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Carbon pool and biomass dynamics associated with deforestation, land use, and agricultural abandonment in the neotropics

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Abstract. Current rates of deforestation and the resulting C emissions in the tropics exceed those of secondary forest regrowth and C sequestration. Changing land-use strategies that would maintain standing forests may be among the least expensive of climate change mitigation options. Further, secondary tropical forests have been suggested to have great value for their potential to sequester atmospheric C. These options require an understanding of and capability to quantify C dynamics at landscape scales. Because of the diversity of physical and biotic features of tropical forests as well as approaches and intensities of land uses within the neotropics, there are tremendous differences in the capacity of different landscapes to store and sequester C. Major gaps in our current knowledge include quantification of C pools, rates and patterns of biomass loss following land-cover change, and quantification of the C storage potential of secondary forests following abandonment. In this paper we present a synthesis and further analyses from recent studies that describe C pools, patterns of C decline associated with land use, and rates of C accumulation following secondary-forest establishment—all information necessary for climate-change mitigation options.

Ecosystem C pools of Neotropical primary forests minimally range from ~141 to 571 Mg/ha, demonstrating tremendous differences in the capacity of different forests to store C. Most of the losses in C and nutrient pools associated with conversion occur when fires are set to remove the slashed forest to prepare sites for crop or pasture establishment. Fires burning slashed primary forests have been found to result in C losses of 62–80% of prefire aboveground pools in dry (deciduous) forest landscapes and 29–57% in wet (evergreen) forest landscapes. Carbon emissions equivalent to the aboveground primary-forest pool arise from repeated fires occurring in the first 4 to 10 years following conversion. Feedbacks of climate change, land-cover change, and increasing habitat fragmentation may result in increases of both the area burned and the total quantity of biomass consumed per unit area by fire. These effects may well limit the capacity for future tropical forests to sequester C and nutrients.

Key words: C storage potential of secondary forests; carbon sequestration; clean development mechanism (CDM); ecosystem C-pool quantification; fire ecology; land-use/land-cover change; nutrient pools; pastures; REDD strategies; secondary forests; tropical forests; sources and sinks of atmospheric C.

Introduction

Tropical forest landscapes are characterized by a remarkably high degree of biological diversity and variation in forest structure. The richness of life forms (plants, insects, microorganisms, vertebrates, etc.) also contributes to the complexity and variation of how and where carbon (C) is partitioned within ecosystems and the manner in which it is cycled. The size and dynamics of C pools within ecosystems are related to a multitude of processes and interactions between the biota and physical features, including geomorphology, soils (texture, parent materials), climate (temperature and precipitation), and natural disturbances.

Lewis (2006) stated that it is remarkable how little is known about the rate of tropical deforestation and the conversion of natural forest to other land uses. The dramatic climatic and structural variation in the tropics that contributes to the high degree of biological diversity also contributes to difficulties in the characterization and assessment of C pools in the neotropics. Uncertainties in the rates of deforestation, patterns of C loss following land-cover change, and rates of secondary-forest growth are critical data gaps limiting our understanding of the role of tropical forests as sources and sinks of atmospheric C.

We define "ecosystem C pools" as the sum of all organically derived C present in soils, roots, and aboveground components. Given the difficulties involved, few studies have quantified total ecosystem C pools. For example, few studies have quantified animal C pools in tropical ecosystems (estimated to be <1% by

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Uhl and Parker [1986]). Frequently, belowground pools are incompletely measured where only surface soils (10–50 cm in depth) are sampled (see Silver et al. 2000, Marin-Spiotta et al. 2008). Rarely are soil C pools measured to bedrock or depths as great as 100 cm. In addition, roots and non-tree components of aboveground biomass are often not included in estimates of C pools. Nevertheless, a global body of literature exists to begin to appreciate the inherent variation that exists in ecosystem C pools at multiple spatial scales and under different land uses. This is important because successful design and implementation of a "clean development mechanism (CDM) under the Kyoto Protocol or future strategies designed to reduce emissions through deforestation and forest degradation (REDD) requires an understanding of C dynamics including both the size of C pools and the rates of C sequestration (Kanninen et al. 2007, UNFCCC 2008).

Ecosystem C pools decline when tropical forest landscapes are logged or converted to agriculture or pasture. Forests shift in function from that of a C sink to that of a source of atmospheric C. Losses of biomass, C, and nutrients occur through harvest, burning, decomposition, and erosion (Kauffman et al. 1995, Maass 1995, Fearnside 1996). Conversely, a shift in land use from agricultural production to secondary forest results in the reaccumulation of ecosystem C (Hughes et al. 1999, Marin-Spiotta et al. 2008). Despite the importance of Neotropical forests to global C cycling, the impacts of land management on C dynamics are poorly understood (Guild et al. 1998, Kauffman et al. 2003, Marin-Spiotta et al. 2008). One of the difficulties includes the inability of generalized models of C dynamics to adequately encompass the diversity of tropical forest types (e.g., life zones) occurring across broad elevation and precipitation gradients, coupled with the diversity of historical and contemporary approaches to land use.

The most promising regions for C offsets under CDM are degraded pastures or agricultural lands that currently provide marginal rates of economic return. Yet few studies have measured C pools in degraded pastures or croplands in the neotropics (but see Kauffman et al. 1998*b*, Hughes et al. 2000*b*, 2002, Jaramillo et al. 2003). Site-history attributes are likely critical determinants of C storage potential (McGrath et al. 2001). Knowledge of site history should begin with an understanding of the patterns of C loss associated with deforestation and land use. Additionally, it is important to know how the intensity and duration of land use coupled with climate and physical factors inherent in the site will affect rates of sequestration, and the time periods required to attain the site potential (i.e., the maximum C-storage potential). Because land use may affect both the rate of sequestration of C pools (Uhl et al. 1988) and the maximum C-storage potential, remnant primary (undisturbed) forests may not accurately reflect the potential pool sizes of abandoned sites with intensive land-use histories.

In this paper we describe C pools in a variety of primary tropical forests, losses associated with land use, and rates of sequestration in secondary forests. We utilize many examples from the literature but emphasize results from studies conducted by the authors in tropical dry forests (western Mexico and northeastern Brazil), moist forests (Brazilian Amazon), and wet forests (eastern Mexico). We focus on describing the range and variation of C pools in Neotropical landscapes and address the sources of uncertainty associated with quantifying C dynamics at spatial scales ranging from the local (site) level to the entirety of the neotropics. The objectives of this paper are to describe C pools and dynamics of common Neotropical ecosystems and land-use/land-cover types that typify landscapes where C sequestration or strategies that reduce emissions through deforestation or forest degradation or other CDMs may become an economically viable option to land management and climate-change mitigation.

Variation in C Pools

Across Neotropical forest landscapes

Total aboveground biomass (TAGB) is highly variable among Neotropical ecosystems ranging from <5 to >600 Mg/ha (aboveground C pools would comprise ~48% of this total). Soil pools range from 76 Mg C/ha in dry forests with shallow soils <60 cm in depth (Jaramillo et al. 2003) to >268 Mg C/ha in wet forests of Venezuela (Delaney et al. 1997) and Costa Rica (J. B. Kauffman, *unpublished data*). Reviewing ecosystem C pools (aboveground + belowground pools), we found that intact Neotropical forests vary by more than four-fold (Fig. 1). Total C pools ranged from 141 Mg/ha in Mexican tropical dry forest to 571 Mg/ha in Venezuelan tropical lower montane moist forest (Delaney et al. 1997, Jaramillo et al. 2003).

Comparison of the Brazilian Cerrado with other Neotropical ecosystems illustrates relationships of disturbance regimes, species composition, and C-pool distribution. The Brazilian Cerrado is a mosaic of grassland, savanna, and woodland communities with a disturbance regime characterized by a presence of frequent fires (Coutinho 1978). In Cerrado woodlands, belowground C comprised 95–99% of the total ecosystem C pool (de Castro 1995). In contrast, soil C pools (typically measured to 1 m) comprised only 39–77% of the total C of Neotropical forest types, where fires of natural origin (i.e., lightning) are rare (Fig. 1).

Even among forests with similar climates or within the same life zone (sensu Holdridge et al. 1971), C pools vary markedly in magnitude and distribution. For example, total ecosystem C pools of moist forest types ranged from 249 to 488 Mg/ha (Fig. 1). Estimates for the TAGB of individual stands of primary tropical moist forest vary over four-fold, from 140 to 660 Mg/ha (e.g., Fearnside et al. 1993, Cummings et al. 2002, Rice et al. 2004).

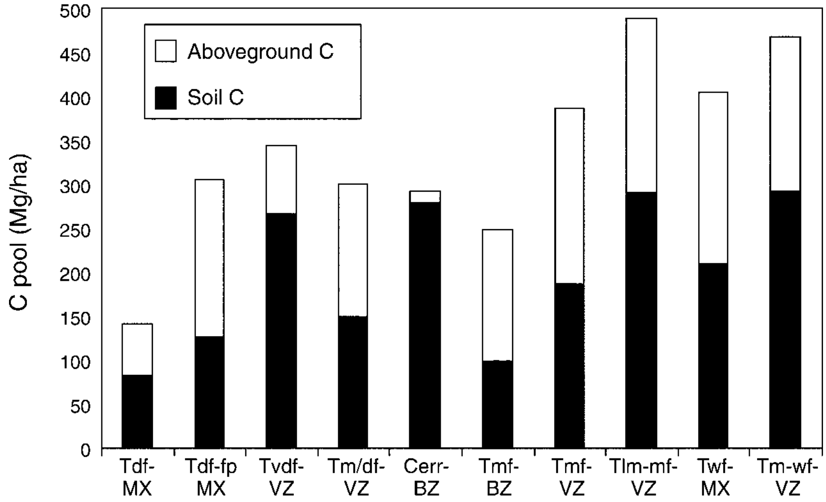

FIG. 1. Examples of total ecosystem C pools of intact forests segregated by life zones of the neotropics. The ecosystems include: Tdf-MX, subtropical dry forest, Mexico; Tdf-fp-MX, tropical floodplain forest in Tdf, Mexico; Tvdf-VZ, tropical very dry forest, Venezuela; Tm/df-VZ, transitional moist/dry forest, Venezuela; Cerr-BZ, Cerrado, Brazil; Tmf-BZ, tropical moist forest, Brazil; Tmf-BZ, tropical moist forest, Venezuela; Tlm-mf-VZ, transitional tropical lower montane/moist forest, Venezuela; Twf-MX, tropical wet forest, Mexico; and Tm-wf-VZ, transitional tropical montane/wet forest, Venezuela. All Venezuelan examples are from Delaney et al. (1997). Tropical dry forests are from Jaramillo et al. (2003); Cerrado data are from de Castro (1995); tropical moist forest, Brazil, data are from Hughes et al. (2002); and tropical wet forest, Mexico, data are from Hughes et al. (2000*b*).

Relatively few studies have quantified forest C pools in the dry and very wet extremes of the tropical precipitation gradient, thereby constraining development of realistic models of C dynamics in these ecosystems, and limiting the capacity to scale C dynamics at regional or national levels. Hughes et al. (2000*b*) estimated that C pools in Mexican tropical wet forest (mean precipitation of 4700 mm) were 195 ± 24 Mg/ha (mean ± SE) for total aboveground pools and 210 ± 49 Mg/ha for belowground pools (Fig. 1). Even though tropical dry forests encompass ~43% of all tropical forests, few measurements of ecosystem C pools exist within this vegetation type. Estimates of ecosystem C pools in Neotropical dry forests range from 141 to 344 Mg/ha (Delaney et al. 1997, Jaramillo et al. 2003).

At local to watershed scales

Accurate regional-scale estimates of C pools must account for the variation in biomass and C pools that exists at local scales (Table 1). For example, within a 1-km^2 area in the Brazilian Cerrado, total aboveground biomass (TAGB) ranged from 5 Mg/ha in pure grassland (Campo limpo) to 25 Mg/ha in dense woodland (Cerrado sensu stricto) (de Castro and Kauffman 1998). Total ecosystem C pools in these two sites were 255 and 293 Mg/ha, respectively (de Castro 1995). Within a given watershed or local area, the TAGB of tropical evergreen forests (moist, wet, and rain forests) can differ by over 250 Mg/ha (Table 1). Cummings et al. (2002) found that TAGB of tropical moist forest in northern Rondonia, Brazil varied from 288 to 534 Mg/ha. In this region of the Amazon, the mean TAGB of two adjacent slashed primary forest plots (each ~3 ha in area) differed by more than 100 Mg/ha (399 and 290 Mg/ha; Kauffman et al. 1995, Guild et al. 1998). Soil C pools (to 1 m in depth) of primary forests in this northern Rondonia location varied from 87 to 110 Mg/ha; soil texture explained most of the variation in C pool size in this study (Hughes et al. 2002). Based on data presented in Cummings et al. (2002) and Hughes et al. (2002), we estimate ecosystem C pools of primary tropical moist forest in northern Rondonia would, at a minimum, vary from 230 to 375 Mg C/ha. Similarly, Heider (2001) reported that TAGB of 18 Mexican tropical wet forests ranged from 309 to 550 Mg/ha (Table 1). In this area (within 10 km of the Los Tuxtlas Biological Station, Veracruz), aboveground C pools ranged from 149 to 267 Mg/ha while soil C pools ranged from 178 to 307 Mg/ha; total ecosystem C pools of these primary forest stands varied by >200 Mg/ha, ranging from 333 to 571 Mg/ha (Hughes et al. 2000*b*, Heider 2001). The wide range in variation of C pools suggests that a degraded pasture from a productive site with only a few megagrams of aboveground C per hectare could contain as much ecosystem C as a primary forest on a less productive site in close proximity. These studies also suggest that regional C models that assume C pools and sequestration rates to be equivalent for forests in the same life zone or even same local area could result in large errors.

Aboveground biomass and C pools are dramatically lower in pastures compared to the primary forest they replace following land-use conversion. The TAGB of pastures in the neotropics has been shown to range from ~7 to 119 Mg/ha (Table 1). Ecosystem C pools of pastures converted from evergreen forests range from 96

TABLE 1. Total aboveground biomass (TAGB) of common Neotropical land-cover types.

Forest type/land cover and location	TAGB (Mg/ha) Mean ± SE	TAGB (Mg/ha) Range	N†	Data source
Primary forests				
Tropical dry (Chamela, Mexico)	112 ± 10	93–126	3	Jaramillo et al. (2003)
Cerrado (Brasilia, Brazil)	16 ± 10	5–25	4	de Castro and Kauffman (1998)
Tropical moist (Rondonia, Brazil)‡	341 ± 24	288–534	20	Cummings et al. (2002)
Tropical wet (Los Tuxtlas, Mexico)	416 ± 24	320–545	12	Heider (2001)
Tropical wet-rain (Los Tuxtlas, Mexico)	434 ± 22	379–502	6	Heider (2001)
Montane rain (cloud forest) (Los Tuxtlas, Mexico)	346 ± 1	344–345	2	Heider (2001)
Pastures				
Tropical dry (Chamela, Mexico)	27 ± 4	20–34	4	Jaramillo et al. (2003)
Tropical moist (Rondonia Brazil)	74 ± 12	53–119	5	Guild et al. (1998)
Tropical wet (Los Tuxtlas, Mexico)	24 ± 6	6.5–48	7	Hughes et al. (2000*b*)
Cornfield				
Tropical wet (Los Tuxtlas, Mexico)	23 ± 9	5–34	4	Hughes et al. (2000*b*)
Secondary forests				
Tropical dry (Serra Talhada, Brazil)	74	74	1	Kauffman et al. (1993)
Tropical moist (Rondonia, Brazil)	109 ± 13	63–178	7	Hughes et al. (2000*a*)
Tropical wet (Los Tuxtlas, Mexico)	149 ± 35	5–293	11	Hughes et al. (2000*b*)

Notes: Each cover type example is a summary of data collected from a relatively small geographical area demonstrating the degree of local/regional variation in TAGB of cover types. Plots comprising each data point were usually <10 km from each other.

† *N* is the number of sites sampled.

‡ Data from this study represent plots sampled in an area with ~150-km radius.

Mg/ha in tropical moist forest landscapes (Rondonia, Brazil) to 178 Mg/ha in tropical wet forests (Los Tuxtlas, Mexico) (Hughes et al. 2000*b*, 2002). These values represent a reduction in C pool size of from ~39% to 44% of the primary forest they replaced, respectively. In tropical dry forests, mean ecosystem C pools of primary forests and pastures were 141 and 108 Mg/ha (i.e., the ecosystem C pools of pastures were equivalent to ~77% of that of primary forests; Jaramillo et al. 2003).

The sizes of C pools in secondary forests vary more than any other land-cover type in tropical forest landscapes. This is because of wide ranges in age since abandonment and variation in land-use history (Cifuentes 2008). For example, Hughes et al. (1999) found that TAGB of tropical wet secondary forests in Mexico ranged from 5 Mg/ha for ~1-yr-old secondary forest to 286 Mg/ha for a 50-yr-old forest. Along this chronosequence, ecosystem C pools ranged from 167 Mg/ha (8-yr-old forest) to 341 Mg/ha (50-yr-old forest). Along a tropical secondary-forest chronosequence in premontane rain forests, Costa Rica, Cifuentes (2008) reported ecosystem C pools to range from 248 Mg/ha in a secondary forest (<1 yr since abandonment) to 423 Mg/ha in a 50-yr-old secondary forest. Differences in these C pools were largely attributable to sequestration of aboveground C pools. While there were clear relationships between secondary-forest age and aboveground C in these studies, no such relationship existed with soil C pools. To accurately predict biomass and C pools, it would be extremely valuable, if not necessary, to determine secondary-forest age, structure, soil type, and land-use history (Uhl et al. 1988, Hughes et al. 1999, Silver et al. 2000).

C DISTRIBUTION WITHIN TROPICAL-FOREST PATCHES

Among tropical forests there is great spatial variability in both the total size of C pools, and the components where C is sequestered (Fig. 2). In tropical moist and wet forests, the majority of total aboveground biomass (TAGB) and aboveground C are usually contained in large trees (i.e., those >30 cm dbh) (Heider 2001, Cummings et al. 2002, Fig. 2). Tropical dry forests contrast with moist and wet forests in that a greater proportion of aboveground C pools are distributed in smaller trees and dead wood (Jaramillo et al. 2003). While dead wood comprised 27–29% of the TAGB in a Mexican dry forest (Jaramillo et al. 2003), Delaney et al. (1997) found that dead wood comprised <18% of the TAGB in similar vegetation types in Venezuela. In Mexican tropical dry forests, dead-to-live ratios of aboveground biomass range from 0.32 to 0.61 (Maass et al. 2002, Jaramillo et al. 2003). In studies reporting results from numerous sampled evergreen tropical-forest stands, mean dead-to-live ratios were 0.14 (tropical moist forest, Amazon) and 0.07 (tropical wet forest, Mexico) (Heider 2001, Cummings et al. 2002, Fig. 2). However, in an eastern Amazon moist forest stand, Rice et al. (2004) reported a dead-to-live ratio similar to that of dry forests (0.25) and suggested that the higher proportion compared with other moist and wet forests was possibly related to drought-induced mortality associated with the strong El Niño Southern Oscillation events of the 1990s.

The wide range in biomass of similar components between stands in a given watershed or landscape suggests that structural generalities such as those in Fig. 2 are of limited value for extrapolating to larger

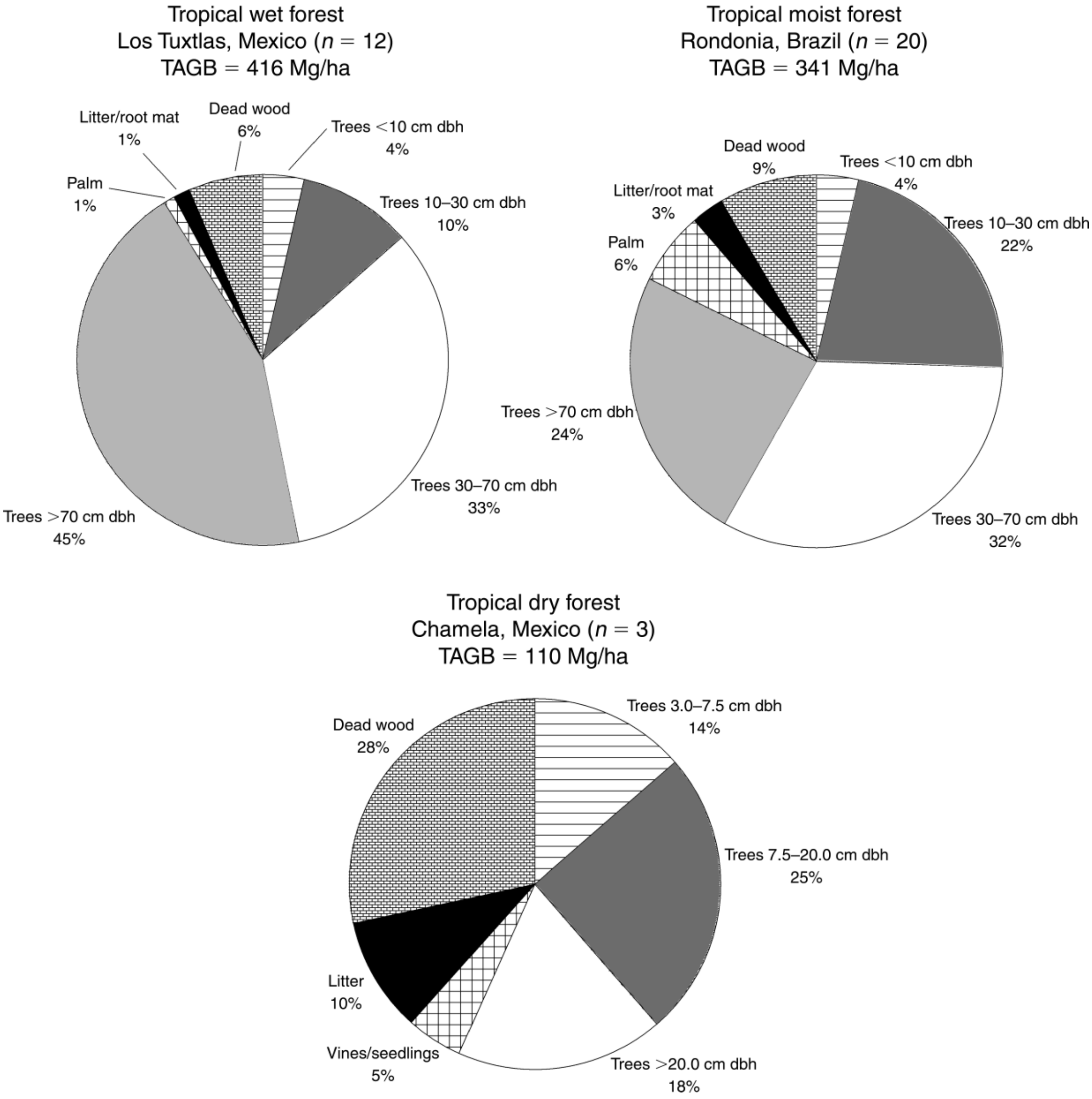

FIG. 2. The distribution of aboveground biomass (%) within intact tropical wet and dry forests, Mexico, and tropical moist forests, Brazil. Data are from Heider (2001), Jaramillo et al. (2003), and Cummings et al. (2002), respectively. TAGB = total aboveground biomass; n = the number of stands comprising the mean biomass of each figure.

spatial scales. For example, Cummings et al. (2002) reported that palm biomass averaged 6% of the TAGB in 20 sampled Amazonian primary tropical moist forests, expressing a broad range within individual stands (from 1 to 95 Mg/ha, or 0.2% to 29% of the TAGB). Similar variability was found in large trees (>100 cm dbh), with site-level ranges from 0% to 42% of the TAGB for this size class (density averaged 1.9 trees/ha). In primary tropical wet forests of eastern Mexico, Heider (2001) found that biomass of individual large trees (>130 cm dbh) ranged from 11 to 43 Mg. In these forests, mean TAGB of trees >130 cm dbh was 50 Mg/ha (range: 19–126 Mg/ha). This is equivalent to 11% (range: 2–23%) of TAGB even though the density of these large trees was only ~2.4 trees/ha. Given the significant contribution of large trees to TAGB and their relative scarcity within tropical forests, plot-level studies designed to estimate C pools must utilize plots of sufficient size to effectively capture variation associated with large trees (Brown et al. 1995, Clark and Clark 2000).

It has been suggested that forest inventories (of commercial tree volume) can be utilized to predict forest biomass and C pools (Brown and Lugo 1984, Brown 1997). This approach is based upon the assumption that forest inventories are correlated with ecosystem C pools.

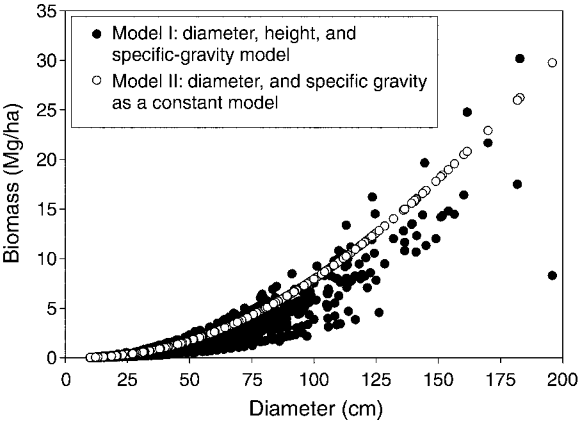

FIG. 3. Estimated biomass for 2973 trees (≥10 cm dbh) measured in 18 0.78-ha plots in primary tropical wet forests, Los Tuxtlas, Mexico. Values were based upon equations using field-measured diameter, height, and specific gravity of wood (Model I) and a model using diameter with a regional average value for wood density (Model II) (Chave et al. 2005).

Few studies have been conducted to determine the strength of the relationship between data reported in inventories and ground-based measurements of biomass. One such example involves those studies that have utilized the massive Brazilian forest inventory—Projeto RADAMBRASIL (Departamento Nacional de Produção Mineral 1978)—to estimate C pools of Amazonian forest (e.g., Houghton et al. 2000). Based upon field measurements designed to test the utility of inventory values for predicting C pools, Cummings (1998) did not find a statistically significant relationship between the volume data reported in the forest inventory and forest biomass measured in the field at 20 RADAMBRASIL sites in Rondonia, Brazil. These findings underscore the need for caution when using conventional forest inventories as well as the need for inclusion of all ecosystem components to estimate C pools when conducting assessments for CDM (Kyoto Protocol clean development mechanism)/REDD (reduced emission through deforestation or forest degradation) options.

Obstacles to utilizing forest inventories stem from the difficulty of predicting total ecosystem pools based solely upon volumes of large, commercially valuable trees. The density of commercially valuable trees can be variable and not necessarily correlated to biomass. Across all tropical forests, there are no strong universal relationships between large trees (commercial and noncommercial) and other forest components. For example, the biomass of many understory components (e.g., wood, small trees) is suggested to be positively and linearly related to forest overstory biomass (Fearnside 1996, Brown 1997, Laurance et al. 1997). However, Kauffman et al. (1998*a*) reported a negative relationship between downed wood and overstory tree biomass (i.e., when a tree falls, the mass of standing trees decreases but downed wood mass increases). Similarly, Rice et al. (2004) suggested that biometric studies of tropical forests that neglect to account for coarse wood debris would be unlikely to accurately determine the C balance of tropical forests.

Ecosystem structure, and hence C pools of other land-cover types (e.g., pastures and croplands) vary greatly across landscapes (Table 1). For example, the TAGB of cornfields converted from tropical wet forest in Mexico varied from 5 to 42 Mg/ha. Pastures in the same landscape ranged from 7 to 48 Mg/ha (Hughes et al. 2000*b*). The differences in TAGB among sites were largely due to the presence or absence of remnant trees and residual large dead wood that originated from the forest that formerly occupied the sites. This underscores the importance of including residual wood and complete inventory of large-tree components in estimations of ecosystem C pools for these land-cover types. In Amazonian pastures, Kauffman et al. (1998*b*) and Guild et al. (1998) reported high degrees of variation in the TAGB of Amazonian pastures, ranging from ~10 to 236 Mg/ha. In pastures (<20 years old), they found that residual wood comprised from 47% to 87% of TAGB; pasture grasses were a comparatively minor component of TAGB at these sites. Wood debris, and hence TAGB, in pastures is related to pasture age; recently formed pastures typically have a larger quantity of residual wood comprising a significant proportion of the aboveground C pool compared to older pastures. The decline in large wood is largely the result of frequent fires, decomposition, and pasture management (Kauffman et al. 1998*b*, Jaramillo et al. 2003).

UNCERTAINTIES IN MEASURING TREE BIOMASS

Narrowing the uncertainties and potential errors associated with the quantification of forest biomass is needed to improve the accuracy of C estimates at local, regional, and global scales. Much of the uncertainty in biomass quantification is related to the selection of variables to be measured in the field as well as sampling a sufficient area to comprehensively and accurately describe all of the of aboveground components. Because trees in tropical ecosystems are diverse in composition and structure, and account for a large proportion of C pools (Fig. 3), they represent a large potential source of error in biomass estimation (Chave et al. 2005).

It is important to recognize that equations that use different variables of tree structure (i.e., combinations of diameter, height, and the specific gravity of wood) often result in large differences in biomass estimates. To illustrate these differences, we analyzed tree data from 18 wet forest sites in Los Tuxtlas, Mexico (Heider 2001) to compare how tree biomass estimates differed using two equations. The first equation included diameter, height, and specific gravity for each tree (Model I, Chave et al. 2005). The second equation utilized diameter as the sole independent variable, applying a regional average wood specific gravity (Model II, Chave et al. 2005). For the 2973 trees >10 cm dbh measured in the study, tree biomass significantly diverged according to which model was used (Fig. 3). Model II (dbh and regional wood-density values only) generally yielded higher predictions of individual tree biomass. At the stand level, this difference translated to Model I TAGB estimates being ~82% those of Model II predictions (range: 55–96%). Using the equations in Brown (1997) and Brown et al. (1989) for this analysis also yielded similar results of higher biomass estimates using diameter-only equations compared to those employing height, diameter, and species-specific wood density (Heider 2001). Chambers et al. (2001) suggested that biomass estimations using equations where diameter is the sole parameter are likely adequate when sampling in the region in which the equations were developed. Where regional models do not exist, Chave et al. (2005) recommended using published or regional estimates of specific gravity to improve model estimates. However, our analysis suggests that this will yield higher estimates of biomass than models that include tree height and species-specific wood density values.

PATTERNS OF C LOSS ASSOCIATED WITH LAND-USE/LAND-COVER CHANGE

The use of fire is one of the most ubiquitous management practices in tropical landscapes, and the greatest and most rapid rates of C and nutrient depletion associated with land conversion occurs during fire events (Kauffman et al. 1995, Cochrane et al. 1999; Table 2). Fires are purposely set to clear forest slash for crop or pasture establishment, resulting in dramatic inputs of CO_2 and other radiative forcing (greenhouse) gasses to the atmosphere (Ward et al. 1992). Fire is also utilized in established pastures to invigorate grasses, and to control weeds and insects (Uhl and Buschbacher 1985, Kauffman et al. 1998*b*). When forests are cut, the quantity of biomass consumed by slash fires varies with climate and forest type. In the Brazilian Amazon, fires in primary-forest slash have been found to consume from 29% to 57% of the total aboveground biomass (TAGB) (Fearnside et al. 1993, Kauffman et al. 1995, Guild et al. 1998; Table 2). Carbon losses from Amazonian slash fires ranged from 58 to 112 Mg/ha and N losses ranged from 817 to 1605 kg/ha (Kauffman et al. 1995, Guild et al. 1998). Because the trees are smaller and the climate is drier in tropical dry forests, the proportion of TAGB consumed by fire is higher. Kauffman et al. (2003) reported slash fires in Mexican dry forests consumed 62 to 80% of the TAGB. At these Mexican dry-forest sites, C losses ranged from 35 to 52 Mg/ha and N losses ranged from 603 to 793 kg/ha (Steele 2000).

Secondary-forest cover is increasing in many areas of the tropics (Marin-Spiotta et al. 2008). However, these areas are vulnerable to deforestation and a return to active land use. Fires associated with conversion of secondary forests to pastures or shifting agriculture have been found to consume proportionately greater quantities of aboveground biomass than fires burning slashed primary forests (Table 2). A greater proportion of the TAGB of secondary forests is consumed by fire because a higher proportion of fuels are composed of younger and smaller trees, resulting in a fuel load with a higher surface-to-volume ratio. Therefore, slashed secondary-forest fuels have a higher rate of moisture loss before fires, resulting in a higher proportion of the TAGB susceptible to combustion (Kauffman et al. 1995, Hughes et al. 2000*a*). In Amazonia, Hughes et al. (2000*a*) found fires consumed 42% to 88% of the TAGB in slashed secondary forests. In a 13-yr-old slashed tropical secondary dry forest of northeast Brazil, Kauffman et al. (1993) reported 77% to 95% of the TAGB was consumed by fire.

The quantity of biomass consumed, and amounts of C released to the atmosphere by fires occurring in cattle pastures can be quite high, and is dependent upon land-use history and climate. Prior land uses affect the quantity of biomass present while climate conditions affect the microsite characteristics to allow available biomass to burn. Variation in land-use history is reflected in studies in the Brazilian Amazon where the range in biomass consumption by pasture fires was 24 to 45 Mg/ha (20% to 84% of the TAGB) (Barbosa and Fearnside 1996, Kauffman et al. 1998*b*). Grass biomass was nearly completely consumed by fires (i.e., a combustion factor of >96%), while lower quantities of residual wood debris were consumed (9% to 66%). Losses of C from fires at these sites ranged from 9 to 21 Mg/ha, and N losses ranged from 88 to 261 kg/ha (Table 2). Similarly, in pastures derived from primary tropical dry forests, 63% to 75% of the TAGB was consumed by fire (Kauffman et al. 2003). C losses from pasture fires in tropical dry forest landscapes were 10 to 12 Mg/ha, and losses of N during these pasture fires were 179 to 220 kg/ha (Steele 2000). Few additional studies of ecosystem effects by pasture fires and the depletion of C pools following land conversion exist in other Neotropical forest types which further constrains our understanding of C dynamics associated with land use in these landscapes.

In the first 10 years following forest conversion to pasture, it is common practice to set fires every 2–3 years to promote grass growth and remove residual wood debris (Guild et al. 1998). It is also commonplace to observe burns where fire accidentally spreads onto adjacent lands (Uhl and Buschbacher 1985, Kauffman et al. 1998*b*, Cochrane et al. 1999). Because of these frequent fires, pastures remain sources of atmospheric C for many years (Fig. 4). Based on studies of forest and pasture biomass and their fates following fire, we have developed generalized patterns of aboveground biomass decline following forest conversion to pasture (Fig. 4). Dynamics of land-cover change from tropical evergreen moist forest to pasture are based on results from studies conducted in Para and Rondonia, Brazil (Guild et al. 1998, Kauffman et al. 1998*b*, Cummings et al. 2002). The aboveground biomass dynamics of land-cover change in tropical dry forest landscapes are based upon

TABLE 2. The total aboveground biomass (TAGB), number of sampled sites or fires (*N*), combustion factor (CF), and losses of C and nutrients associated with anthropogenic fires in common land-cover/land-use types of the neotropics.

Forest type/land cover	*N*	TAGB (Mg/ha)	CF† (%)	Site losses through burning C (Mg/ha)	 N (kg/ha)
Primary forests					
Tropical dry (Chamela, México)	2	127 ± 8	72 ± 9	43 ± 8	673 ± 93
Tropical moist (Rondonia and Para, Brazil)	4	345 ± 30	51 ± 3	87 ± 10	1218 ± 151
Tropical moist (Rondonia, Brazil)	2	377 ± 22	51 ± 4	92 ± 11	1216 ± 152
Pastures/natural grassland and savannas					
Tropical dry (Chamela, México)	2	36 ± 6	69 ± 6	10.5 ± 1.0	132 ± 3
Tropical moist (Rondônia, Brazil)	1	66	31	9.7	93
Tropical moist (Rondônia, Brazil)	3	82 ± 20	50 ± 18	16.0 ± 2.9	235 ± 16
Cerrado, natural grasslands, Brazil‡	2	7.4 ± 1.9	88 ± 4	3.3 ± 0.01	23 ± 0.7
Cerrado, woodland savannas, Brazil‡	2	24.9 ± 0.1	44 ± 11	2.7 ± 0.02	25 ± 1
Secondary forests					
Tropical dry forest (Brazil)	3	74 ± 0.1	87 ± 5	28 ± 2	495 ± 33
Tropical moist forest (Brazil)	6	110 ± 15	59 ± 6	29 ± 4	531 ± 58

Notes: Nutrient losses are calculated as the nutrient pools before fire − the uncombusted post fire mass + ash. Therefore, numbers do not reflect additional site losses such as wind or water erosion. The data are means ± SE; nd indicates that no data were collected.

† Percentage of biomass consumed.

‡ Natural grasslands in the Cerrado are classified as "Campo Limpo" and "Campo Sujo" which contain few woody species. The Cerrado woodland/savannas ("Cerrado Sensu Stricto" and Campo Cerrado") are dominated by an open forest overstory.

studies in Chamela, Mexico, by Ellingson et al. (2000), Steele (2000), Jaramillo et al. (2003), and Kauffman et al. (2003). Net biomass accumulation between pasture fires is calculated as the rate of vegetation growth minus losses through decomposition. In the dry forest, decomposition was roughly equivalent to biomass accumulation during the first two years after the initial slash fire (Kauffman et al. 2003, Fig. 4). During the time periods between subsequent fires, net aboveground biomass accumulation averaged 6 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$. In pastures formed in tropical moist forest landscapes, the mean rate of biomass accumulation between fires was 8.9 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$. Pasture regrowth consisted of grasses, seedlings of invasive woody plants, and sprouting trees, vines, and shrubs. Based upon a review of the literature, interviews with local landowners, and personal observations in both Brazil and Mexico, we assumed fires would occur every 2 years for the first 10 years (Uhl and Buschbacher 1985, Guild et al. 1998, Kauffman et al. 1998*b*, 2003). While this simple model provides a reasonable description of patterns and rates of biomass decline, there will be variation in dynamics due to differing initial levels of forest biomass, the quantities of biomass consumed by fire, the frequencies of burning, and differing approaches to land use.

When forests are converted to pastures in tropical dry forest landscapes, losses of biomass, C pools, and nutrients are greatest from the initial slash fire (Fig. 4). Kauffman et al. (2003) reported that during the initial 2.5 years following conversion from tropical dry primary forest to pasture, an equivalent of 87% to 94% of the TAGB of the primary forest was consumed by two fires (the initial slash fire followed by the first pasture burn). Total aboveground C losses during the initial 2.5 years of land-cover change were 47–61 Mg/ha; total N losses via combustion were 752–938 kg/ha. An amount of biomass equivalent to the TAGB of the primary dry forest is predicted to be consumed by fires by the fourth year following pasture establishment (Fig. 4). During the first 10 years of pasture establishment in dry forest, the cumulative biomass consumed by fires is predicted to be 135% of the biomass of the primary forest (172 Mg/ha); ∼53% of this total biomass is consumed during the initial slash fire (Fig. 4).

In pastures derived from Amazonian tropical evergreen forest, residual wood debris typically remains on site longer than in pastures derived from dry forest. Nevertheless, in the first six years of pasture establishment, fires were predicted to consume as much biomass (and release as much C) as is present in the TAGB of primary tropical moist forests. During the first 10 years of pasture establishment in Amazonian moist forest landscapes, we predict that the total C input into the atmosphere via slash and subsequent pasture fires would be ∼210 Mg/ha (from 420 Mg/ha of biomass consumed by fire). This is equivalent to 123% of the primary forest TAGB. Of the total quantity of biomass lost by fire, ∼39% of the biomass would be consumed during the initial fire burning primary forest slash. The remaining 61% of C loss would occur during subsequent pasture fires, underscoring their important role in affecting C dynamics in this landscape. Similarly in the northern Amazon, Barbosa and Fearnside (1996) predicted ∼90% of the C in the original forest biomass would be released by the end of the first decade of pasture establishment.

While declines in aboveground C pools as a result of deforestation and land conversion are dramatic, the patterns of response by soil C are equivocal (Trumbore et al. 1995, McGrath et al. 2001). Some studies have reported increases in soil C pools with land conversion

Table 2. Extended.

Site losses through burning				
P (kg/ha)	S (kg/ha)	Ca (kg/ha)	K (kg/ha)	Data source
11 ± 2	46 ± 6	444 ± 116	165 ± 32	Kauffman et al. (2003), Steele (2000)
11 ± 3	115 ± 8	67 ± 18	39 ± 21	Kauffman et al. (1995)
nd	99 ± 13	nd	nd	Guild et al. (1988)
4.9 ± 0.2	13.5 ± 2.5	110 ± 10	72 ± 25	Kauffman et al. (2003), Steele (2000)
nd	4	nd	nd	Guild et al. (1998)
5.4 ± 3.2	20.0 ± 2.6	8.7 ± 4.7	21.7 ± 6.4	Kauffman et al. (1998*b*)
1.0 ± 0.1	3.1 ± 0.1	nd	nd	de Castro and Kauffman (1998), Kauffman et al. (1994)
1.3 ± 0.3	3.8 ± 0.4	nd	nd	de Castro and Kauffman (1998), Kauffman et al. (1994)
14 ± 7	nd	nd	nd	Kauffman et al. (1993)
12 ± 2	35 ± 3	72 ± 20	47 ± 12	Hughes et al. (2000*a*)

while others have found no changes, or decreases. Compared with aboveground pool losses, gross changes in soil C following land-cover change are usually an order of magnitude lower. Land conversion results in a change in the origin of C substrate inputs from forest (tree) to pasture (grass). This in turn results in a change in the composition and structure of the soil C pool (e.g., Garcia-Oliva et al. 1994, Trumbore et al. 1995). However, changes in the mass of soil C pools resulting from contemporary land uses appear to be relatively minor compared to changes in aboveground pools.

Rates of C Accumulation Following Land-Use Abandonment

Secondary forests have become one of the dominant land-cover types in the tropics (Marin-Spiotta et al. 2008). It has been estimated that ~9 million hectares of secondary forests are formed annually within the tropical regions of the world (Brown and Lugo 1990, Silver et al. 2000). As such, these forests may have the potential to regain large amounts of terrestrial C. Lugo and Brown (1992) estimated that secondary forests in the tropics have the capacity to sequester between 0.6 and 1.4 Pg of C annually. This represents between 40% and 90% of the estimated annual C emissions resulting from biomass burning in those regions. Given the importance of secondary forests in the dynamics of terrestrial C sequestration, we need to gain more insight into the variables that affect such dynamics and identify what current knowledge gaps constrain our ability to monitor and predict C sequestration in regenerating forest systems.

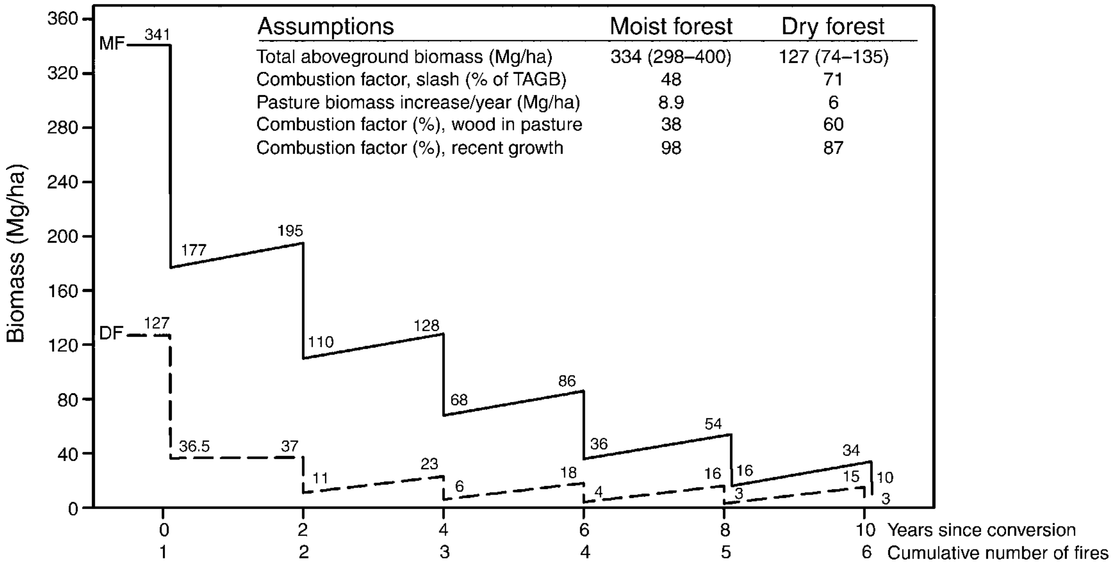

Fig. 4. The temporal dynamics of C pools associated with land-use/land-cover change from forest to pasture in tropical moist forest (MF), Brazil, and in tropical dry forest (DF), Mexico, landscapes.

Influence of Climate Change and Land Use on Rates of C Sequestration in Secondary Forests

One of the major gaps in our current knowledge regarding secondary forests concerns the amount of C they are capable of storing. Will secondary forests formerly occupied by pasture or agriculture have the potential to store an amount of C that is equivalent to the pool of the primary forest they replaced? Further, how will global climate change affect rates of C sequestration in secondary forests? With increases in temperature, increased frequency and duration of El Niño events, and possible changes in precipitation, both the potential C pool size and rates of C sequestration in secondary forest may be different from that measured from chronosequence studies of extant secondary forests (Cifuentes 2008).

Duration of land use represents one of the most important variables affecting C accumulation in regenerating forests in the tropics (Uhl and Jordan 1984, Uhl et al. 1988, Hughes et al. 1999). Rates of C sequestration have been shown to markedly decrease for abandoned sites with relatively long durations of land use. In a study conducted in the Brazilian state of Para, Uhl et al. (1988) reported that secondary forests of sites that had experienced relatively light intensities of land use had mean rates of aboveground biomass accumulation of 10.5 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$, while sites that experienced moderate land use had rates of 4.4 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$, and sites that experienced high intensity land use had rates of 3.3 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$. In tropical wet forests of southeastern Mexico, Hughes et al. (1999) found that duration of land use prior to abandonment strongly affected rates of aboveground biomass accumulation; sites with 1–7 years of land use attained the approximate biomass of primary forests within 31 years of abandonment, while sites that experienced 13–31 years of land use prior to abandonment required ~79 years to reach an equivalent level of aboveground biomass. However, primary forests and regenerating secondary forests are substantially different with regard to structure. While aboveground biomass of 20- to 50-yr-old secondary forests in tropical Mexico had roughly 65% of the biomass contained in primary forests of the area, they were quite different with regard to the structure and distribution of that biomass. Trees >70 cm dbh accounted for 44% of total aboveground biomass (TAGB) in primary forests but only 8% of TAGB in the older secondary forests. This has implications for changes in microclimate, fuels structure, and a higher potential risk of fires originating from adjacent lands under active use.

While aboveground C pools of secondary forests increase following abandonment, total soil C pools change to a much smaller degree. Along a secondary-forest chronosequence from 6 months to 50 years, Hughes et al. (1999) found that aboveground C pools ranged from 2 to 136 Mg/ha. These pools were positively correlated with forest age and negatively correlated with duration of land use prior to abandonment. In contrast, soil C pools (to 1 m depth) of these same forests ranged from 139 to 249 Mg/ha, and patterns of variation were not related to either forest age or duration of land use (Hughes et al. 1999). Similarly, De Camargo et al. (1999) found that differences in soil C pools among primary-forest, pasture, and secondary-forest sites of different ages were small and within uncertainties of their measurements. In Amazonia, Buschbacher et al. (1988) also found that surface soil organic-matter concentrations were similar among primary- and secondary-forest sites having experienced different levels of land-use intensity. Based upon analysis of soil pools in Amazonia, Hughes et al. (2002) and McGrath et al. (2001) concluded that soil C (and nutrient) pools were most strongly and positively related to clay content. Silver et al. (2000) predicted soil C accumulation rates in regenerating tropical forests ranged from 0.2 to 1.0 $\mathrm{Mg\ C \cdot ha^{-1} \cdot yr^{-1}}$ in secondary forests. These rates are within the sampling errors of most studies that have examined C dynamics along chronosequences of time since land-use abandonment. Marin-Spiotta et al. (2008) cautioned that bulk soil C measurements are often too coarse to detect changes over forest successional time periods, and may lead to the erroneous conclusion that soil C has not responded to land-use change.

Soil fertility has been shown to affect rates of C sequestration in secondary forests. Saldarriaga et al. (1988) suggested that the relatively low rates of aboveground biomass accumulation in late successional secondary forests were related to the highly weathered soils of the Amazon Basin, which tend to be low in available concentrations of soil cations (K, Ca, and Mg). In contrast, in relatively young volcanic soils in Mexico, rates of aboveground biomass accumulation in regenerating forests remained high for up to 50 years following abandonment (Hughes et al. 1999). Improved modeling efforts to describe the effects of soil characteristics (i.e., fertility, texture, chemistry) and prior land use on rates of aboveground biomass accumulation would greatly improve our ability to predict C sequestration across landscapes and regions.

It is important that scientists and policy makers gain a better understanding of C dynamics in the tropics. Feedbacks and synergistic influences of past land use with climate change, and how they influence potential rates of sequestration and storage is a crucial gap in understanding C dynamics (Lewis et al. 2004). Also of great uncertainty is the role of land use and the future of secondary forests, particularly in areas where subsistence agriculture is the dominant land use. One cannot assume that secondary forests will not be converted to other land uses in the future. Secondary forests may be little more than ephemeral stages of land use (i.e., a relatively brief fallow phase) and therefore not a relevant long-term C sink.

The great variation in structure, composition, and successional dynamics among forests in tropical landscapes complicates the prediction and monitoring of C dynamics (rates of C sequestration and loss). When scaling up beyond the individual patch level, the variation in rates of C sequestration associated with biota, climate, edaphic factors, land-use history, future changing land uses, and global climate change compound the uncertainties in C-dynamics modeling. Additional studies that link feedbacks between climatic, physical, biotic, and anthropogenic factors to C-dynamics in forest landscapes are needed to decrease these uncertainties and refine our understanding of the value of CDM C-offset/C-recovery projects.

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