season occurs between March and May in which monthly rainfall usually does not exceed 150 mm. Mean monthly temperatures vary 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 grading to steep slopes. Volcán San Martín Tuxtla 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).

Potential vegetation of the study area is classified as ''selva alta perennifolia'' (tall evergreen forest), and is characterized by a closed canopy 30–35 m in height (Gomez-Pompa 1973). Common 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 plectostachyus* and *Panicum maximum*. Although broadleaf herbicide is sometimes applied to inhibit non-grass vegetation, pastures are typically maintained by manual removal of woody species and/or burning (Guevara et al. 1992). Stocking rates of cattle in pastures typically range from 2 to 4 head per hectare, and grazing rotations of 15–30 d of use followed by 15–40 d of rest are common (Guevara et al. 1997).

Corn (*Zea mays*) 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 a second rotation during the dry season as well. Cultivation in the Los Tuxtlas Region is typically long-lived: some 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 shift-

TABLE 1. Land-use histories of pastures and cornfields sampled in the Los Tuxtlas Region of Mexico.

Site code†	Land-use history prior to sampling‡	Land-use period (yr)§
Pasture sites		
P-8	8 yr pasture	8
P-9	1 yr as cornfield; 8 yr as pasture	9
P-10	1 yr as cornfield; 9 yr as pasture	10
P-28	9 yr as cornfield; 5 yr as second-growth forest; 14 yr as pasture	28
P-33a	27 yr as cornfield; 6 yr as pasture	33
P-33b	3 yr cornfield; 30 yr as pasture	33
P-40	40 yr as pasture	40
Cornfield sites		
C-3	3 yr as cornfield	3
C-5	5 yr as cornfield	5
C-32	32 yr as cornfield	32
C-45	45 yr as cornfield	45

† Numerical values in the label of each site indicate the years of land use following deforestation.
‡ 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.
§ Land-use period refers to years prior to sampling.

ing cultivation. According to landholders, fertilizers had never been applied to any of the pasture and cornfield sites sampled in this study.

METHODS

Total aboveground biomass (TAGB) and aboveground pools of C, N, S, and P were estimated in four forest, seven pasture, and four cornfield sites. 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 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 three forest (SN, SB, and SP), four pasture (P-8, P-9, P-33a, and P-33b), and three cornfield (C-5, C-32, C-45) sites. Pools of P were also quantified in soils, but only to a depth of 10 cm, and only at three forest (SN, SB, and SP) and two pasture (P-8 and P-33a) sites.

Plot layouts

Aboveground biomass and elemental pools in forests were quantified using a nested plot design. At each site, diameter at breast height (dbh, 1.3 m) was measured for all trees ≥30 cm dbh present within a 105 × 75 m plot (i.e., ∼0.79 ha). A 25 × 105 m subplot was established in the central portion of the larger plot, and dbh of all trees ≥10 and <30 cm dbh were measured within this subplot. In cases where individual trees had large buttresses, diameter was measured above the buttress.

Downed woody debris was measured along sixteen 15-m sampling planes placed at 15-m intervals along each of two 105-m transects within each 105 × 75 m plot. Diameter was recorded for all wood ≥7.6 cm in diameter that crossed each 15-m transect; wood was divided into sound and rotten classes based on degree of decomposition. Wood debris particles ≥2.54 and <7.6 cm in diameter that intersected a 10-m section of each 15-m transect were counted. Biomass of woody debris was calculated at each 15-m transect using planar-intersect techniques (Van Wagner 1968, Brown and Roussopoulous 1974; Table 2). Average values for specific gravity of each of three woody-debris particle classes (2.45–≥7.6 cm diam., ≥7.6-cm diam. sound, and ≥7.6-cm diam. rotten) were determined from samples collected at random from forest sites.

Biomass of trees, lianas, and palms at least 1.3 m in height but <10 cm dbh was quantified through measurement of dbh and/or height of all individuals within 2 × 10 m transects located adjacent to each of the 16 woody-debris transects at each site. 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 × 50 cm microplots placed at the 5-m point along each woody-debris transect line (n = 16 microplots/site).

TAGB and elemental pools of pastures were quantified in a 60 × 90 m plot established in the center of each sampled pasture. All trees, lianas, and palms ≥1.3 m in height were measured in this large plot. Woody debris was sampled along 15-m transects placed at 10-m intervals along three 90-m transects within the 60 × 90 m plot (n = 30 microplots/pasture). 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 microplots/pasture).

At each cornfield site, biomass of trees, lianas, and palms ≥1.3 m in height was measured within one 30 × 60 m plot. Sites were sampled immediately prior to the harvest. Consequently, biomass and elemental pools represent the maximum annual biomass value at each site. Corn biomass was measured in fifteen 5 × 5 m subplots distributed among five 25-m transects running perpendicular to the 60-m side of the large plot at 15-m intervals. All corn stalks within each subplot were counted, and an average dry-mass value for each corn stalk was obtained from samples of 20 stalks collected at random from each site. Woody debris was measured along 15-m transects placed at a randomly selected corner of each 5 × 5 m subplot (n = 15 transects); methods followed those described for forest sites. The combined biomass of litter, graminoids, and other non-corn vegetation <1.3 m in height was measured in 50 × 50 cm microplots placed at a randomly selected corner of each 5 × 5 m subplot (n = 15 microplots).

TABLE 2. Equations to determine components of aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. All biomass is expressed as dry mass.

Parameter†	Equation‡	Correction factor, CF§	R^2
Height of trees > 10 cm dbh	$4.722 \ln(D^2) - 13.323$	none	0.70
Biomass (Mg)			
Trees ≥ 10 cm dbh[b]	$[\exp(-2.409 + 0.9522 \ln(D^2 H \mathrm{Sg}))]\mathrm{CF} \times 10^{-3}$	1.03	0.99
Cecropia ≥ 10 cm dbh (wood)[u]	$[\exp(-3.78 + 0.95 \ln(D^2) + 1.00 \ln(H)] \times 10^{-3}$	none	0.88
Cecropia ≥ 10 cm dbh (leaf)[u]	$[-0.56 + 0.02(D^2) + 0.04(H)] \times 10^{-3}$	none	0.98
Standing dead trees ≥ 10 cm dbh	$\pi[(D/2)^2]H(0.42)$	none	none
Trees < 10 cm dbh	$[\exp(4.9375 + 1.0583 \ln(D^2))]\mathrm{CF} \times 10^{-6}$	1.14	0.93
Dead trees < 10 cm dbh	$[\exp(4.6014 + 1.1204 \ln(D^2))]\mathrm{CF} \times 10^{-6}$	1.11	0.95
Palms	$[\exp(3.6272 + 0.5768 \ln(D^2 H))]\mathrm{CF} \times 10^{-6}$	1.02	0.73
Dead palms	$[\exp(-0.5285 + 0.9907 \ln(D^2 H))] \times 10^{-6}$	none	0.98
Lianas[p]	$(10^{0.12+0.91 \log_{10}(\mathrm{BA})}) \times 10^{-3}$	none	0.82
Tree leaves[c]	$\exp(-1.897 + 0.836 \ln(D^2 H)) \times 10^{-3}$	none	0.85
Sapling wood	$\exp(4.7472 + 1.0915 \ln(D^2))\mathrm{CF} \times 10^{-6}$	1.13	0.93
Sapling leaves	$\exp(3.0473 + 0.7778 \ln(D^2))\mathrm{CF} \times 10^{-6}$	1.45	0.71
Liana leaves[p]	$[(0.109\mathrm{BA}) - 0.376] \times 10^{-3}$	none	none
Wood debris 2.45–7.6 cm diam.[v]	$\mathrm{Sg} \times [(\pi^2 N S \mathrm{Cs} d^2)/8\mathrm{L}] \times 10^2$	none	none
Wood debris ≥ 7.6 cm diam.[v]	$\mathrm{Sg} \times [\pi^2 \mathrm{sumD}^2 S \mathrm{Cs} d^2)/8L] \times 10^2$	none	none

† All information is based on this study unless indicated by the following superscript letters: b = Brown et al. 1989, c = Crow 1978, p = Putz 1983, u = Uhl et al. 1988, v = VanWagner 1968.

‡ Definitions (and units) for symbols used in equations: BA = basal area (cm^2); Cs = slope correction factor (square root of $[1 + (\%\ \mathrm{slope}/100)^2]$; D = diameter breast height (cm); d = quadratic mean diameter of wood debris (cm); H = height (m); L = transect length (cm); N = number of pieces of wood debris intersected per transect; S = secant of wood debris tilt; Sg = specific gravity of wood ($\mathrm{g/cm}^3$); sumD^2 = sum of wood debris diameters-squared (cm^2).

§ CF = exp(MSE/2). See *Methods*: *Parameter calculations* for further explanation. A value given in this column is to be substituted in the equation on the same line.

Soil sampling

C, N, S, and P mass in mineral soil was determined from five sample points placed at 10-m intervals along a 50-m transect located in the center of each 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 by compositing four subsamples collected 1 m from each sampling point in each cardinal direction. At each sample point, deep soils were collected from one of the four locations from which surface soils had been sampled. Soil bulk density was determined at each site from samples of known volume collected at five points located within each site.

Parameter calculations

Biomass of trees ≥10 cm in diameter at breast height (dbh) was estimated 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). In addition to dbh, each tree ≥10 cm dbh encountered during sampling procedures was identified to species in order to assign species-specific wood-density values to each tree. The majority of wood-density values were provided by T. 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 Brown (1997). Heights of trees ≥10 cm dbh were determined using a predictive model developed from 553 trees sampled during this study and by Bongers et al. (1988). Due to the unusual form of *Cecropia obtusifolia,* genus-specific models for wood and leaf biomass developed by Uhl et al. (1988) were used (Table 2). Correction factors were included in several of the allometric models to account for bias introduced during conversion from logarithmic to arithmetic units (Baskerville 1972). In certain cases correction factors were not employed because they either were not available from cited sources or they failed to improve the predictability of the respective models (Table 2).

Biomass of live and dead trees ≥1.3 m in height but <10 cm dbh was calculated using a regression equation developed from measures of 66 trees harvested in the Los Tuxtlas Region. Biomass of palms was calculated from a regression equation developed from 15 *Astrocaryum mexicanum* individuals harvested within the region (Table 2).

Surface-layer biomass was defined as litter and vegetation <1.3 m in height (i.e., seedlings). At forest sites, litter and seedling components were collected

TABLE 3. Concentrations (mean ± 1 SE) of C, N, S, and P in components of aboveground biomass in forest, pasture, and cornfield sites in the Los Tuxtlas Region of Mexico.

Vegetation component	C (%)	N (mg/g)	S (mg/g)	P (mg/g)
Litter, forest sites	46.15 ± 0.88	17.29 ± 1.16	1.59 ± 0.16	0.70 ± 0.07
Herbs, forest sites	42.52 ± 0.24	19.05 ± 1.01	2.88 ± 0.16	1.18 ± 0.13
Surface layer, pastures	43.68 ± 0.33	13.34 ± 0.74	2.27 ± 0.38	1.73 ± 0.27
Surface layer, cornfields	42.48 ± 0.46	14.06 ± 0.84	1.29 ± 0.26	1.42 ± 0.34
Palm (stem biomass)	47.32 ± 0.30	7.00 ± 1.29	1.10 ± 0.16	1.00 ± 0.18
Trees < 10 cm, leaf	43.05 ± 0.84	26.04 ± 0.98	4.05 ± 0.30	1.48 ± 0.14
Trees ≥ 10 cm, leaf	46.25 ± 0.51	25.14 ± 0.76	2.99 ± 0.17	1.35 ± 0.11
Trees < 10 cm, wood	45.82 ± 0.25	8.01 ± 0.28	1.53 ± 0.19	0.73 ± 0.07
Trees ≥ 10 cm, wood	48.58 ± 0.13	3.20 ± 0.18	0.45 ± 0.10	0.19 ± 0.02
Corn plant	44.59 ± 0.29	9.34 ± 1.13	0.83 ± 0.16	1.36 ± 0.29
Corn cob	45.97 ± 0.13	5.97 ± 1.06	0.43 ± 0.17	1.01 ± 0.29
Corn grain	44.43 ± 0.54	16.69 ± 0.64	1.12 ± 0.15	2.11 ± 0.12
Wood debris diameter class				
2.55–7.6 cm	49.16 ± 0.28	4.93 ± 0.31	0.49 ± 0.04	0.25 ± 0.02
≥7.6 cm (sound)	50.12 ± 0.33	3.73 ± 0.43	0.19 ± 0.02	0.36 ± 0.19
≥7.6 cm (rotten)	49.29 ± 0.63	5.64 ± 0.68	0.42 ± 0.09	0.31 ± 0.06

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 leaves collected from randomly selected individuals at two of the 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. Leaf samples were collected by climbing into the tree canopy. Five composite samples, each consisting of subsamples taken from eight trees, were collected at each site.

C, N, S, and P pools of all biomass components were calculated by multiplying the biomass of each component by its respective C and nutrient concentration (Table 3). Leaf biomass of each tree ≥10 cm dbh was determined using a regression equation developed by Crow (1978) (Table 2). 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 each of two sites. Samples were composited to provide five leaf and five wood samples per site. C, N, S, and P pools in palms were calculated by multiplying palm biomass by elemental concentrations measured in stem tissue sampled from 15 randomly selected *A. mexicanum* individuals. Elemental pools of leaf and stem 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 in wood debris were determined from five composited samples for each class collected at random within forest sites. Elemental concentrations of surface-layer components were determined from five composited samples obtained from biomass samples. Elemental concentrations of corn biomass were determined at each cornfield site from five composited tissue samples obtained from 20 corn plants selected at random in each site.

Mass of C, N, S, and P in soils was calculated by multiplying mean concentrations of those elements at each depth by the corresponding mean soil bulk density value for each depth at each site (Table 4).

TABLE 4. Concentrations (mean ± 1 SE) of C, N, S, and P, and bulk density of soils in forests, pastures, and cornfields of the Los Tuxtlas Region of Mexico.

Element, by soil depth (cm)	Forest	Pasture	Cornfield
Carbon (%)			
>0–2.5 cm	7.8 ± 1.7	6.5 ± 0.9	5.4 ± 0.8
>2.5–10 cm	5.0 ± 1.5	4.6 ± 0.5	4.6 ± 0.8
>10–30 cm	3.5 ± 1.4	2.5 ± 0.6	3.5 ± 0.7
>30–50 cm	2.6 ± 1.1	1.6 ± 0.4	2.3 ± 0.4
>50–100 cm	1.9 ± 0.8	1.1 ± 0.2	1.7 ± 0.3
Nitrogen (mg/g)			
>0–2.5 cm	7.04 ± 1.66	6.17 ± 1.01	5.10 ± 0.91
>2.5–10 cm	5.00 ± 1.62	4.43 ± 0.56	4.63 ± 0.91
>10–30 cm	3.57 ± 1.58	2.56 ± 0.74	3.69 ± 0.92
>30–50 cm	2.43 ± 1.01	1.47 ± 0.42	2.21 ± 0.45
>50–100 cm	1.66 ± 0.68	1.05 ± 0.22	1.54 ± 0.36
Sulfur (mg/g)			
>0–2.5 cm	0.83 ± 0.18	0.79 ± 0.10	0.74 ± 0.09
>2.5–10 cm	0.65 ± 0.17	0.61 ± 0.08	0.70 ± 0.07
>10–30 cm	0.52 ± 0.18	0.40 ± 0.06	0.58 ± 0.05
>30–50 cm	0.44 ± 0.17	0.32 ± 0.11	0.46 ± 0.08
>50–100 cm	0.42 ± 0.17	0.33 ± 0.08	0.41 ± 0.08
Phosphorus (mg/g)†			
>0–2.5 cm	1.27 ± 0.04	1.42 ± 0.14	···
>2.5–10 cm	1.34 ± 0.11	1.34 ± 0.18	···
Bulk density (g/cm^3)			
>0–10 cm	0.85 ± 0.13	0.85 ± 0.04	0.92 ± 0.08
>10–30 cm	0.86 ± 0.13	0.93 ± 0.10	0.87 ± 0.06
>30–50 cm	0.87 ± 0.10	1.00 ± 0.13	0.95 ± 0.07
>50–100 cm	0.84 ± 0.11	1.03 ± 0.11	0.96 ± 0.11

† P concentrations were determined for surface soil layers only and were not measured in cornfield sites.

TABLE 5. Total aboveground biomass and stem densities of primary forest sites in the Los Tuxtlas Region, Mexico.

Forest site	Litter	Seedling	Surface layer†	Woody debris	Palm	Liana	Tree, by dbh <10 cm
Biomass (Mg/ha)							
SL	7.1	2.4	9.5	22.9	5.9	0.9	13.6
SN	6.3	0.8	7.2	9.1	5.8	6.6	4.3
SB	5.3	0.6	5.9	2.7	7.2	2.1	1.7
SP	5.8	0.6	6.4	22.6	1.9	3.3	4.3
Mean ± 1 SE	6.1 ± 0.4	1.1 ± 0.4	7.3 ± 0.8	14 ± 5.1	5.2 ± 1.2	3.2 ± 1.2	6.0 ± 2.6
Stem density (individuals /ha)							
SL					1438	656	4938
SN					1094	3281	2594
SB					1563	2281	1563
SP					375	3219	3719
Mean ± 1 SE					1117 ± 267	2359 ± 612	3203 ± 727

† The surface-layer category represents the sum of litter and seedling components.
‡ Total biomass represents the sum of all biomass components; total stem density represents the sum for trees >10 cm dbh.

Laboratory and statistical analysis

All soil and vegetation samples were oven dried to a constant weight at a temperature of 65°C. Vegetation samples were ground to pass through a 40-mesh (0.55-mm mesh) screen using a Tecator Cyclotec 1093 sample mill (Tecator, Herndon, Virginia, USA). Soil samples were sieved to remove roots >2 mm in diameter and ground to pass through a 60-mesh (250-μm pore size) screen. 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 CNS analyzer (Fisons Instruments, Danvers, Massachusetts, USA) (Nelson and Sommers 1982). Total P concentrations were determined using a Kjeldahl digestion procedure followed by colorimetric analysis (Olson and Sommers 1982).

To simplify our interpretation of the consequences of land-use change in the Los Tuxtlas Region, we provide values as means ± 1 SE throughout our presentation of the differences/similarities in TAGB, C, N, S, and P pools between land-cover types. Further statistical tests (e.g., ANOVA) were avoided because sites within pasture and cornfield groups could not be considered as true replicates due to their divergent ages and land-use histories (Hurlbert 1984).

RESULTS

Total aboveground biomass

Total aboveground biomass (TAGB) averaged 403 Mg/ha in undisturbed primary forests (Table 5) and was ~20 times greater than average TAGB values of both pastures and cornfields (Tables 3 and 4). However, TAGB was highly variable among forest sites, ranging from 320 to 545 Mg/ha. Conversion of forest to pasture or agriculture resulted in declines of nearly 95% of TAGB, or 380 Mg/ha. The mean TAGB of pastures was nearly identical to that of cornfields; pasture TAGB averaged 24 Mg/ha, while cornfield TAGB averaged 23 Mg/ha (Table 6).

In forest sites, trees ≥30 cm in diameter at breast height (dbh) comprised ~80% of TAGB, and trees ≥70 cm dbh comprised ~45% of TAGB (Table 3). In contrast, the combined biomass of the surface layer (i.e., litter, graminoids, and seedlings <1.3 m in height), woody debris, palm, liana, and trees <10 cm dbh accounted for only ~9% of forest TAGB.

TAGB of pastures and cornfields was also highly variable among sites of each of those vegetation types. It ranged from 7 to 48 Mg/ha in pastures and from 5 to 42 Mg/ha in cornfields. The combined biomass of woody debris and trees ≥10 cm dbh was the most substantial and variable set of components, ranging from 0 to 38 Mg/ha and 0 to 36 Mg/ha in pastures and cornfields, respectively. In contrast, non-woody biomass (i.e., the surface-layer and corn biomass) ranged from 5 to 12 Mg/ha in pastures and from 5 to 13 Mg/ha in cornfields. In pastures, the combined biomass of litter, graminoids, and seedlings <1.3 m in height (i.e., the surface layer) accounted for an average of 30% of TAGB; corn biomass accounted for an average of 25% of TAGB in cornfields. Combined palm and liana biomass was negligible or nonexistent in both pasture and cornfield sites (Table 6).

Mass of aboveground C, N, S, and P pools

Distribution of aboveground C pools was similar to those of TAGB. Total aboveground C of forest sites ranged from 155 to 264 Mg/ha. Trees ≥30 cm dbh accounted for 80% of the total aboveground C mass of forest sites, and variation in total aboveground C between sites was primarily due to variation in the mass of C in trees ≥70 cm (Table 7). Aboveground C mass was 18 times higher in primary forests relative to cornfields and pastures. Average C mass of pastures was nearly identical to that of cornfields (11 Mg/ha), and the combined pools of woody debris and trees ≥10 cm dbh accounted for the majority of aboveground C mass in each land-cover type. On average, conversion of forests to pastures or cornfields resulted in a loss of 94% of aboveground C mass, or 184 Mg/ha.

TABLE 5. Extended.

Tree, by dbh			
≥10–30 cm	≥30–70 cm	≥70 cm	Total‡
57.3	128.9	114.5	353.6
27.3	134.3	125.7	320.2
48.8	142.6	182.0	392.9
51.7	170.4	284.2	544.7
46 ± 6.6	144 ± 9.2	177 ± 39	403 ± 50
469	67	15	551
187	95	22	304
248	88	23	358
274	111	28	413
306 ± 62	92 ± 10	23 ± 2.7	421 ± 55

Total aboveground pools of N in forests, pastures, and cornfields averaged 1705, 161, and 152 kg/ha, respectively. Reductions in N due to forest conversion were slightly lower than reductions in C; N pools of pastures and cornfields represented 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 mass 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 7). Total aboveground pools of S in forests, pastures, and cornfields sites were 227, 25, and 11 kg/ha, respectively. In pastures, the surface layer contained the majority of aboveground S (67%), and the majority of aboveground S in cornfields was distributed between the surface layer and corn biomass components (68% of total). Mass of S in forests was concentrated in trees ≥10 cm dbh (83% of total).

Total aboveground mass of P averaged 105 kg/ha in forests, 17 kg/ha in pastures, and 18 kg/ha in cornfields. Site conversion resulted in an average decline of 83% of aboveground P pools. In forests, ~78% of the total mass of P was concentrated in trees ≥10 cm dbh. In contrast, ~74% of the aboveground P of pastures was in the surface layer, and 67% of total P of cornfields was in the combined mass of surface-layer and corn biomass (Table 7).

Mass of C, N, S, and P in soils

In contrast to the dynamics of aboveground pools, we did not detect a strong influence of land use on soil C and nutrient pools. Total mass of soil C to a 1-m depth in forests, pastures, and cornfields averaged 210, 167, and 200 Mg/ha, respectively (Table 8). Total soil N to a 1-m depth ranged between 16 and 20 Mg/ha for the three land-cover types. Total soil S to a 1-m depth ranged between 3 and 4 Mg/ha. Although C, N, and S pools were lower, on average, in pastures compared to forests and cornfields, this was primarily due to the influence of high values in one forest site (SP) and one cornfield site (C-32). These two sites had much larger soil C, N, and S pools than any of the other sites we sampled and consequently increased both the mean and, more importantly, standard error values of forest and cornfield sites relative to those of pasture sites (Table 9).

In addition, duration of land use did not decrease soil pools within the available span of land-use periods. Mass of C, N, and S in sites that had experienced relatively longer periods of land use (i.e., P-33a, P-33b, C-32, and C-45) averaged 205, 20, and 4 Mg/ha, respectively. In sites that had experienced relatively shorter periods of land use (i.e., P-8, P-9, and C-5), C, N, and S pools averaged 149, 14, and 3 Mg/ha re-

TABLE 6. Total aboveground biomass (Mg/ha) of pasture and cornfield sites in the Los Tuxtlas Region, Mexico.

Site	Surface layer†	Corn			Woody debris	Palm	Liana	Tree, dbh‡		Total
		Plant	Cob	Grain				<10 cm	≥10 cm	
Pastures										
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 ± 1.1	···	···	···	3.3 ± 2.1	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.2	13 ± 5.8	24 ± 6
Cornfields										
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 ± 0.7	4.5 ± 1.1	0.4 ± 0.1	1.0 ± 0.3	14 ± 8.3	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.5	23 ± 9

† The surface-layer category represents the sum of litter, grass, and seedling components.
‡ Means are reported ± 1 SE.

TABLE 7. Mass of C, N, S, and P in aboveground biomass of forest, pasture, and cornfield sites in the Los Tuxtlas Region, Mexico. Values are means ± 1 SE.

Component	Forest	Pasture	Cornfield
Carbon (Mg/ha)			
Surface layer†	3.3 ± 0.4	3.3 ± 0.5	1.1 ± 0.3
Litter	2.8 ± 0.2	···	···
Seedlings	0.5 ± 0.2	···	···
Woody debris	7.1 ± 2.5	1.6 ± 1.1	6.8 ± 4.1
Corn biomass	0.0 ± 0.0	0.0 ± 0.0	2.6 ± 0.6
Palm	2.5 ± 0.5	0.0 ± 0.0	0.1 ± 0.1
Liana	1.5 ± 0.6	0.0 ± 0.0	0.0 ± 0.0
Tree			
<10 cm	2.7 ± 1.2	0.2 ± 0.1	0.0 ± 0.0
≥10–30 cm	22.4 ± 3.2	0.9 ± 0.3	0.3 ± 0.2
≥30–70 cm	69.9 ± 4.5	2.2 ± 1.3	0.0 ± 0.0
≥70 cm	85.7 ± 18.8	3.1 ± 2.0	0.0 ± 0.0
Total	195.1 ± 24.2	11.3 ± 3.0	10.9 ± 4.4
Nitrogen (kg/ha)			
Surface layer	126 ± 10	93 ± 9	35 ± 8
Litter	105 ± 5	···	···
Seedlings	21 ± 8	···	···
Woody debris	60 ± 20	15 ± 10	53 ± 32
Corn biomass	0 ± 0	0 ± 0	61 ± 17
Palm	36 ± 8	0 ± 0	1 ± 1
Liana	28 ± 11	0 ± 0	0 ± 0
Tree			
<10 cm	56 ± 24	4 ± 2	0 ± 0
≥10–30 cm	192 ± 28	8 ± 2	3 ± 2
≥30–70 cm	554 ± 37	17 ± 10	0 ± 0
≥70 cm	653 ± 140	24 ± 16	0 ± 0
Total	1705 ± 165	161 ± 24	152 ± 43
Sulfur (kg/ha)			
Surface layer†	12.9 ± 1.6	16.8 ± 3.6	3.3 ± 1.1
Litter	9.7 ± 0.8	n.a	n.a
Seedlings	3.1 ± 1.3	n.a	n.a
Woody debris	3.7 ± 1.2	1.0 ± 0.7	3.0 ± 1.8
Corn biomass	0.0 ± 0.0	0.0 ± 0.0	4.5 ± 0.7
Palm	5.7 ± 1.3	0.0 ± 0.0	0.2 ± 0.2
Liana	5.1 ± 2.0	0.0 ± 0.0	0.0 ± 0.0
Tree			
<10 cm	10.3 ± 4.4	0.8 ± 0.3	0.0 ± 0.0
≥10–30 cm	25.7 ± 3.7	1.0 ± 0.3	0.4 ± 0.3
≥30–70 cm	75.0 ± 4.9	2.3 ± 1.4	0.0 ± 0.0
≥70 cm	89.0 ± 19.2	3.3 ± 2.1	0.0 ± 0.0
Total	227.4 ± 22.5	25.2 ± 4.4	11.4 ± 2.4
Phosphorus (kg/ha)			
Surface layer†	5.6 ± 0.8	12.4 ± 1.9	4.1 ± 2.0
Litter	4.3 ± 0.5	n.a	n.a
Seedlings	1.3 ± 0.5	n.a	n.a
Woody debris	4.9 ± 1.8	1.1 ± 0.7	4.7 ± 2.9
Corn biomass	0.0 ± 0.0	0.0 ± 0.0	7.9 ± 1.6
Palm	5.4 ± 1.2	0.0 ± 0.0	0.2 ± 0.2
Liana	2.4 ± 0.9	0.0 ± 0.0	0.0 ± 0.0
Tree			
<10 cm	4.5 ± 2.0	0.4 ± 0.1	0.0 ± 0.0
≥10–30 cm	11.2 ± 1.6	0.4 ± 0.1	0.9 ± 0.7
≥30–70 cm	32.5 ± 2.1	1.0 ± 0.6	0.0 ± 0.0
≥70 cm	38.5 ± 8.3	1.4 ± 0.9	0.0 ± 0.0
Total	105.0 ± 9.2	16.8 ± 2.4	17.8 ± 4.9

† In forest sites, litter and seedling pools were sampled separately. The surface-layer pool is the sum of these two components.

spectively (Table 9). In all land-cover types, ~50% of soil C and N occurred between 0 and 30 cm, and roughly 30% of C and N was located in the 50–100 cm depth. Approximately 40% of soil S was located within the 0–30 cm soil-depth range, and 30–50% was located between 50 and 100 cm (Table 8).

DISCUSSION

Total aboveground biomass in forests

The mean total aboveground biomass (TAGB) of forests sampled in this study—(403 Mg/ha)—is at the high end of the range of TAGB for tropical evergreen forests (TEFs) located elsewhere in tropical America. Cummings (1998) reported a mean of 345 Mg/ha for 20 intact forest sites within Rondonia, Brazil. Other estimates of TAGB in primary forests of the Amazon Basin range from 264 to 363 (Uhl et al. 1988, Jordan 1989). Estimates of TAGB in TEFs of Puerto Rico, Costa Rica, and Panama were 365, 382, and 326 Mg/ha, respectively (Ovington and Olson 1970, Golley et al. 1975, P. Werner, *unpublished data* cited by Jordan 1989). Because biomass of primary forests in the Los Tuxtlas Region of Mexico was 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.

Variation among the four forest sites was primarily due to variation in trees ≥70 cm in diameter at breast height (dbh); this vegetation component represented the largest contribution to TAGB and was also the most highly variable of components among those sites. Densities of large trees ranged from 15 to 28 individuals/ha, and large trees accounted for between 32% and 52% of forest TAGB (Table 3). TAGB was dominated by trees ≥30 cm dbh which comprised 80% of TAGB. The 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 ~58% of TAGB, and trees ≥70 cm dbh accounted for only 20% of TAGB (Cummings 1998).

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 (7–15%). Woody debris, in particular, proved to be a minor component of forest biomass, accounting for a mean of only 3% of TAGB. In contrast, woody debris accounted for an average of 12% of TAGB in TEFs of Rondonia, Brazil (Cummings 1998).

Regarding potential sources of error in our estimates of TAGB, and particularly large-tree biomass, one must consider the error introduced by the allometric equation used to predict biomass of trees ≥10 cm dbh (Brown et al. 1989). The error estimates (1 SE) reported throughout our results refer only to statistical uncertainty derived from our sample design and do not incorporate potential errors introduced by allometric models. Biomass values of the pan tropical sample of trees used to produce the Brown et al. model were shown to be highly correlated with the combined var-

TABLE 8. Mass of C, N, S, and P in soils of forests, pastures, and cornfields in the Los Tuxtlas Region, Mexico. Values are means ± 1 SE.

Depth	Forest	Pasture	Cornfield
Carbon (Mg/ha)			
0–2.5 cm	15.4 ± 0.8	13.6 ± 1.2	12.6 ± 3.0
>2.5–10 cm	28.5 ± 3.6	28.9 ± 2.0	32.5 ± 8.4
>10–30 cm	53.0 ± 12.6	43.1 ± 3.2	60.4 ± 12.0
>30–50 cm	40.3 ± 11.1	28.1 ± 2.4	42.8 ± 6.7
>50–100 cm	73.1 ± 21.8	52.9 ± 5.9	52.0 ± 26.2
Total to 1 m	210.3 ± 49.2	166.6 ± 9.0	200.3 ± 47.6
Nitrogen (Mg/ha)			
0–2.5 cm	1.4 ± 0.1	1.3 ± 0.2	1.2 ± 0.3
>2.5–10 cm	2.9 ± 0.4	2.8 ± 0.2	3.3 ± 1.0
>10–30 cm	5.4 ± 1.5	4.3 ± 0.6	6.5 ± 1.7
>30–50 cm	3.8 ± 1.1	2.6 ± 0.3	4.2 ± 0.8
>50–100 cm	6.4 ± 1.9	5.0 ± 0.5	4.9 ± 2.5
Total to 1 m	19.8 ± 4.9	16.0 ± 1.2	19.9 ± 5.4
Sulfur (Mg/ha)			
0–2.5 cm	0.16 ± 0.01	0.16 ± 0.02	0.17 ± 0.04
>2.5–10 cm	0.38 ± 0.03	0.38 ± 0.03	0.49 ± 0.10
>10–30 cm	0.80 ± 0.14	0.70 ± 0.07	1.01 ± 0.12
>30–50 cm	0.70 ± 0.17	0.54 ± 0.09	0.87 ± 0.14
>50–100 cm	1.58 ± 0.46	1.57 ± 0.18	1.28 ± 0.65
Total to 1 m	3.63 ± 0.80	3.36 ± 0.32	3.84 ± 0.86
Phosphorus (Mg/ha)†			
0–2.5 cm	0.27 ± 0.04	0.32 ± 0.03	···
>2.5–10 cm	0.86 ± 0.19	0.89 ± 0.12	···
Total to 10 cm	1.13 ± 0.23	1.21 ± 0.15	···

† Mass of P was determined only to a 10-cm depth and was not sampled in cornfields.

iables of diameter, height, and wood specific gravity (Adjusted $R^2 = 0.99$). However, the sample size of 94 trees was relatively small, and only a small number of trees ≥70 cm dbh were included in this data set. In the future, potential errors resulting from the use of such allometric models would be substantially reduced by additions of large-tree data points to these models. This would likely be the single most effective means to improve plot scale estimates of tropical evergreen forest biomass.

Mass of C, N, S, and P in forest sites

Mass of C in aboveground biomass and soils of forests averaged 195 and 210 Mg/ha, respectively, and were substantially higher than previous estimates of C in TAGB (162 Mg/ha) and soils (70 Mg/ha) of TEFs in Mexico by Masera et al. (1997). In addition, they were substantially higher than mean values for C mass in aboveground biomass (150 Mg/ha) and soils (104 Mg/ha) obtained from tropical regions outside of Mexico and used by Riley et al. (1997) to model landscape-level C dynamics in the Los Tuxtlas Region. We quantified losses of ~95% of aboveground C as a result of conversion of forest to non-forest vegetation in the Los Tuxtlas region.

TABLE 9. Mass (Mg/ha) of C, N, and S in soils to 1-m depth at specific forest, pasture, and cornfield study sites in the Los Tuxtlas Region, Mexico. Values are means ± 1 SE.

Site	Carbon	Nitrogen	Sulfur
Forests			
SP	307 ± 15.2	29.3 ± 1.6	5.2 ± 0.17
SB	146 ± 1.0	13.0 ± 0.1	2.8 ± 0.08
SN	178 ± 11.4	17.3 ± 1.1	2.8 ± 0.10
Pastures			
P-8	163 ± 22.8	15.0 ± 2.0	2.6 ± 0.20
P-9	154 ± 9.8	14.6 ± 0.9	3.5 ± 0.28
P-33a	193 ± 8.5	19.6 ± 0.7	3.6 ± 0.28
P-33b	157 ± 11.1	14.6 ± 1.0	3.1 ± 0.18
Cornfields			
C-5	130 ± 3.6	13.0 ± 0.4	2.4 ± 0.09
C-32	291 ± 9.8	30.6 ± 1.2	5.4 ± 0.25
C-45	180 ± 6.2	16.2 ± 0.5	3.7 ± 0.13

Absolute losses of aboveground biomass and C mass due to the conversion of forests to pastures or cropland averaged 380 and 184 Mg/ha, respectively. These average losses are substantially greater than those in the Brazilian Amazon, where conversion of TEFs to pastures resulted in average losses of 275 Mg/ha of biomass and 135 Mg/ha of C (Kauffman et al. 1995, 1998, Guild et al. 1998). The higher losses associated with land-use change in the Los Tuxtlas Region relative to the Brazilian Amazon are due to both larger biomass and C mass in forests and smaller pools in pastures and croplands of the Los Tuxtlas Region vs. those in the Brazilian Amazon.

Soil carbon mass in forests of the Los Tuxtlas Region were large relative to C pools in forest soils measured elsewhere in the tropics. 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 from a variety of climatic regimes (Brown et al. 1993). Sánchez et al. (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). Soil C pools 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 the foci of land-use activities in tropical regions (Sánchez 1989).

In contrast to the roughly equal distribution of C mass between total aboveground biomass and soils, the majority of the N mass in forest sites was located in soil pools of all three land-cover types. Mass of N in TAGB was 1705 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 ~20 Mg/ha, N mass was 10 times higher in soils to a 1-m depth than in TAGB of forest sites. In addition, N mass in forest soils of the Los Tuxtlas Region was 2–3 times the amount of soil N to a 1-m depth found in tropical soils (Sánchez et al. 1983). As with soil C, the large soil N mass in forests of Los Tuxtlas is 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 in 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 coincided with large pools in soils; total P in surface soils was nearly 10-fold higher than in surface soils (i.e., 0–10 cm in depth) of forests in the Amazon reported by Kauffman et al. (1995).

Aboveground 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 (Buschbacher 1984, Fearnside 1992), but lower than values reported by Kauffman et al. (1998) for young pastures of the Amazon Basin (53–119 Mg/ha). The higher biomass of Amazonian pastures was due to larger amounts of residual downed woody debris at these sites compared to those of the Los Tuxtlas Region.

The average TAGB in cornfields (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 (Houghton et al. 1983, Fearnside and Guimarães 1996). Although TAGB of crops is small relative to that of forests, the variability across landscapes and regions is potentially very high. Increased resolution of cropland biomass and dynamics is needed to 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 woody 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 roughly 70% of TAGB, but was nonexistent in old cornfields. Woody debris is an important component in croplands and pastures throughout other regions of tropical America as well. For example, woody debris accounted for between 47% and 87% of TAGB in pastures of the Brazilian Amazon (Kauffman et al. 1998).

In pastures of the Los Tuxtlas Region, remnant trees ≥10 cm dbh accounted for a substantial portion of TAGB and C mass. On average, they comprised >50% of TAGB, and accounted for 75% of the TAGB in three of the seven pastures sampled. In addition, remnant trees in pastures of Los Tuxtlas are important foci for the regeneration of woody species (Guevara et al. 1992), and provide forage and shade for cattle, fruit for human consumption, and wood products for small landholders. Together, woody debris and remnant trees represent significant fractions of aboveground biomass and elemental pools of pastures and croplands, and quantification of the fate of these biomass components is critical to understanding the ecosystem dynamics following deforestation in the Los Tuxtlas Region and other regions of the tropics.

C, N, and S mass of soils in pastures and cornfields

Results from this study indicate that deforestation and land-use activities had a negligible impact on total C, N, and S soil pools in the Los Tuxtlas Region. Mass of these elements was highly variable and not substantially different among forest, pasture, and cornfield sites. These findings do not support previous estimates that C mass in soils would be reduced 20–50% following deforestation and land use (Schlesinger 1984, Detwiler 1986, Riley et al. 1997). In addition, although our sample sizes were relatively small and values were highly variable, soil C, N, and S mass was not substantially different among sites that differed in land-use type (i.e., pastures, cornfields), nor did they decrease with increased duration of land use. This latter result is remarkable in that four of the seven sites had experienced human land use for periods >30 yr. Conversely, it may be the case that the pastures and cornfields sampled in this study had simply not experienced sufficiently long periods of land use to cause significant losses of soil C, N, and S mass. Sampling soils of older pastures and cornfields in the future may indicate significant losses of C and nutrients from those soils. While constraints in land-use duration or differences in site characteristics that were not measured in this study may partially obscure losses resulting from land use, the lack of change in elemental pools of soils following deforestation regardless of the sampled periods of land use is likely due to the inherent capacity of Andosols to retain large amounts of soil organic matter regardless of land-use practices (Vitousek and Sanford 1986, Sánchez 1989, Veldkamp 1994).

In the Los Tuxtlas Region, R. Ahedo (*unpublished data*) found that root biomass to a 1-m depth in primary forests averaged 22 Mg/ha, and C mass of roots averaged 9 Mg/ha. These pools represent only 5% of the aboveground component for each of the respective pools in primary forests, and are substantially smaller than proposed values of 60 Mg/ha for belowground biomass of TEFs in Mexico (Masera et al. 1997). While conversion of forests to pastures resulted in losses of 81% of root biomass and C pools (R. Ahedo, *unpublished data*), the absolute losses of these pools were relatively small when compared to changes in aboveground pools in response to land-use change.

Aboveground vs. soil-pool dynamics

This study has characterized the differential responses of aboveground and soil pools of biomass, C, and nutrients to land-use change. Aboveground pools were greatly diminished by forest conversion, while soil pools remained relatively stable. Losses of C resulting from forest conversion represented nearly half (∼184 Mg/ha) of the combined aboveground and soil pools. These losses are high because nearly 50% of the total ecosystem C was stored in TAGB, and ∼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 pools during conversion of forests to pastures or cornfields were substantial, the fractions of the combined aboveground and soil pools of those elements lost were relatively small. This was due to the fact that the vast majority of N, S, and P pools were located in soils and were not significantly altered by land-use change. These results are similar to findings of other studies that demonstrated that changes in ecosystem pools are primarily driven by losses of aboveground biomass while soil pools of elements are affected to a much smaller degree (Kauffman et al. 1995, 1998, Trumbore et al. 1995).

Conclusions

Dirzo and García (1992) estimated that ∼91% of the 850-km^2 northern Los Tuxtlas Region will be deforested by the year 2000. 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 substantially reduced, the Los Tuxtlas Region will continue to function as a net source of C, N, and S to the atmosphere.

Acknowledgments

We thank Annalee Hughes and numerous members of the Sinaca family of Ejido Laguna Escondida, Veracruz, Mexico, for their assistance during all stages of fieldwork. 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. Tomas Carmona-Valdovinos, Raul Ahedo, and Franz Bongers provided previously unpublished data for the benefit of this project. Lisa Ellingson and Dian Cummings conducted much of the laboratory analysis, and Rodolfo Dirzo, Richard Waring, Greg Aplet, Michael Cairnes, Anthony Janetos, and two anonymous reviewers provided thoughtful reviews of previous drafts of the manuscript. We are also indebted to Rodolfo Dirzo for his invaluable assistance in facilitating the various stages of this project. 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

Barajas-Morales, J. 1987. Wood specific gravity in species from two tropical forests in Mexico. IAWA 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, Mexico. 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. United Nations 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.

Buschbacher, R. J. 1984. Changes in productivity and nutrient cycling following conversion of Amazon rainforest to pasture. Dissertation. University of Georgia, Athens, Georgia, USA.

Crews, T. E., K. Kitayama, J. H. Fownes, R. 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 Hawai'i. Ecology **76**:1407–1424.

Crow, T. R. 1978. Common regressions to estimate tree biomass in tropical stands. Forest Science **24**:110–114.

Crutzen, P. J., and M. O. Andreae. 1990. Biomass burning in the tropics: impact on atmospheric chemistry and biogeochemical cycles. Science **250**:1669–1678.

Cummings, D. L. 1998. Total aboveground biomass, forest volume, and tree density of Amazonian tropical forest delineated by projecto RADAMBRASIL in Northern Rondonia, Brazil. Thesis. Oregon State University, Corvallis Oregon, USA.

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 Mexico. Conservation Biology **6**:84–90.

Dirzo, R., E. González Soriano, and R. C. Vogt. 1997. Introducción general. Pages 3–6 *in* E. Gonzalez-Soriano, R. Dirzo, and R.C. Vogt, editors. Historia Natural de Los Tuxtlas. Universidad Nacional Autónoma de México, México, D.F., Mexico.

Dixon, R. K., S. Brown, R. A. Houghton, A. M. Solomon, M. C. Trexler and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. Science **263**:185–190.

Dixon, R. K., and J. Wisniewski. 1995. Global forest systems: an uncertain response to atmospheric pollutants and global climate change? Water, Air, and Soil Pollution **85**:101–110.

FAO/UNESCO. 1975. Soil maps of the world. Volume III. Mexico and Central America. Food and Agriculture Organization/UNESCO, Paris, France.

Fearnside, P. M. 1992. Carbon emissions and sequestration in forests: case studies from seven developing countries. 2. Brazil. U.S. Enviromental Protection Agency, Climate Change Division, Washington, D.C., USA.

Fearnside, P. M., and W. M. Guimarães. 1996. Carbon uptake by secondary forests in Brazilian Amazonia. Forest Ecology and Management **80**:35–46.

García, E. 1970. Los Climas del estado de Veracruz (según el sistema de clasificación climático de Koppen, modificado por la autora). Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Botánica **41**:3–42.

Golley, F. B., J. T. McGinnis, R. C. Clements, G. I. Child, and M. J. Duever. 1975. Mineral cycling in a tropical moist forest ecosystem. University of Georgia Press, Athens, Georgia, USA.

Gómez-Pompa, A. 1973. Ecology of the vegetation of Veracruz. Pages 73–148 *in* A. Graham, editor. Vegetation and vegetational history in northern Latin America. Elsevier, Amsterdam, The Netherlands.

Guevara, S., J. Laborde, D. Liesenfeld, and O. Barrera. 1997. Potreros 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 D.F., Mexico.

Guevara, S., J. Meave, P. Moreno-Casasola, and J. Laborde. 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. Journal of Vegetation Science **3**:655–664.

Guild, L. S., J. B. Kauffman, L. J. Ellingson, D. L. Cummings, and E. A. Castro. 1998. Dynamics associated with total aboveground biomass, C, and nutrient pools, and biomass burning in primary forest and pasture in Rondônia, Brazil during SCAR-B. Journal of Geophysical Research, **103**: 32091–32100.

Hao, W. M., M. H. Liu, and P. J. Crutzen. 1990. Estimates of annual and regional releases of CO_2 and other trace gases to the atmosphere from fires in the tropics, based on the FAO statistics for the period 1975–1980. Pages 440–462 *in* J. G. Goldammer, editor. Fire in the tropical biota: ecosystem processes and global challenges. Ecological studies 84. Springer-Verlag, New York, New York, USA.

Houghton, R. A., J. E. Hobbie, J. M. Melillo, B. Moore, B. J. Peterson, G. R. Shaver, and G. M. Woodwell. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: a net release of CO_2 to the atmosphere. Ecological Monographs **53**:235–262.

Hurlbert, S. J. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

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, D. F., Mexico.

Jordan, C. F. 1989. An Amazonian rain forest: the structure and function of a nutrient stressed ecosystem and the impact of slash-and-burn agriculture. Man and the biosphere series. Volume 2. Parthenon, Paris, France.

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, R. Babbitt. 1995. Fire in the Brazilian Amazon. 1. Biomass, nutrient pools, and losses in slashed primary forests. Oecologia **104**: 397–408.

Kauffman, J. B., and C. Uhl. 1990. Interaction of anthropogenic activities, fire, and rain forests in the Amazon Basin. Pages 117–133 *in* J.G. Goldammer, editor. Fire in the tropical biota: ecosystem processes and global challenges. Ecological Studies 84. Springer-Verlag, New York, New York, USA.

Levine, J. S. 1990. Global biomass burning: atmospheric, climatic and biospheric implications. EOS **71**:1075–1077.

Masera, O. R., M. J. Ordóñez, and R. Dirzo. 1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. Climatic Change **35**:265–295.

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, Madison, Wisconsin, USA.

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 Madison, Wisconsin, USA.

Ovington, J. D., and J. S. Olson. 1970. Biomass and chemical content of El Verde lower montane rain forest plants. Pages H53-H77 *in* H. T. Odum and R. F. Pigeon, editors. A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico. National Technical Information Service, Springfield Virginia, USA.

Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochemical Cycles **7**:811–841.

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. Garcia. 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.

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., M. P. Gichuru, and L. B. Katz. 1982. Organic matter in major soils of the tropical and temperate regions. International Congress of Soil Science **12**:99–114.

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.

Schimel, D., I. G. Enting, M. Heimann, T. M. L. Wigley, D. Raynaud, D. Alves, and U. Siegenthaler. 1995. CO_2 and the carbon cycle. Pages 39–66 *in* J.T. Houghton, L.G. Meira Filho, J. Bruce, H. Lee, B.A. Callander, E. Haites, N. Harris, and K. Maskell, editors. Climate change 1994: radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios. Cambridge University Press, Cambridge, UK.

Schlesinger, W. H. 1984. Soil organic matter: a source of atmosphere CO_2. Pages 111–127 *in* G. M. Woodwell, editor. The role of terrestrial vegetation in the global carbon cycle: measurement by remote sensing. SCOPE. John Wiley & Sons, 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, D.F., Mexico.

Townsend, A. R., P. M. Vitousek, and S. E. Trumbore. 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawai'i. Ecology **76**:721–733.

Trumbore, S. E., E. A. Davidson, P. Barbosa de Carmargo, D. E. Nepstad, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles **9**:515–528.

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.

Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. Forest Science **14**:20–26.

Veldkamp, E. 1994. Organic carbon turnover in three tropical soils under pasture after deforestation. Soil Science Society of America Journal **58**:175–180.

Vitousek, P. M. and R. L. Sanford, Jr. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics **17**:137–167.

Ward, D. E., R. A. Susott, J. B. Kauffman, R. E. Babbit, D. L. Cummings, B. Dias, B. N. Holben, Y. J. Kaufman, R. A. Rasmussen, and A. W. Setzer. 1992. Smoke and fire characteristics for Cerrado and deforestation burns in Brazil: Base-B Experiment. Journal of Geophysical Research **97**:14601–14619.