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Biomass, Carbon, and Nitrogen Pools in Mexican Tropical Dry Forest Landscapes

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ABSTRACT

Tropical dry forest is the most widely distributed land-cover type in the tropics. As the rate of land-use/land-cover change from forest to pasture or agriculture accelerates worldwide, it is becoming increasingly important to quantify the ecosystem biomass and carbon (C) and nitrogen (N) pools of both intact forests and converted sites. In the central coastal region of México, we sampled total aboveground biomass (TAGB), and the N and C pools of two floodplain forests, three upland dry forests, and four pastures converted from dry forest. We also sampled belowground biomass and soil C and N pools in two sites of each land-cover type. The TAGB of floodplain forests was as high as 416 Mg ha^{-1}, whereas the TAGB of the dry forest ranged from 94 to 126 Mg ha^{-1}. The TAGB of pastures derived from dry forest ranged from 20 to 34 Mg ha^{-1}. Dead wood (standing and downed combined) comprised 27%–29% of the TABG of dry forest but only about 10% in floodplain forest. Root biomass averaged 32.0 Mg ha^{-1} in floodplain forest, 17.1 Mg ha^{-1} in dry forest, and 5.8 Mg ha^{-1} in pasture. Although total root biomass was similar between sites within land-cover types, root distribution varied by depth and by size class. The highest proportion of root biomass occurred in the top 20 cm of soil in all sites. Total aboveground and root C pools, respectively, were 12 and 2.2 Mg ha^{-1} in pasture and reached 180 and 12.9 Mg ha^{-1} in floodplain forest. Total aboveground and root pools, respectively, were 149 and 47 kg ha^{-1} in pasture and reached 2623 and 264 kg ha^{-1} in floodplain forest. Soil organic C pools were greater in pastures than in dry forest, but soil N pools were similar when calculated for the same soil depths. Total ecosystem C pools were 306. The Mg ha^{-1} in floodplain forest, 141 Mg ha^{-1} in dry forest, and 124 Mg ha^{-1} in pasture. Soil C comprised 37%–90% of the total ecosystem C, whereas soil N comprised 85%–98% of the total. The N pools lack of a consistent decrease in soil pools caused by land-use change suggests that C and N losses result from the burning of aboveground biomass. We estimate that in México, dry forest landscapes store approximately 2.3 Pg C, which is about equal to the C stored by the evergreen forests of that country (approximately 2.4 Pg C). Potential C emissions to the atmosphere from the burning of biomass in the dry tropical landscapes of México may amount to 708 Tg C, as compared with 569 Tg C from evergreen forests.

Key words: tropical dry forest; tropical floodplain forest; tropical pastures; biomass; soil carbon; soil nitrogen; carbon pools; nitrogen pools; land-use change; deforestation.

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Introduction

The impact of land-use/land-cover change on biogeochemical cycles, particularly the carbon (C) and nitrogen (N) cycles, has been the subject of much attention in recent years (Vitousek and others 1997; Houghton 1999 and references therein; Walker and Steffen 1999). Quantification of the changes in pool size and fluxes of C and nutrients is fundamental to the understanding of the effects of land-use/land-cover change on ecosystem function. Inventories of pools and fluxes should be as complete as possible, but often only parts of ecosystems are investigated (Schulze and others 1999).

Dry forests are the most widely distributed land-cover type in the tropics. Tropical and subtropical dry forests are found in frost-free areas where the mean annual biotemperature (a calculation that reduces the effects of extreme temperatures) (Holdridge 1967 in Murphy and Lugo 1995) is higher than 17°C, the annual rainfall ranges from 250 to 2000 mm, and the ratio of potential evaporation to precipitation ranges from 1 to 2 (Murphy and Lugo 1986a, 1995). By these criteria, 49% of the vegetation of Central America and the Caribbean is considered dry forest, and about 42% of all tropical vegetation worldwide is dry forest (Murphy and Lugo 1995). Of the tropical forests of México, 64% are dry and 36% are evergreen forests (Masera and others 2001). Tropical dry forests are among the most heavily utilized and perturbed by human activities; a far greater proportion of dry forests has been degraded or converted than moist and wet forests (Murphy and Lugo 1986a; Maass 1995; Mooney and others 1995). In México, it has been estimated that only 27% of the area originally covered by tropical dry forests remained intact by the beginning of the 1990s (Trejo and Dirzo 2000). Ironically, they remain among the least studied of tropical ecosystems (Mooney and others 1995).

As in most regions of the Neotropics, rates of land conversion and land-cover change are very high in México. It has been estimated that 1.4%–1.9% of all Mexican tropical deciduous forest, and as much as 3.8% in the Chamela region (an area dominated by dry forest), is being converted annually to agriculture, pasture, or other uses (Masera and others 1997; Trejo and Dirzo 2000). Because of their broad areal extent within the tropical regions of the world, tropical dry forests are not only valuable in terms of their biological diversity, but also function as C sinks and sources of atmospheric C. Therefore, it is important to quantify the structure, biomass, and C pools of both intact dry forests and recently converted pastures.

Roots are an important component of ecosystem dynamics in tropical dry forests (Cuevas 1995), where they typically represent a larger percentage of the total biomass (33%) than in tropical lowland forests (12%) (Sanford and Cuevas 1996). Recent syntheses of the research on root biomass and distribution (Jackson and others 1996; Cairns and others 1997) suggest that some vegetation types, including tropical dry forests, have gone relatively unstudied. Indeed, there are very few estimates of root biomass below the top 20 cm of soil (for example, see Murphy and Lugo 1986b; Castellanos and others 1991; De Castro and Kauffman 1998).

This paper is part of a larger research project to quantify the dynamics of ecosystem biomass and the C and N pools of Mexican tropical forest landscapes (Hughes and others 1999, 2000; Jaramillo and others forthcoming). The objectives of this study were to quantify ecosystem pools in three distinct land-cover types of the Chamela region of the central Pacific coast of México: upland tropical dry forest, floodplain forests, and cattle pasture. To accomplish this, we quantified tree density, basal area, total aboveground biomass, and aboveground C and N pools. In addition, we quantified root biomass, root C and N pools, and soil organic C and N pools. From these data, we calculated total ecosystem biomass and C and N pools in forests and pastures.

Methods

Study Area

The study was conducted in the Chamela region, near the Pacific coast of Jalisco, México. All intact forest sites (except one) were sampled in the Estación de Biología Chamela of the Instituto de Biología, UNAM (19°30'N, 105°03'W). The pastures and one dry forest site were located in the Ejido San Mateo, approximately 10 km north of the station. The climate is highly seasonal and has a pronounced dry season. Precipitation averages 679 mm, distributed mostly from June to October; on average, about 31% of the total annual precipitation falls in September (García-Oliva and others 1995). Mean temperature is approximately 25°C, with a less than 5°C difference between the coolest and warmest months.

The landscape consists of low hills (50–160 m elevation) with steep convex slopes. The predominant lithology is Tertiary volcanic of rhyolitic and rhyodacitic composition and tuff (Campo 1995). Upland soils are relatively young, shallow (0.5–1-m depth) Typic Ustorthents. They are poorly structured, sandy loam in texture, derived from rhyolite, and have a pH of 6–6.5 (Solís 1993). Floodplain soils are alluvial, sandy (65%–75% sand), and relatively deep (1–1.5 m). They can be Typic Ustorthents or Typic Ustifluvents and are slightly more acidic than the upland soils, with a pH of 5.5–6.0 (C. Siebe personal communication).

The flora of the Chamela region is comprised of at least 1120 vascular plant species, 554 genera, and 124 families (Lott 1993). The plant families with the greatest number of species are the Leguminosae, Euphorbiaceae, Rubiaceae, and Bignoniaceae, and more than 10% of the species are endemic to the states of Jalisco and Colima, México.

Three land-cover types were sampled in this study. These included intact stands (with no recent human disturbances) of both upland dry forest and floodplain forest. In addition, we sampled cattle pastures derived from dry forest, which is the most common type of land conversion in the region. The dry forest, located on upland soils, is dominated by deciduous trees, 4–15 m in height, with a well-developed understory (Lott and others 1987). Common tree species include *Bursera* spp., *Jatropha standleyi, Caesalpinia eriostachys, C. coriaria, Cordia alliodora,* and *Lonchocarpus constrictus.* With few exceptions, species are leafless for several months each year; their phenology is driven by water availability (Bullock and Solís-Magallanes 1990). The floodplain forest, which corresponds to the "arroyo forest" of Lott and others (1987) and the "selva mediana subcaducifolia" (Miranda and Hernández X. 1963), occurs in the level floodplains with deeper soils and is composed of both evergreen and deciduous trees between 15 and 40 m high. Common tree species include *Brosimum alicastrum, Tabebuia donnell-smithii, T. rosea, Thouinidium decandrum, Astronium graveolens, Cynometra oaxacana,* and *Ficus insipida*. The floodplain forest once formed complex mosaics with dry forest, but extensive floodplain areas have been converted to agricultural and horticultural fields (Challenger 1998). Lianas are abundant in both forest types.

Following the conversion of dry forest via slash-and-burn, pastures are initially seeded with a mix of corn (*Zea mays*) and tropical forage grasses. Corn is harvested after the first growing season; thereafter, sites are used for cattle production. The perennial forage grasses commonly used are the C_4 species *Panicum maximum* Jacq. (guinea grass), which is considered highly palatable for cattle; *Cenchrus ciliaris* L. (buffel grass); and *Andropogon gayanus* L. The recommended stocking rate for pastures in this area is 1.9 ha per animal unit per year (COTECOCA 1989). Actual stocking rates vary due to rainfall variability and pasture age. A type of rotational grazing is common practice, but it is constrained by the individual landowner's resources (that is, owning an adequate number of pastures or having sufficient money to rent them).

Measurements

We sampled aboveground biomass in three intact stands of dry forest. The sites were named for the position on the slope in which they were located: Ridgeline, Middle Slope, and Lower Slope. The Ridgeline site was located at the Ejido San Mateo; the other sites were located at the Chamela Biological Station. We sampled aboveground biomass of two intact floodplain forests, the Búho and Garrapata sites, both of which were located at the Chamela Biological Station. Aboveground pools of three cattle pastures were also sampled. The ages of the pastures were not replicated and varied from recently converted pasture (1 year since conversion) to some of the oldest pastures in the region (13 years). The three pasture sites were Don Mario (13 years), La Vista (4 years), and El Cielo (sampled twice at ages of 1 and 2 years). The El Cielo site in fact occupied the same area as the Ridgeline dry forest site, which had been deforested and converted to pasture. This pasture was grazed for 2 months each year by a herd of 40 animals. Soils and root sampling were conducted in two dry forest sites (Middle Slope and Lower Slope), two floodplain sites (Búho and Garrapata), and two pastures (La Vista and Don Mario). One sampling was conducted for each land-cover type.

Aboveground biomass. All data were collected during the dry season, when leaves were absent from deciduous trees and litter mass was at its maximum. Because of their variable vegetation structure, plot sizes and approaches to the quantification of aboveground biomass varied for each of the forest types and pastures.

Tropical Floodplain Forest

The biomass of the more structurally diverse floodplain forests was measured in a nested design, closely following the methods used to determine total aboveground biomass (TAGB) of tropical evergreen forests described in Cummings and others (2002) and Hughes and others (2000). The diameter of trees greater than 30 cm diameter at breast height (dbh) were measured in a 75 × 105 m plot with large calipers and dbh tapes. The diameter of trees (and vines) 10–30 cm dbh were measured in a 25 × 105 m plot that was nested within the center of the larger plot. Subcanopy trees (more than

1.3 m in height but less than 10 cm dbh) were measured in 2 × 10 m plots located every 15 m along two transects 105 m in length (n = 16 plots) and 25 m apart. Both live and dead trees were sampled in this manner. Biomass of all trees was determined from allometric equations based on diameter (at 1.3 m) and tree height. The biomass of trees greater than 10 cm dbh was calculated using equations for tropical moist forest in Brown and others (1989). Vine biomass was determined using the equations developed by Putz (1983). Biomass of trees less than 10 cm dbh was calculated using the equations for small tropical evergreen forest trees developed by Jordan and Uhl (1978). Mass of dead trees was calculated as the trunk volume multiplied by the specific gravity of dead wood. For analysis and site description, we partitioned trees into categories based on their dbh (less than 10 cm, 10–30 cm, 30–50 cm, and more than 50 cm).

The aboveground biomass of plants less than 1.3 m high (tree and vine seedlings) was measured in sixteen 50 × 50 cm microplots established at the beginning of each subcanopy tree transect. All seedlings growing in the microplots were cut at ground level, placed in a paper bag, and transported to the laboratory for drying and weighing. Similarly, forest litter was collected in the same plot. In this study, "litter" is defined as all detached and dead leaves, flowers, fruits, seeds, bark fragments, and dead wood less than 2.5 cm in diameter. Downed wood debris was sampled using the planar intercept technique established at these same points (n = 16 transects per site) (Brown and Roussoupoulous 1974; Kauffman and others 1988; Van Wagner 1978). Each 15-m transect began at the same random point where the microplots were placed. The direction of the transect was randomly determined. All downed wood more than 7.5 cm in diameter that intersected the transect was measured; wood was partitioned into sound and rotten classes based on degree of decomposition. Wood pieces 2.5–7.5 cm in diameter that intersected a 10-m section of the transect were counted. Diameter for this size class was estimated through calculation of the quadratic mean diameter of 100 wood particles of this diameter range. Specific gravity for each class was determined through measurement of 50 randomly collected pieces. Specific gravity of the wood 2.5–7.5 cm in diameter was 0.42 g cm^3; for wood more than 7.5 cm in diameter, it was 0.52 g cm^3. No rotten wood was encountered in either of the two tropical floodplain forests.

Tropical Dry Forest

For all dry forest stands, TAGB was estimated in a 50 × 240 m macroplot. At 15-m intervals along the 240-m side of the macroplot, 2 × 50 m plots (or belt transects) were established (n = 16 per plot). All tree trunks with a diameter greater than 3 cm at 1.3 m in height were measured in each of these 2 × 50 m plots (Martínez-Yrízar and others 1992). From these data, we calculated basal area, tree density, and aboveground tree biomass. Aboveground tree biomass was determined using equations developed at Chamela by Martínez-Yrízar and others (1992). For the analysis, we separated trees into three different classes based on dbh—3–7.5, 7.5–20, and more than 20 cm. The height and diameter of all dead trees were measured in each plot. Mass of dead trees was calculated from determination of the trunk volume and large dead wood specific gravity.

Plants less than 3 cm dbh were sampled in sixteen 50 × 50 cm microplots. Microplots were randomly located at a point along the edge of the 50-m tree biomass plots. All plants with a dbh less than 3 cm rooted in the microplot were clipped at ground level, placed in a paper bag, and returned to the laboratory. In the laboratory, they were placed in drying ovens at 60°C. Litter mass was also collected in these microplots. All forest plants and litter samples occurring in the microplots were dried in the laboratory at 60°C.

Following the methods described above, dead wood was sampled nondestructively using the planar intercept technique. Specific gravity of the downed wood was 0.59 g cm^3 for sound wood 2.5–7.5 cm in diameter, 0.71 g cm^3 for sound wood more than 7.5 cm in diameter; and 0.61 g cm^3 for rotten wood more than 7.5 cm in diameter.

Pastures

The TAGB for the La Vista and Don Mario pastures was calculated from measurements in a 50 × 90 m macroplot established in the center of the pastures. Tree biomass was calculated via measurement of all trees that occurred in this large plot, using the same equations employed for dry forest. Mass of stumps was calculated through measurement of their volume and multiplied by the specific gravity of dead wood. Three 90-m transects were established, one on each edge and one bisecting the plot. At 10-m intervals along each transect, we collected grass/surface litter biomass in a 50 × 50 cm microplot (n = 10 per transect and 30 per pasture). All grass/litter materials consisting of live grass, dead grass, live and dead dicots, manure, and wood debris less than 2.5 cm in diameter were placed in a paper bag and transported to the laboratory for drying and mass determination. Wood debris was measured using the planar intercept technique. At the same point where grass/litter was collected, a transect in a random direction was measured following the same methods previously described for wood in dry forest. To calculate biomass, volume derived from the transects was multiplied by specific gravity of wood. Mean specific gravity of wood in pastures was 0.73 g cm^3 for wood 2.5–7.5 cm in diameter, 0.77 g cm^3 for sound wood more than 7.5 cm in diameter, and 0.23 g cm^3 for rotten wood more than 7.5 cm in diameter. In the El Cielo pasture, TAGB was collected in a similar manner, but with more transects and microplots. Grass/litter mass was calculated from 120 microplots measuring 50 × 50 cm, and wood mass was calculated from 120 planar intercept transects. Plot size for tree mass determination in these pastures was approximately 3 ha.

Root biomass. Sampling was conducted at the sites during the dry season between November 1994 and May 1995 (two in each land-cover type). A 60 × 50 m plot was established in the same area where aboveground biomass had been measured previously. One of the 60-m sides was used as a baseline, and five 50-m lines, spaced 15 m apart, were marked. One sampling point was located randomly along each line, and a 2 × 0.50 m microplot was carefully excavated. To ensure unbiased sampling, the direction of the long axis of each microplot was also determined randomly. Five microplots were excavated per site. We sampled roots in 10-cm intervals down to the 20-cm depth and at 20-cm intervals thereafter. The final depths varied according to site conditions, but most sampling in dry forest was done to a depth of 60 cm, where a hardpan layer was often encountered, making further excavation extremely difficult. By contrast, pits generally reached 120 cm in floodplain forests and 80 cm in pastures.

Roots were separated in the field by sieving the soil through a wire mesh. Roots were placed in plastic bags and transported to the laboratory at the field station. No attempt was made to separate live from dead roots. In the laboratory, roots collected at each depth were carefully washed and separated manually into the following four diameter classes: 4.0 mm or less, 4.1–10.0 mm; 10.1–20.0 mm, and more than 20 mm. Roots were then placed in paper bags and oven-dried at 70°C. Very large roots were weighed fresh and a subsample was dried. Fine roots (1 mm or less) were sampled separately to a depth of 40 cm with a soil core (5 cm in diameter) because the trench sampling underestimated their biomass. About 90% of the fine-root biomass in dry forest occurred within this soil depth (Castellanos and others 1991). Fine roots were separated on trays according to two different mesh sizes (2- and 0.8-mm), collected with tweezers, and placed in a petri dish with water to eliminate soil particles. They were then oven dried at 70°C.

Nutrient concentration and pools. In the laboratory, all aboveground samples were first dried to a constant weight at 65°C. Samples were then ground to pass through a 40-mesh (0.55-mm opening) screen using a Tecator Cyclotec 1093 sample mill (Tecator, Herdon, VA, USA). Samples of litter were collected from each site (n = 40 from the El Cielo pasture and Ridgeline forest; n = 6 for all other sites). The C and N concentrations of all tree and wood samples in forests were determined from samples collected from the Ridgeline forest (n = 40 for each component). The C and N concentrations of all wood components for pastures were collected in the El Cielo pasture (n = 40 for each component). Total C and N concentrations of each sample were determined using the induction furnace method with a Carlo-Erba NA series 1500 CNS analyzer (Fisions Instruments, Danvers, MA, USA) (Nelson and Sommers 1996).

To determine root C and N concentrations, samples were collected from two randomly selected microplots at each site and finely ground. Soils were sieved through a 2-mm mesh and dried at 80°C for 48 h. Total C in roots and soil was determined in a carbon analyzer (CM 5012; UIC, Inc.). Total N was determined with a Kjeldahl procedure and colorimetrically in a Technicon autoanalyzer. Inorganic C concentration was negligible (less than 0.001%) in the Chamela soils. Soil N concentrations were determined in two randomly chosen microplots from each site. Soil bulk density was determined at each depth in all microplots. Soil C and N pools were calculated from concentration and bulk density data. To compare soil pools between pastures and dry forest sites, bulk density was corrected for compaction effects (Detwiller 1986) in the 13-year-old Don Mario pasture, which showed a higher soil bulk density than dry forest.

Root C and N concentrations were analyzed with a posteriori analysis of variance (ANOVA) to determine differences due to diameter class and land-cover type. Means were compared with Tukey's HSD test when the ANOVA showed significant ($P <$ 0.05) treatment effects. All values are shown as means ± SE.

The TAGB, total root biomass, and the total-ecosystem biomass of all sites were calculated based on the sum of the mass of all individual components.

Table 1. Basal Area ($m^2\ ha^{-1}$) and Density (ha^{-1}) of Trees and Vines in Tropical Floodplain Forest

	Basal Area			Density		
	Garrapata	Búho	Mean	Garrapata	Búho	Mean
Live trees (dbh)						
0–10 cm	3.99 ± 1.34	6.56 ± 1.21	5.28 ± 1.29	6781 ± 816	12969 ± 1667	9875 ± 3094
10–30 cm	8.80	10.85	9.83 ± 1.025	335	456	396 ± 61
30–50 cm	6.96	6.56	6.76 ± 0.20	60	63	61 ± 2
> 50 cm	11.33	2.02	6.68 ± 4.66	28	6	17 ± 11
Live vines (dbh)						
0–10 cm	2.16 ± 0.66	1.56 ± 0.33	1.86 ± 0.30	6063 ± 1171	5344 ± 1192	5704 ± 360
10–30 cm	0.07	0	0.4 ± 0.04	4	0	2 ± 2
Dead trees (dbh)						
0–10 cm	0.08 ± 0.06	0.24 ± 0.18	0.16 ± 0.08	219 ± 108	438 ± 124	329 ± 110
10–30 cm	0.29	1.00	0.65 ± 0.36	23	42	33 ± 10
30–50 cm	0.23	0.28	0.26 ± 0.03	3	3	3 ± 0
> 50 cm	0	0.27	0.14 ± 0.14	0	1	0.5 ± 0.5
Dead vines (dbh)						
0–10 cm	0 ± 0	0.04 ± 0.03	0.02 ± 0.02	0 ± 0	188 ± 107	94 ± 94
Total	34.65	29.38	31.65 ± 2.27	13516	19472	16513 ± 2977

dbh, diameter at breast height
Values are the mean ± SE.

Similarly, the C and N pools in the biomass of each site were calculated by multiplying the mean concentration of each component by its respective mass.

Results

Density and Basal Area

The density of trees and vines, respectively, in the floodplain forests was 13,516 and 19,472 ha^{-1} (Table 1). approximately four- to fivefold greater than that of the dry forests (Table 2). Total basal area of the two floodplain forests, respectively, was 34.7 and 29.4 $m^2\ ha^{-1}$, or about 74% greater than that of the dry forests. Trees and vines less than 10 cm dbh comprised the greatest proportion of the plant density (a mean of 94% and 95% of the total plant density in the Búho and Garrapata sites, respectively). However, these plants comprised only 27% and 18%, respectively, of the total basal area of the sites. Mean density of trees greater than 30 cm dbh was 78 ha^{-1}, or less than 0.5% of the total tree density. Although density of trees greater than 50 cm dbh was only 28 ha^{-1} at the Garrapata site, they occupied 33% of the basal area. In contrast, at the Búho site, trees greater than 50 cm dbh comprised only 6.9% of the stand basal area. At this site, trees with a dbh of 10–30 cm comprised the largest proportion of stand basal area.

Mean basal area of the dry forests ranged from 20.8 to 27.1 $m^2\ ha^{-1}$ and increased from the Ridgeline plots to the Lower Slope plots (Table 2). Tree density (more than 3 cm dbh) in dry forests ranged from 3270 to 4325 ha^{-1}. The most abundant size class of trees was the 3.0–7.5-cm one (around 61% of the total tree density), whereas trees in the 7.5–20.5-cm size class comprised the greatest proportion of the basal area. Trees larger than 20.5 cm dbh comprised only around 14% of the stand basal area. The mean size of trees was larger in the Lower Slope plot than the Middle Slope or Ridgeline plots. For example, the mean basal area per individual tree in the greater than 20.5 cm dbh size class in the Lower Slope was 0.074 m^2, but it was less than 0.055 m^2 in the others. The density of standing dead trees ranged from 369 to 768 stems ha^{-1}.

Biomass

Aboveground. The semievergreen floodplain forests had a mean TAGB of 375 Mg ha^{-1} (Table 3), which was approximately three- to fourfold greater than in dry forests (Table 4). However, there was a difference of 150 Mg ha^{-1} in the TAGB of the two floodplain forests (Table 3). The greatest difference was in trees more than 50 cm dbh, where the biomass was 187 Mg ha^{-1} in the Garrapata site but only 31 Mg ha^{-1} at the Búho site. On average, trees at least 10 cm dbh comprised 74% of the TAGB. The dead components of the forests comprised 15% of the TAGB. Standing dead and downed wood debris averaged 37 Mg ha^{-1}, or about 10% of the TAGB.

From the Ridgeline to the Lower Slope plots, the total aboveground biomass of dry forest increased from 94 to 126 Mg ha^{-1} (Table 4). Similarly, live TAGB ranged from 60 to 80 Mg ha^{-1}. Trees of the 7.5–20.5 cm dbh class comprised a mean of 25% of the TAGB, whereas trees more than 20.5 cm dbh comprised only 18% of the TAGB. The mass of all dead vegetation components ranged from 34 to 46 Mg ha^{-1} (a mean of around 38% of the TAGB). Standing dead and downed wood averaged approximately 22 Mg ha^{-1}, or 19% of the TAGB. Litter and standing dead trees comprised a mean of 10% and 9% of the TAGB, respectively.

Conversion of dry forest to cattle pasture resulted in dramatic decreases in TAGB (Tables 4 and 5). The TAGB of cattle pastures ranged from 20 to 34 Mg ha^{-1}, or 18%–31% of the mean TAGB of the intact forests they replaced. Of all sampled pastures, we found the greatest TAGB in the 2-year-old El Cielo site and the lowest TAGB in the 13-year-old Don Mario site. The greatest differences in biomass of these two sites was in residual downed wood (more than 7.6 cm in diameter), which originated from the forests that had occupied these sites prior to their conversion to pasture. In addition, biomass of the grass/litter component in the 2-year-old El Cielo site was almost twice that of the other sites. In the younger El Cielo and La Vista pastures, the standing trees/stumps category was comprised largely of stumps. In contrast, at the Don Mario site, this category was made up largely of invasive trees.

On average, biomass of the grass and surface litter comprised only 33% of the TAGB of cattle pastures. Standing trees/stumps comprised 27% of the TAGB. Interestingly, the residual wood debris comprised 53% of the mean TAGB in the 1-year-old El Cielo cattle pasture and 26% of the TAGB in the 13-year-old Don Mario pasture, which had been burned five or six times.

Roots. Root biomass varied by land-cover type and was affected by the conversion of dry forest to pasture. The tropical floodplain forest had the highest root biomass, with a mean of 32 Mg ha^{-1}, whereas root biomass in the tropical dry forest was 17 Mg ha^{-1}. Root biomass in pasture was less than 35% that of the dry forest (6 Mg ha^{-1}). Total root biomass varied only slightly between sites within each land-cover type (Figure 1).

Fine-root (1 mm or less) biomass in the 0–40-cm depth was 1.9 Mg ha^{-1} (Búho) and 1.7 Mg ha^{-1} (Garrapata) in the floodplain forest. It was 1.7 Mg ha^{-1} (Middle Slope) and 1.5 Mg ha^{-1} (Lower Slope)

Table 2. Basal Area (m^3 ha^{-1}) and Density (ha^{-1}) of Trees in Tropical Dry Forest Stands

	Basal Area				Density			
	Ridgeline	Middle Slope	Lower Slope	Mean	Ridgeline	Middle Slope	Lower Slope	Mean
Live trees (dbh)								
3.0–7.5 cm	4.83 ± 0.36	3.95 ± 0.41	4.31 ± 0.46	4.36 ± 0.26	2720 ± 185	2288 ± 244	2431 ± 245	2480 ± 127
7.5–20.5 cm	8.58 ± 0.72	7.92 ± 0.97	12.74 ± 1.31	9.74 ± 1.51	765 ± 72	731 ± 83	1125 ± 103	873 ± 126
> 20.5 cm	3.94 ± 0.87	7.44 ± 2.14	6.01 ± 2.07	5.80 ± 1.02	72 ± 14	150 ± 40	81 ± 25	101 ± 25
Dead trees	3.49 ± 0.54	2.69 ± 0.86	4.00 ± 1.00	3.39 ± 0.38	768 ± 88	513 ± 116	369 ± 52	550 ± 117
Cactus	0 ± 0	0.5 ± 0.4	0 ± 0	0.17 ± 0.17	0 ± 0	38 ± 2	0 ± 0	13 ± 13
Total	20.84	22.50	27.06	23.47 ± 1.86	4325	3270	4006	4071 ± 214

dbh, diameter at breast height
Values are the mean ± SE.

Table 3. Total Aboveground Biomass (Mg ha^{-1}) of Tropical Floodplain Forest

	Garrapata	Búho	Mean
Live biomass			
Trees (dbh)			
0–10 cm	17.04 ± 3.27	28.01 ± 5.32	22.53 ± 5.49
10–30 cm	76.76	94.51	85.64 ± 8.88
30–50 cm	85.99	76.94	81.46 ± 4.53
> 50 cm	186.9	30.63	108.76 ± 78.14
Vines (dbh)			
0–10 cm	22.92 ± 6.69	17.41 ± 3.73	20.17 ± 2.78
10–30 cm	0.56	0	0.28 ± 0.28
Total live	390.17	247.5	318.84 ± 71.34
Necromass			
Standing dead (dbh)			
0–10 cm	0.18 ± 0.13	0.80 ± 0.69	0.49 ± 0.31
10–30 cm	0.79	6.76	3.78 ± 2.99
30–50 cm	1.01	2.18	1.60 ± 0.59
> 50 cm	0	1.64	0.82 ± 0.82
Dead vines (dbh)			
0–10 cm	0.00 ± 0.00	0.16 ± 0.13	0.08 ± 0.08
Litter	13.10 ± 1.10	12.55 ± 1.29	12.83 ± 0.28
Downed wood debris			
2.5–7.6 cm diam.	25.47 ± 5.76	17.85 ± 3.30	21.66 ± 3.81
7.6–20.5 cm diam. sound	20.89 ± 9.99	1.69 ± 0.91	11.29 ± 9.60
7.6–20.5 cm diam. rotten	0.00 ± 0.00	0.41 ± 0.29	0.21 ± 0.21
> 20.5 cm diam.	0.00 ± 0.00	6.56 ± 6.35	3.28 ± 3.28
Total dead	61.44	50.6	56.02 ± 5.42
Total aboveground biomass	451.61	301.1	374.86 ± 76.76

dbh, diameter at breast height
Values are the mean ± SE.

Table 4. Total Aboveground Biomass (Mg ha^{-1}) of Tropical Dry Forest

	Ridgeline	Middle Slope	Lower Slope	Mean
Live biomass				
Seedlings/vines	8.53 ± 2.29	2.26 ± 1.15	5.49 ± 1.93	5.42 ± 1.81
Trees				
3–7.5 cm diam.	15.64 ± 2.20	11.49 ± 1.17	18.00 ± 1.83	15.04 ± 1.90
7.5–20.5 cm diam.	24.28 ± 2.14	23.04 ± 2.81	38.80 ± 4.14	27.71 ± 5.06
> 20.5 cm diam.	11.46 ± 2.52	30.19 ± 10.05	18.45 ± 5.97	20.03 ± 5.46
Cactus	0 ± 0	1.47 ± 1.17	0 ± 0	0.49 ± 0.49
Total live	59.91	68.45	80.74	69.70 ± 6.04
Necromass				
Standing dead	9.21 ± 1.51	7.81 ± 2.51	12.53 ± 2.90	9.85 ± 1.40
Litter	8.29 ± 0.64	13.65 ± 1.84	11.33 ± 0.88	11.09 ± 1.55
Downed wood debris				
2.5–7.6 cm diam.	5.84 ± 0.84	12.76 ± 1.53	10.63 ± 1.83	9.74 ± 2.05
> 7.6 cm diam. sound	7.17 ± 1.77	7.13 ± 3.25	7.96 ± 3.24	7.42 ± 0.27
> 7.6 cm diam. rotten	3.49 ± 1.07	6.52 ± 3.29	3.27 ± 1.57	4.43 ± 1.05
Total dead	34	47.87	45.72	42.53 ± 4.31
Total aboveground biomass	93.91	116.32	126.46	112.23 ± 9.62

Values are the mean ± SD.

Table 5. Total Aboveground Biomass (Mg ha^{-1}) of Pastures Converted from Tropical Dry Forest

	El Cielo (1 y)	El Cielo (2 y)	La Vista (4 y)	Don Mario (13 y)	Mean
Grasses and surface litter	7.1 ± 0.5	13.1 ± 1.1	7.3 ± 0.7	7.9 ± 0.9	8.9 ± 1.4
Downed wood debris					
2.5–7.6 cm diam.	6.2 ± 0.6	5.0 ± 0.8	4.1 ± 0.9	3.4 ± 1.0	4.7 ± 0.6
> 7.6 cm diam.	10.5 ± 1.2	10.5 ± 1.2	2.1 ± 0.7	1.8 ± 0.8	6.2 ± 2.5
Standing trees/stumps	7.7	5.9	8.5	6.7	7.2 ± 0.6
Total	31.4	34.4	22.0	19.9	26.9 ± 3.6

Values are the mean ± SE where appropriate.

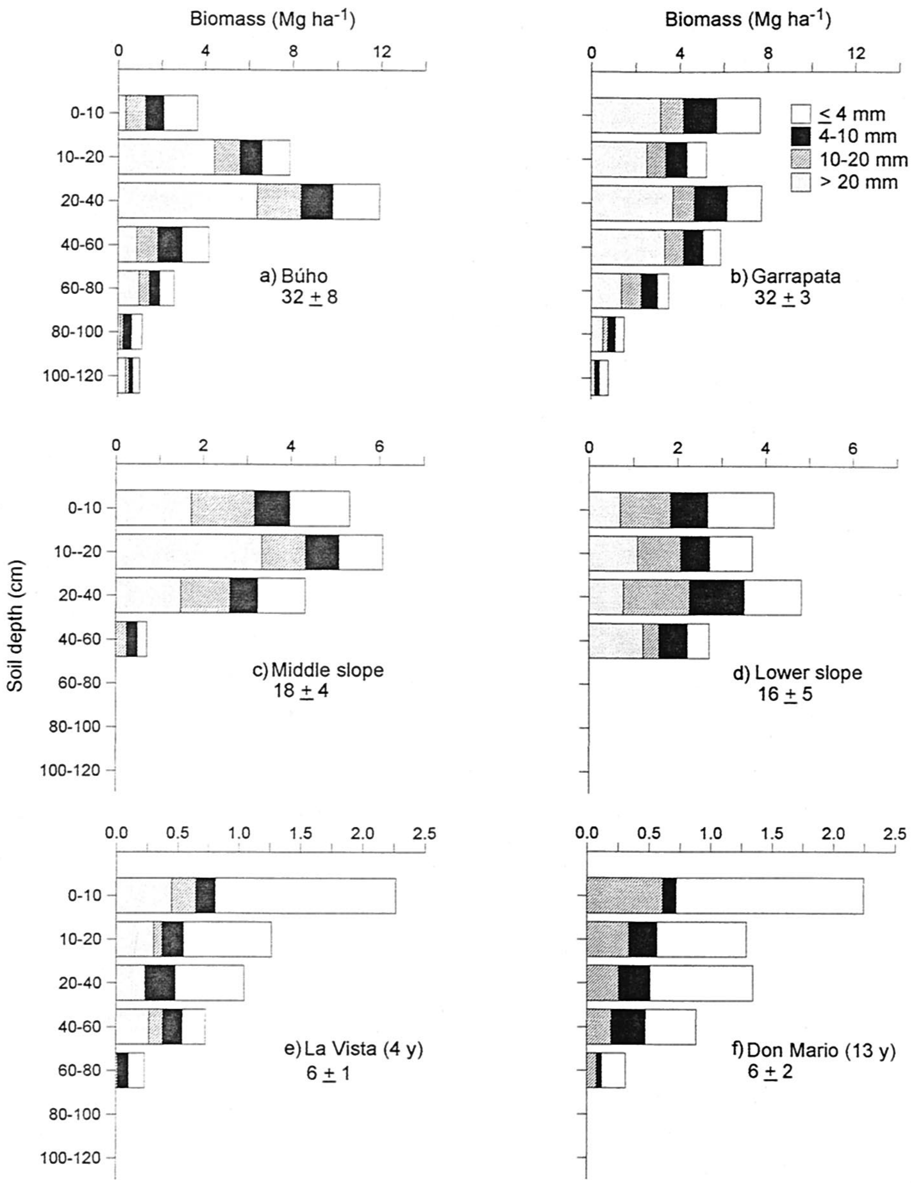

Figure 1. Biomass (Mg ha^{-1}) by root diameter class (mm) and soil depth (cm) in the tropical floodplain forest (**a**, **b**), tropical dry forest (**c**, **d**), and pastures (**e**, **f**) in the Chamela region of western México. Total root biomass (Mg ha^{-1}), (mean ± SE) is included for each site. All values are the means of five microplots per site.

in the dry forest, and it was 1.8 Mg ha^{-1} (La Vista 4-year-old) and 1.9 Mg ha^{-1} (Don Mario 13-year-old) in pasture. Between 40% and 48% of the fine-root biomass occurred in the top 10 cm of soil in the forests, whereas 52%–57% occurred in the top 10 cm of soil in the pastures.

Although total root biomass was similar within land-cover types, root distribution varied by depth and by size class (Figure 1). For example, the highest biomass of small roots (4 mm or less) in the floodplain forests occurred between the 20- and the 40-cm depth in the Búho site (2.1 Mg ha^{-1}) but at the 0–10-cm depth in the Garrapata site (2.0 Mg ha^{-1}). Similarly, the largest roots (more than 20 mm) showed conspicuous differences in their distribution with depth (Figure 1a and b). Total biomass of roots measuring 4 mm or less in floodplain forests was 7.6 Mg ha^{-1} (Búho) and 6.5 Mg ha^{-1} (Garrapata) and represented 24% and 20%, respectively, of the total root biomass. The biomass for the the largest roots (more than 20 mm) was 13.5 Mg ha^{-1} (Búho) and 14.7 Mg ha^{-1} (Garrapata) and represented 42% and 46%, respectively, of the total root biomass. On average, 85% of the total root biomass was found in the top 60 cm of the soil.

We also found site variation in the distribution of root biomass by size class and depth in the dry forest, particularly among the largest root sizes (Figure 1c and d). For example, at the Middle Slope, the greatest biomass of roots greater than 20 mm was in the 10–20-cm depth (3.3 Mg ha^{-1}), whereas in the Lower Slope their maximum value was recorded at 40–60 cm (1.2 Mg ha^{-1}). Total biomass of roots 4 mm or less was 3.6 Mg ha^{-1} at the Middle Slope and 4.3 Mg ha^{-1} at the Lower Slope and comprised 22% and 28%, respectively, of the total root biomass. The biomass of roots more than 20 mm was 6.6 Mg ha^{-1} at the Middle Slope and 3.8 Mg ha^{-1} at the Lower Slope and represented 40% and 25% of the total root biomass, respectively. On average, 88% of root biomass in the dry forests was in the top 40 cm of soil.

The different-aged pastures showed some conspicuous differences in biomass among size classes. The most obvious was the absence of roots larger than 20 mm in the 13-year-old Don Mario pasture (Figure 1e and f), whereas the biomass of these roots in the 4-year-old La Vista pasture was 1.3 Mg ha^{-1}. The biomass distribution of roots 4 mm or less according to depth was very similar between pastures. Their total biomass was 3.1 Mg ha^{-1} at La Vista and 3.7 Mg ha^{-1} at Don Mario and comprised 55% and 61% of the total root biomass, respectively. This was a much higher percentage than in dry forest. Between 80% and 83% of the root biomass in pastures occurred in the top 40 cm of the soil.

The highest proportion of root biomass was concentrated in the top 20 cm of soil at all of the sites and was particularly high in dry forest and pastures, where from 51% to 69% (dry forest) and 58% to 64% (pastures) of the root biomass occurred at this depth.

The root–shoot (R:S) ratios (live + dead roots/live + standing dead biomass) were 0.12 (Búho) and 0.08 (Garrapata) in the floodplain forest, 0.21 (Middle Slope) and 0.19 (Lower Slope) in the dry forest, and 0.35 (La Vista 4-year-old) and 0.42 (Don Mario 13-year-old) in the pasture.

Total ecosystem biomass was highest in the floodplain forest, with 333 Mg ha^{-1} at the Búho site and 484 Mg ha^{-1} at the Garrapata site (mean, 408 Mg ha^{-1}). Total biomass in the dry forest was 133 Mg ha^{-1} at the Middle Slope site and 145 Mg ha^{-1} at the Lower Slope site (mean, 139 Mg ha^{-1}). These values were five times higher than the those for ecosystem biomass of pastures, which were 28 and 26 Mg ha^{-1} in the La Vista and Don Mario sites, respectively (mean, 27 Mg ha^{-1}).

C and N Pools

Aboveground. The C concentrations did not vary greatly among the components that comprised the TAGB of either forests or pastures (Table 6). In forests, C concentrations of components ranged from about 40% to 52%. Carbon concentrations of the aboveground pasture components ranged from about 42% to 48%. Concentrations of N in forests ranged from 0.64% in trees to 1.74% in the litter of floodplain forests. The N concentration in the forest litter was much higher than that of the litter in pastures (1.5% or more in forests and 0.62% in pasture). The N concentration of the biomass components in pastures ranged from 0.44% for the dead wood to 0.64% for standing trees. The C:N ratio in forest litter was approximately 26, as compared to 68 for pasture litter.

Total aboveground C pools ranged from a mean of 12 Mg ha^{-1} in pastures to 180 Mg ha^{-1} in floodplain forests (Figure 2). The mean aboveground C pools of the intact dry forest were 54 Mg ha^{-1}. Aboveground C pools of the pastures were approximately 23% of that of the dry forest. Given the similarity of the C concentrations among biomass components, the distribution of the C pools did not vary greatly from the manner in which biomass was distributed within the land-cover types. Trees comprised 81% of the aboveground C pools in floodplain forest and 63%–70% of the aboveground C pool in dry forest. In the newly converted (1-year-old) El Cielo pasture, residual wood comprised 55% of the 14.7 Mg ha^{-1} C pool. In contrast, wood comprised 27% of the 9 Mg ha^{-1} C pool in the 13-year-old Don Mario pasture. C comprised 47.7%

Table 6. Concentration (%) of Carbon (C) and Nitrogen (N) of Aboveground Components Used to Calculate the Aboveground Pools of Tropical Dry Forest, Floodplain Forest, and Converted Pastures

Site component	C	N	C:N Ratio	Source and Sample Size
Pastures				
Grasses/litter	42.19	0.62	68	Mean of samples from the four pastures ($n \geq 10$/site)
Dead wood 2.5–7.5 cm diam.	48.12	0.44	109	Steele (1998); mean of El Cielo pastures, 1994 ($n = 27$) and 1995 ($n = 10$)
> 7.5 cm diam.	47.84	0.45	106	Steele (1998); mean of El Cielo pastures, 1994 ($n = 35$) and 1995 ($n = 20$)
Trees/stumps	48.09	0.64	75	Calculated by determination of concentrations and biomass proportion of eight stem diameter categories ($n \geq 10$ for each stem size)
Forests				
Seedlings/vines	46.16	1.09	42	Means of dry forest sites ($n = 5$/site)
Trees	48.09	0.64	75	Calculated by determination of concentrations and biomass proportion of eight stem diameter categories ($n \geq 10$ for each stem size)
Standing dead trees	51.58	0.86	60	From Ridgeline forest ($n = 5$)
Litter—TDF	40.11	1.5	27	Site means ($n = 10$/site)
Litter—TFF	44.15	1.74	25	Site means ($n = 8$/site)
Dead wood	49.03	0.68	72	From Ridgeline forest ($n = 5$)
Dead wood 2.5–7.5 cm diam.	49.03	0.68	72	From Ridgeline forest ($n = 5$)
> 7.5 cm diam. sound	51	0.66	77	From Ridgeline forest ($n = 5$)
> 7.5 cm diam. rotten	51.58	0.86	60	From Ridgeline forest ($n = 5$)

TDF, tropical dry forest; TFF, tropical floodplain forest

of the TAGB in floodplain forest, 47.9% in dry forest, and 46.1% in pastures.

Total aboveground N pools in floodplain forest were a mean of 2623 kg ha^{-1}. The mean N pools of dry forest were 873 kg ha^{-1}; pasture N pools were 149 kg ha^{-1}, which was about 17% of the dry forest pools (Figure 2). Aboveground N pools may have been underestimated, particularly in pastures, because the N concentration of foliage would have been higher in the rainy season than in the dry season when the samples were collected. In the two floodplain forests, trees comprised 74% and 76%, respectively, of the total aboveground N pool. In dry forest, the trees comprised 50%–55% of the aboveground N pool. Trees made up a smaller proportion of the total N pool than either biomass or C pools. Conversely, in dry forest, litter comprised 10% of the TAGB but 17%–22% of the total aboveground N pool. Similarly in the two floodplain forests, litter comprised 3.4% of the TAGB but 6.2% and 8.8%, respectively, of the total aboveground N pool (that is, 197 and 188 kg ha^{-1} in the Garrapata and Búho sites, respectively). In pastures, total aboveground N pools ranged from 167 kg ha^{-1} in the El Cielo pasture to 115 kg ha^{-1} in the Don Mario pasture; the principal difference was the smaller N pool in residual wood. At the site level, N comprised 0.70 ± 0.01% and 0.78 ± 0.01% of the aboveground biomass in floodplain and dry forests, respectively. In addition to a decrease in the absolute size of the N pool in pastures, N comprised only 0.55 ± 0.01% of the TAGB. Site level C:N ratios of the TAGB were 68 ± 1 in floodplain forest, 62 ± 1 in dry forest, and 83 ± 2 in cattle pasture.

Roots. Root C concentrations ranged from 33.4% to 43.4% across all sites and size classes (Table 7). There were no differences in root C concentrations among land-cover types (40.1% for floodplain forest, 39.0% for dry forest, and 40.2% for pastures). Comparisons within each land-cover type showed that there were no significant differences between sites within forests. However, the 13-year-old Don Mario pasture had significantly ($P < 0.01$) higher mean root C concentrations (42%) than the 4-year-old La Vista pasture (38%). Averaged over land-cover types, the mean C concentration of small (4 mm or less) roots (38%) was significantly lower ($P < 0.01$) than in the other size classes (40.2%–40.5%).

Root N concentrations varied between 0.49% and 1.65% across all sites and size classes (Table 7). They differed significantly among land-cover types

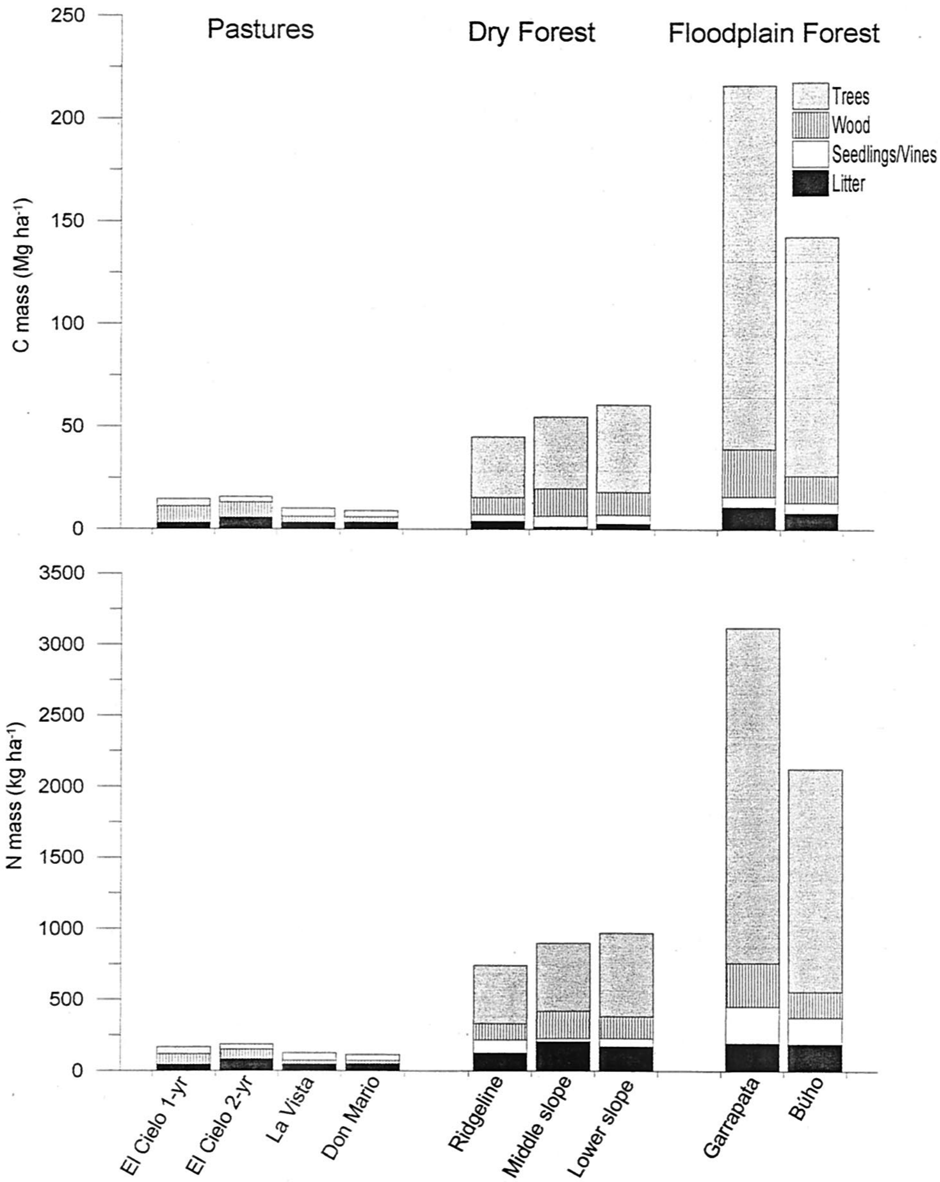

Figure 2. Total aboveground carbon (C) (Mg ha^{-1}) and nitrogen (N) (kg ha^{-1}) pools in pastures, tropical dry forest, and floodplain forest of the Chamela region of western México.

($P < 0.001$) when averaged across diameter class and were higher in the floodplain forest (0.88% ± 0.07) than in the dry forest (0.63% ± 0.03) and pastures (0.78% ± 0.04) ($P < 0.05$). There were also significant ($P < 0.001$) differences among the root size classes when averaged across land-cover types. The largest roots (more than 20 mm) had lower N concentrations than the smallest size classes (4 mm or less and 4–10 mm) ($P < 0.05$). The C:N ratio increased with root diameter class: 39.3 ± 4.0 (4 mm or less), 56.3 ± 4.0 (4–10 mm), 65.9 ± 4.1 (10–20 mm), and 69.4 ± 4.0 (more than 20 mm).

The total root C pool, as was the case with aboveground and root biomass, was greatest in the floodplain forest (13 Mg ha^{-1}), followed by the dry forest (7 Mg ha^{-1}), which was about three times greater than in the pastures (2 Mg ha^{-1}) (Table 8). Similarly, the root N pool was highest in the floodplain forest (264 kg ha^{-1}) followed by the dry forest (106 kg ha^{-1}), which was 2.4 times greater than in the pastures (48 kg ha^{-1}).

Soil. Mean soil C concentrations were slightly lower in dry forest than in floodplain forest and pasture at all depths (Table 9). Soil C concentrations were quite variable between sites within both forest types but were similar between pastures. Concentrations of C were highest in the top 10 cm of the soil (range, 1.63%–3.05%) and decreased with depth. For example, concentrations at the

Table 7. Root Carbon (C) and Nitrogen (N) concentrations (%) by Diameter Class of Tropical Floodplain Forest, Tropical Dry Forest, and Pastures

	Root Diameter							
	≤ 4 mm		4–10 mm		10–20 mm		> 20 mm	
	C	N	C	N	C	N	C	N
Floodplain forest								
Búho	39.6 ± 0.7	1.65 ± 0.27	41.2 ± 0.6	0.91 ± 0.10	40.1 ± 1.5	0.52 ± 0.11	40.3 ± 0.6	0.61 ± 0.08
Garrapata	39.3 ± 0.5	1.10 ± 0.12	39.9 ± 0.6	0.94 ± 0.10	40.5 ± 0.6	0.76 ± 0.05	40.2 ± 0.8	0.52 ± 0.08
Dry forest								
Middle Slope	37.2 ± 1.4	0.88 ± 0.06	41.0 ± 0.4	0.67 ± 0.05	40.8 ± 0.4	0.53 ± 0.05	40.0 ± 2.1	0.57 ± 0.08
Lower Slope	37.8 ± 1.1	0.72 ± 0.05	38.4 ± 1.3	0.53 ± 0.05	38.4 ± 0.5	0.66 ± 0.13	38.7 ± 1.4	0.49 ± 0.10
Pastures								
La Vista (4 y)	33.4 ± 1.4	0.94 ± 0.15	37.0 ± 3.5	0.75 ± 0.10	40.7 ± 1.3	0.59 ± 0.03	40.4 ± 2.1	0.74 ± 0.18
Don Mario (13 y)	41.0 ± 0.9	0.90 ± 0.03	43.4 ± 1.1	0.79 ± 0.05	42.7 ± 1.7	0.70 ± 0.10	NP	NP

NP, not present
Values are the mean ± SE.

Table 8. Total Ecosystem Carbon and Nitrogen Pools in the Tropical Dry Forest Region of Chamela, Jalisco, México

	Tropical Floodplain Forest				Tropical Dry Forest				Pasture			
	Búho	Garrapata	Mean	SE	Middle Slope	Lower Slope	Mean	SE	La Vista	Don Mario	Mean	SE
Carbon (Mg ha^{-1})												
Aboveground	142.8	216.5	179.7	36.9	55.8	60.7	58.3	2.5	10.2	9.1	9.7	0.5
Belowground												
Roots	12.9	12.8	12.9	1.7	6.4	6.9	6.7	1.1	1.9	2.5	2.2	0.4
Soil	80.9	146.6	113.8	32.9	83.7	68.6	76.2	7.6	111.8	113.1	112.5	0.6
Total	236.6	375.9	306.3		145.9	136.2	141.1		123.9	124.7	124.3	
Soil to 60 cm	60.9	100.7	80.8	19.9	83.7	68.6	76.2	7.6	93.8	99.0	96.4	2.6
Total to 60 cm	216.6	330.0	273.3		145.9	136.2	141.1		105.9	110.6	108.3	
Nitrogen (kg ha^{-1})												
Aboveground	2125	3121	2623	498	909	971	940	31	126	115	120	6
Belowground												
Roots	267	261	264	3	99	112	106	6	44	51	47	3
Soil	19602	13857	16730	2873	7107	6211	6659	448	7407	9214	8310	904
Total	21994	17239	19617		8115	7293	7704		7577	9379	8478	
Soil to 60 cm	15300	10070	12685	2615	7107	6211	6659	448	5692	7660	6676	984
Total to 60 cm	17692	13452	15572		8115	7293	7704		5863	7825	6844	

Totals to 60 cm in the soil are included to compare ecosystems at similar depths.

20–40-cm depth were only 47%–64% of those in the top 10 cm of soil.

Soil N concentrations were generally higher in floodplain forest than in dry forest and pasture, down to 40 cm (Table 9). No apparent differences were found between dry forest and pasture. In contrast to C, soil N concentrations were generally more similar between sites within each land-cover type. As for soil C, N concentrations decreased with soil depth in all land-cover types.

Soil bulk densities were generally lowest at the 0–10-cm depth and increased with depth. Among all sites, soil bulk density ranged from 1.13 ± 0.06 g cm^{-3} at 0–10 cm in the floodplain forest Garrapata site to 1.55 ± 0.14 g cm^{-3} at the 40–60-cm depth in the dry forest Middle Slope site (mean ± SE). The

Table 9. Soil Carbon and Nitrogen Concentrations (%) by Depth in Tropical Floodplain Forest, Tropical Dry Forest, and Pastures

		Tropical Floodplain Forest			Tropical Dry Forest			Pasture		
	Depth (cm)	Búho	Garrapata	Mean	Middle Slope	Lower Slope	Mean	La Vista	Don Mario	Mean
Carbon										
	0–10	1.75 ± 0.39	3.05 ± 0.55	2.40	2.54 ± 0.38	1.63 ± 0.28	2.08	2.30 ± 0.35	2.36 ± 0.22	2.33
	10–20	0.83 ± 0.14	1.64 ± 0.27	1.24	1.44 ± 0.18	0.85 ± 0.09	1.14	1.48 ± 0.36	1.33 ± 0.20	1.40
	20–40	0.69 ± 0.18	1.04 ± 0.13	0.86	0.77 ± 0.04	0.66 ± 0.10	0.72	0.85 ± 0.14	0.80 ± 0.14	0.82
	40–60	0.47 ± 0.06	0.72 ± 0.08	0.60	0.57 ± 0.10	0.53 ± 0.11	0.55	0.78 ± 0.09	0.75 ± 0.24	0.76
	60–80	0.32 ± 0.06	0.67 ± 0.05	0.50				0.75 ± 0.10	0.49 ± 0.05	0.62
	80–100	0.28 ± 0.06	0.60 ± 0.06	0.44						
	100–120	0.26 ± 0.03	0.48 ± 0.08	0.37						
Nitrogen										
	0–10	0.39 ± 0.097	0.34 ± 0.089	0.36	0.12 ± 0.002	0.15 ± 0.011	0.14	0.12 ± 0.024	0.14 ± 0.036	0.13
	10–20	0.19 ± 0.017	0.14 ± 0.029	0.16	0.09 ± 0.002	0.11 ± 0.016	0.10	0.05 ± 0.027	0.09 ± 0.004	0.07
	20–40	0.19 ± 0.012	0.11 ± 0.017	0.15	0.07 ± 0.004	0.08 ± 0.006	0.08	0.12 ± 0.051	0.07 ± 0.006	0.10
	40–60	0.15 ± 0.010	0.06 ± 0.004	0.10	0.07 ± 0.003	0.04 ± 0.024	0.06	0.05 ± 0.009	0.07 ± 0.014	0.06
	60–80	0.05 ± 0.005	0.05 ± 0.005	0.05				0.06 ± 0.013	0.06 ± 0.014	0.06
	80–100	0.05 ± 0.009	0.04 ± 0.006	0.04						
	100–120	0.06 ± 0.003	0.03 ± 0.009	0.04						

Values are the mean ± SE.

Table 10. Proportional Distribution of Soil Carbon (C) and Nitrogen (N) with Depth in the Tropical Dry Forest Region of Chamela, Jalisco, México

		Floodplain Forest		Dry Forest		Pasture	
	Depth (cm)	Búho	Garrapata	Middle Slope	Lower Slope	La Vista	Don Mario
Soil C							
	0–10	0.24	0.24	0.36	0.32	0.25	0.28
	10–20	0.13	0.14	0.23	0.18	0.17	0.18
	20–40	0.20	0.17	0.23	0.27	0.20	0.22
	40–60	0.14	0.12	0.18	0.23	0.19	0.20
	60–80	0.10	0.12			0.19	0.12
	80–100	0.09	0.11				
	100–120	0.09	0.09				
Soil N							
	0–10	0.24	0.28	0.22	0.28	0.20	0.21
	10–20	0.13	0.13	0.18	0.24	0.12	0.14
	20–40	0.22	0.20	0.28	0.29	0.26	0.23
	40–60	0.19	0.12	0.32	0.18	0.19	0.25
	60–80	0.07	0.10			0.23	0.17
	80–100	0.07	0.10				
	100–120	0.09	0.07				

Columns may not add to 1 due to rounding errors.

14-year-old Don Mario pasture had consistently higher bulk densities than the dry forest sites.

A high proportion of the soil C pool (0.37–0.59) was in the top 20 cm of soil in all land-cover types (Table 10). Soil C pools were higher in floodplain forests (113.8 Mg ha^{-1}) and pasture (112.5 Mg ha^{-1}) than in dry forest (76.2 Mg ha^{-1}) (Table 8). The soil C pool corrected for soil bulk density for the Don Mario pasture (see Methods) was 92 Mg ha^{-1} to a 60-cm depth. After correction, mean soil C pools in pastures were still 17 Mg ha^{-1} higher than in dry forest at similar depths. Soil C pools were greatest at the Garrapata floodplain forest site (147 $\pm$ 15 Mg ha^{-1}) and lowest at the Lower Slope dry forest site (69 $\pm$ 10 Mg ha^{-1}).

As for soil C, a high proportion of the soil N pools (0.32–0.52) were in the top 20 cm of the soil (Table 10). Soil N pools were highest in the floodplain forest (16.7 Mg ha^{-1}) and lowest in the dry forest (6.7 Mg ha^{-1}) (Table 8). However, soil N pools calculated for the same soil depths were very similar between dry forest and pasture (around 6.7 Mg ha^{-1}). The smallest soil N pool was in the 4-year-old La Vista pasture. When corrected for soil bulk density, the soil N pool in the 13-year-old Don Mario pasture at 60-cm depth was 7.1 Mg ha^{-1} and very similar to that in the Middle Slope (dry forest).

The floodplain forest had the highest total-ecosystem (biomass + soil) C and N pools, even when comparisons were made for similar soil depths (Table 8). Total-ecosystem C pools, after standardizing for soil depth and correcting for bulk density (the Don Mario pasture), were higher in dry forest than in pasture by about 35 Mg ha^{-1}. This represents a 25% loss in the total-ecosystem C pools when dry forests are converted to pasture. Ecosystem N pools were greater in dry forest by about 1430 kg ha^{-1} when compared to the 4-year-old La Vista pasture, but the difference was much smaller when compared to the 13-year-old Don Mario pasture. Total ecosystem N losses from dry forest represented a mean of 24% when compared to the La Vista site but 1%–11% when compared to the Don Mario site.

Discussion

Aboveground and Root Biomass

There were marked differences in the aboveground biomass and structure of the dry and floodplain forests. The TAGB and the C and N pools of the tall semideciduous floodplain forest were three to four times greater than the shorter deciduous dry forest. These differences in biomass and structure between upland and floodplain forests of this dry forest region are likely much greater than those of moist and wet forest types. For example, in the southwestern Brazilian Amazon, Cummings and others (2002) reported that floodplain forests had a TAGB of 288–408 Mg ha^{-1}, a value quite similar to that found for upland forests (287–488 Mg ha^{-1}). Globally, floodplain forests (riparian zones) are known to be zones of high biotic diversity and productivity (Naiman and Décamps 1996). In tropical moist forest landscapes, floodplain forests are important to both the terrestrial and aquatic biota (Junk and others 1989). The conversion of floodplain forests to agriculture or pasture is of particular concern because so few floodplain forests remain in this region of México.

Our measurements of biomass for dry forest are similar to those reported in other studies of the Neotropics (Kauffman and others 1993; Martínez-Yrízar 1995; Delaney and others 1997). In global reviews by Martínez-Yrízar (1995) and Murphy and Lugo (1986a), the aboveground phytomass of dry forests ranged from approximately 23 to 273 Mg ha^{-1}. Our estimates of live biomass (60–82 Mg ha^{-1}) as well as TAGB would fall within the lower end of this range. In contrast, the TAGB of the Chamela floodplain forests (301–451 Mg ha^{-1}) exceeded the range of biomass reported for dry forests of the world. However, this was expected because the geomorphic position of these forests was such that water availability exceeded that available only via precipitation.

Litter in the three dry forest sites sampled in this study ranged from 8.3 to 13.7 Mg ha^{-1}. Martínez-Yrízar (1995) reported that global estimates of litter standing crop ranged from 3.2 to 12.3 Mg ha^{-1}. The litter mass at the Middle Slope site (13.7 Mg ha^{-1}, which included both leaf litter and wood less than 2.5 cm in diameter) exceeded this global range. However, we sampled surface litter toward the end of the dry season, when litter standing crop would be expected to be at its annual maximum (Martínez-Yrízar and Sarukhán 1993). The total surface biomass (deadwood + litter) of forests in this study was 24.8–40.0 Mg ha^{-1}, a figure that also far exceeds any other studies of surface litter/wood in dry forests (Martínez-Yrízar 1995; Delaney and others 1997).

The proportion of the TAGB composed of dead mass was similar among the three sampled dry forests (36%–41%). In contrast, the dead mass in floodplain forest comprised only about 15% of the TAGB. This percentage was similar to that for moist and wet forests, where dead mass comprised only a small fraction of the TAGB (Delaney and others 1997; Hughes and others 2000). For example, Hughes and others (2000) reported that dead mass accounted for only 5% of the TAGB (mean, 403 Mg ha^{-1}) in three tropical wet forest sites in southeastern México. Similarly, Cummings and others (2002) reported that nonliving vegetation comprised about 11% of the TAGB of 20 intact evergreen forests of the Brazilian Amazon. Dead wood (standing and downed combined) of dry forest ranged from 26 to 34 Mg ha^{-1}, a value similar to the 27 Mg ha^{-1} estimated by Maass and others (forthcoming) for another dry forest site in Chamela. Dead wood comprised 27%–29% of the TAGB of the dry forests sampled in this study. This is a much greater percentage than has been reported for Venezuelan dry forests (Delaney and others 1997). Delaney and others (1997) found that dead wood in dry forests (that is, thorn woodland, dry forest, and moist/dry transition forests) ranged from 2.4 to 6.6 Mg ha^{-1}. As a percent of the aboveground biomass, they reported that dead wood comprised a mean of 18%–2%. In the dry forests sampled in this study, components of dead vegetation comprised a mean of 39% of the total aboveground C pool and 49% of the aboveground N pool. The dead components of these dry forests apparently are important ecosystem pools of C and nutrients.

There are no previous reports concerning the root biomass of floodplain forests in México, so comparisons with similar forests cannot be made. However, in a recent global analysis of root distributions (Jackson and others 1996), the root biomass of floodplain forest (32 Mg ha^{-1}) was within the upper half of the biomass values reported for tropical evergreen forest. Root biomass in floodplain forest was similar to the mean value reported for tropical lowland forests by Sanford and Cuevas (1996), but if was significantly lower than in the Brazilian Cerrado Denso (semideciduous woodland–savanna) (De Castro and Kauffman 1998). Interestingly, root biomass of the floodplain forest in this study was greater than in the tropical evergreen forest of Los Tuxtlas, México, which was estimated using similar field approaches (22.3 Mg ha^{-1}) (Jaramillo and others forthcoming). This difference may result from the greater water availability, higher soil fertility, or different species characteristic of evergreen forest zones (Hughes and others 2000) versus dry forest landscapes. Despite the difference in root mass between these two forests, the relative abundance of roots in surface soils (top 40 cm) was very similar; 64%–72% of the root biomass in floodplain forest was found at this depth, as compared to 68% in evergreen forest (Jaramillo and others forthcoming). Similar values have also been reported for the top 30 cm of soil in Brazilian woodland–savannas (71%) (De Castro and Kauffman 1998) and tropical evergreen forest (69%) (Jackson and others 1996).

In contrast, up to 95% of the root biomass of old-growth Amazonian forests is concentrated in the top 20 cm of the mineral soil and the root mat (Sanford 1989).

Our estimate of 17 Mg ha^{-1} for the root biomass of dry forest was lower than the 31 Mg ha^{-1} reported by Castellanos and others (1991) for another dry forest site in Chamela. This difference likely reflects the heterogeneity in the distribution of plant species in this forest (Lott and others 1987; Balvanera and others 2002) and variations in soil depth and soil element concentrations, as well as site selection or sampling approaches. We think that soil depth may not be the main factor, since a relatively small fraction of the root biomass was found at lower depths. These differences could simply be the result of site selection and hence reflect the variation in root biomass of dry forest in this region. In addition, the two sites sampled by Castellanos and others (1991) were from 100-m^2 plots on the same slope, whereas our microplots were located within 3000-m^2 plots in sites at least 1 km apart. The root mass of the dry forest in our study was toward the lower end of the range of values found in other tropical dry forests (see Sanford and Cuevas 1996); moreover, it was also lower than the mean of 41 Mg ha^{-1} reported by Jackson and others (1996) for tropical deciduous forest.

The conversion of tropical dry forest to pasture not only led to a 66% reduction in root biomass but also an important change in the allocation of biomass among root-size classes and in the root-size class distribution. For example, although the absolute amount of biomass accounted for by fine and small roots (4 mm or less) was not very different for dry forest and pasture, these smaller roots did comprise a greater proportion of the total root biomass in pastures (that is, 55% and 61% in pastures versus 23% and 24% for dry forest sites). A similarly high proportion of biomass in the smallest roots in pastures—56%—has been reported for tropical grasslands (Campo Limpo) in Brazil (De Castro and Kauffman 1998).

Large roots (more than 20 mm in diameter) accounted for 23% of the biomass in the 4-year-old La Vista pasture, but they were not present in the 13-year-old Don Mario pasture. These roots were likely dead remnants from the dry forest that existed prior to conversion. Results from a ^{13}C study in nearby pastures suggested that forest roots persist for up to 7 years after disturbance by slash-and-burn (Garcia-Oliva and others 1994). Taken together, these results imply that large roots from the original forest decompose between 7 and 13 years after forest transformation.

The root–shoot ratios (R.S) calculated in this study clearly reflected, as expected, the higher allocation of biomass to aboveground structures in the forests, particularly in the floodplain forest. The R.S ratios in floodplain forest were low compared to the values reported for evergreen forest by Jackson and others (1996) and Cairns and others (1997) but similar to those of Edwards and Grubb (1982). The R.S ratios for dry forest in this study were lower than the 0.42 reported by Castellanos and others (1991), even if we considered only aboveground live biomas,. as they did. The R.S ratios of our sites were also lower than the average global value of 0.34 for tropical deciduous forest (Jackson and others 1996).

C and N Pools

The soil C pools of the two floodplain forests in Chamela (81 and 147 Mg ha,$^{-1}$ respectively) were lower than those of the lower montane tropical forest in Venezuela (253 Mg ha^{-1}) (Delaney and others 1997) and the tropical evergreen forest of the Los Tuxtlas, México (210 Mg ha^{-1}) (Hughes and others 2000). However, they were similar to those recorded for the top 50–100 cm of soil in tropical humid forests in Malaysia, Amazonia, and elsewhere (see Nykvist 1997; Fearnside and Barbosa 1998; and references in both). Soil N pools in floodplain forests, calculated for a 60-cm depth, were generally greater than those recorded to 50-cm depths in various tropical rainforests and summarized by Nykvist (1997). However, the N pool of the Búho site (18 Mg ha^{-1}, calculated to 1-m depth) in floodplain forest was similar to the mean of 20 Mg ha^{-1} recorded in the tropical evergreen forest of Los Tuxtlas, México, at a similar depth (Hughes and others 2000).

The soil C pools of dry forest (84 and 69 Mg ha^{-1}) were also lower than the 233 Mg ha^{-1} of the "very dry" tropical forests in Venezuela (Delaney and others 1997) and the 158 Mg ha^{-1} global estimate for the top 1 m of soil for tropical deciduous forests (Jobbágy and Jackson 2000). The low soil C pools in dry forest may be related to the intense morphodynamic processes that dominate in Chamela; these processes maintain shallow, stony soils that have low retention of organic matter and no development of a B horizon (Cotler and others forthcoming). The 6.7 Mg ha^{-1} soil N pool in the dry forest of this study was comparable to the 9.1 Mg ha^{-1} of the Guánica dry forest (Lugo and Murphy 1986).

The quantification of the total-ecosystem C and N pools of tropical forests and pastures is important because the amount of C stored belowground is usually greater than that on the forest floor and in the aboveground biomass (Schlesinger 1997). In this study, soil organic C pools (excluding root C) comprised 37% (floodplain forest), 54% (dry forest), and 90% (pasture), respectively, of the total-ecosystem C, while soil N pools comprised 85% (floodplain forest), 86% (dry forest), and 98% (pasture), respectively, of the total-ecosystem N pool. In a study of Mexican tropical wet forests (Los Tuxtlas), Hughes and others (2000) showed that 51% and 92%, respectively, of total-ecoystem C and N was contained in soils. They also reported that in pastures soil pools comprised 94% and 99% of the total C and N pools, respectively—values similar to the ones obtained for pastures in this study. Another ecosystem-level study in a tropical evergreen forest in Sabah, Malaysia, revealed that soil pools contained 41% and 83% of the total-ecosystem C and N pools, respectively (Nykvist 1997). Delaney and others (1997) reported that 35%–66% of the total C was stored in the soil of tropical moist and lower montane forests of Venezuela, with a corresponding range of 63%–72% for "very dry" tropical forest. Our finding that 86% of the N ecosystem pool in the Chamela dry forest was in soil is similar to the 88% rate reported for the Guánica dry forest in Puerto Rico (Lugo and Murphy 1986). These results indicate that a very high percentage of N in tropical ecosystems (whether humid or dry) is stored in the mineral soils, whereas the proportion of C in the soil pools is more variable. This finding has obvious implications because of the rapid loss of aboveground biomass associated with land-use change in both tropical dry forests (Kauffman and others 1993, forthcoming) and tropical evergreen forests (Kauffman and others 1995; Hughes and others 2000).

The Effect of Land-Use/Land-Cover Change

Land-use/land-cover change affects the three major ecosystem pools of C and N—aboveground biomass, belowground biomass, and soil. Aboveground C and N pools in the cattle pastures were approximately 23% and 18%, respectively, of the C and N pools in the dry forests. When dry forests were converted to pasture, there was a greater proportional decline in N than in C. Nitrogen comprised 0.78% of the TAGB in dry forest but only 0.51% of the TAGB in pasture. This difference was also reflected in the C:N ratio, which was higher for aboveground biomass in pasture than in dry forest (83 and 62, respectively). Conversion of tropical moist forest to pasture also results in larger decreases in vegetation N than vegetation C. For example, in their study of the Brazilian Amazon (Rondonia), Kauffman and others (1995, 1998) reported that N comprised 0.67%–0.71% of the TAGB in primary forest but only 0.51%–0.57% in pasture.

Root C and N pools in cattle pasture were 33% and 44%, respectively, of the C and N pools in the roots of dry forest. In contrast to aboveground pools, there was a greater proportional decline in C than in N. In dry forest, N comprised 0.62% of the root biomass; but it was 0.80% of the root mass in pasture. This difference was reflected in the C:N ratio, which was lower for root biomass in pasture than for dry forest (53 and 64, respectively). The differential effect of land-use change on C and N was also evident in the belowground (root + soil)/aboveground ratios of C and N. Although the C ratio shifted from 1.4 in dry forest to 11.8 in pasture, the N ratio increased from 7.2 to 69.6. As these results indicate, not only does the conversion of forest to pasture cause declines in both aboveground and root ecosystem pools, but other ecosystem processes, such as nutrient turnover and decomposition rates, are also affected.

Land-use/land-cover change does not necessarily lead to reduced soil C in the tropics (Lugo and others 1986; Neill and others 1996; Scholes and others 1999; Hughes and others 2000), particularly when forests are converted to pasture land (Murty and others 2002). Soil C pools in dry forest were approximately 20% lower than those in pastures derived from dry forest, even when the two types of land use are compared for the same total soil depth and the results are corrected for differences in soil bulk density. Our finding that there was no soil C decrease following forest-to-pasture conversion is in accord with the results of Garcia-Oliva and others (1994), who found an increase in soil organic matter content in the top 6 cm of soil in 1–3-y-old pastures and C contents similar to the forest in 7- and 11-y-old pastures in Chamela. Veldkamp (1994) suggested that the decomposition of tree roots in the first few years after clearing provides an extra input of soil organic C in tropical humid forest, which could be the case in our study as well. However, we cannot completely rule out the effect of site differences on our results.

At the whole-ecosystem level, our estimates indicate that there is an ecosystem C loss of around 25% (35 Mg C ha^{-1}) after the conversion of dry forest to pasture. Total ecosystem N losses were variable and depended on pasture age, but ranged from 1% to 24%. Although we did not quantify the impacts of land-use change on floodplain forest, significant C and N losses would be expected, from biomass burning alone, given the relatively large pools of aboveground C and N at this type of site. Clearly, we also need to consider older pastures to better quantify the longer-term trends in ecosystem C and N pools. Our finding that there was no consistent decrease in soil pools of C and N that could be attributed to land-use change indicates that the more significant C and N losses actually derive from aboveground biomass burning, as was shown for the tropical evergreen forests of Los Tuxtlas, México (Hughes and others 2000). It also suggests that any evaluation of potential C storage in dry forest landscapes must consider the key role of soil.

Unmanaged dry forest occupies an estimated area of 15.3×10^6 ha in México (Masera and others 2001), of which a conservative 5% may be floodplain forest (Challenger 1998). With an ecosystem C pool of 141 Mg ha^{-1} for dry forest and 306 Mg ha^{-1} for floodplain forest, total C storage in dry forest landscapes would amount to about 2.3 Pg C. By the same reasoning, the ecosystem C pool of 414 Mg ha^{-1} for tropical evergreen forest (Hughes and others 2000; Jaramillo and others forthcoming), which occupies an estimated 5.7×10^6 ha of unmanaged land (Masera and others 2001), results in a C storage of about 2.4 Pg C. Thus the C stocks stored in dry forest landscapes represent approximately 96% of the C stock in the tropical evergreen forest region of México. The available evidence suggests that C release to the atmosphere from the deforestation of Mexican tropical forests is primarily due to aboveground biomass burning. Given a mean biomass combustion factor of 72% for dry forest (Kauffman and other forthcoming) and a mean combustion factor of 51% for evergreen forests (Kauffman and others 1995; Guild and others 1998), we calculate that C emissions to the atmosphere of approximately 708 Tg C could result from biomass burning in the dry tropical landscapes of México, as compared to emissions of approximately 569 Tg C for the evergreen forests. This high rate of potential C emissions underscores the urgent need to find alternatives to current land-use practices in the Mexican dry tropics that would alleviate the significant pressures exerted by the trend toward widespread deforestation.

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