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Loss of carbon sequestration potential after several decades of shifting cultivation in the Southern Yucatán

James M. Eaton, Deborah Lawrence *

Department of Environmental Sciences, University of Virginia, PO Box 400123, Charlottesville, Virginia 22904-4123, USA

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ABSTRACT

Cumulative losses from shifting cultivation in the tropics can affect the local to regional to global balance of carbon and nutrient cycles. We determined whether shifting cultivation in the Southern Yucatán causes feedbacks that limit future forest productivity and carbon sequestration potential. Specifically, we tested how the recovery of carbon stocks changes with each additional cultivation-fallow cycle. Live aboveground biomass, coarse woody debris, fine woody debris, forest floor litter and soil were sampled in 53 sites (39 secondary forests 2–25 years old, with one to four cultivation-fallow cycles, and 14 mature forests) along a precipitation gradient in Campeche and Quintana Roo, Mexico. From the first to the third or fourth cultivation-fallow cycle, mean carbon stocks in live aboveground biomass debris declined 64%. From the first to the third cycle, coarse woody debris declined by 85%. Despite declining inputs to soil with each cultivation-fallow cycle, soil carbon stocks did not further decline after the initial conversion from mature to secondary forest. The combined aboveground and soil carbon stock declined almost 36% after conversion from mature forest, however two additional cultivation cycles did not promote further significant decline, largely because of the stability of the soil carbon pool. Although age was the dominant factor in predicting total carbon stocks of secondary forests under shifting cultivation, the number of cultivation-fallow cycles should not be neglected. Understanding change beyond the first cycle of deforestation will enhance forest management at a local scale by improving predictions of secondary forest productivity and related agricultural productivity. A multi-cycle approach to deforestation is critical for regional and national evaluation of forest-based carbon sequestration. Finally, models of the global carbon cycle can be better constrained with more accurate quantification of carbon fluxes from land-use change.

1. Introduction

Land-use and land-cover change, primarily in forests, account for the second largest human-induced flux of carbon dioxide to the atmosphere, following the combustion of fossil fuels (Houghton and Skole, 1990; Canadell et al., 2007; IPCC, 2007). Yet, complete carbon inventories in secondary forests are still rare in many rapidly changing regions (Hughes et al., 1999, 2000b; Markewitz et al., 2004), including the seasonally dry tropical forests that represent 42% of tropical forests globally (Murphy and Lugo, 1986). The Maya Forest, spanning southern Mexico, Belize and Guatemala, is the second largest contiguous neotropical forest following Amazonia, and is considered a hot spot for both biodiversity and deforestation (Achard et al., 1998; Cincotta et al., 2000). The forest is being fragmented due to shifting cultivation, illegal logging and clearing of forest for pasture (Rodstrom et al., 1998; Turner et al., 2001). Land-use is altering the structure and function of these forest ecosystems (Read and Lawrence, 2003; Lawrence, 2005a; Lawrence et al., 2007) with potential feedbacks on the future carbon balance. More immediately, if productivity declines, both livelihoods and forest may suffer as farmers adapt. In this study, we analyzed the effect of shifting cultivation, the major cause of deforestation, on carbon stocks in the tropical dry forests of the southern Yucatán, focusing on both the history of cultivation and time since the most recent disturbance.

Accurate estimates of global carbon emissions depend on quantifying the carbon stocks in secondary forests. At the end of the 20th century, degraded and secondary forests accounted for roughly 60% of tropical forested areas (ITTO, 2002). They are increasingly regarded as an important carbon sink following the original losses associated with forest clearing. Estimated carbon emissions for Mexico vary by a factor of five, due in part to the misapplication of deforestation rates to different types of forest and in part to the paucity of data on carbon emissions from the

* Corresponding author. Tel.: +1 434 924 0581; fax: +1 434 982 2137.
E-mail address: dl3c@virginia.edu (D. Lawrence).

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forest sector (Masera et al., 1997). Quantifying the stocks of carbon in Mexico's different forest types (Cairns et al., 2000) will decrease this uncertainty. Addressing this uncertainty is critical as many tropical deforestation hotspots enter their third, fourth, or fifth decade of land-use change. Many tropical landscapes are now subject to a new, intensive disturbance regime; however the effect of repeated disturbance may be exacerbated in a drier environment. Houghton et al. (1991a,b) suggest an emphasis on explicitly sampling forests of several ages and land-use histories to reduce unquantified differences that lead to uncertainty in estimates of net carbon emissions.

The objective of this study was to test whether the number of prior cultivation-fallow cycles affects the recovery of carbon stocks in the Southern Yucatán Peninsular Region (SYPR). To this end, we simultaneously examined the influence of forest age and number of prior cultivation-fallow cycles while controlling for rainfall regime. We combined original and previously published data to estimate carbon in live aboveground biomass, woody debris, forest floor litter and soil. Previous research on these sites has demonstrated that live aboveground biomass increases rapidly with forest age (Read and Lawrence, 2003). Since both fine woody debris and forest floor litter mass are derived from live aboveground biomass, we hypothesized that age would be the dominant factor in determining the amount of carbon in these pools. Given that Yucatán forests are adapted to disturbance by hurricanes (and perhaps a long history of Mayan occupation), we did not expect that live aboveground biomass carbon would decline with an increase in the number of cultivation-fallow cycles. We hypothesized that repeated disturbance (increasing the cumulative number of burns) would decrease the carbon stored in coarse woody debris (Eaton and Lawrence, 2006). We expected soil organic carbon (SOC) stocks to increase in older forests after a period of loss following cultivation (e.g. Pregitizer and Euskirchen, 2004), but we were uncertain as to whether the fallow period is long enough to allow full recovery of SOC between cycles.

2. Methods

2.1. Study sites

We sampled three ejidos of southeastern Mexico, spanning a precipitation gradient in the states of Campeche and Quintana Roo: El Refugio (ER, ca. 890 mm/yr), Nicolás Bravo (NB, ca. 1150 mm/yr) and Arroyo Negro (AN, ca. 1400 mm/yr) (see Lawrence and Foster, 2002). The area is classified as tropical dry forest (Holdridge et al., 1971) with a mean annual temperature of 25 °C. Remote sensing indicates that the region is a patchwork of open agricultural land, secondary forests and mature forests, which still dominated 89% of the landscape in 1997 (Turner et al., 2001). The SYPR is mostly upland forested terrain classified as *Selva mediana subperennifolia* (medium semi-evergreen forest, Xuluc-Tolosa et al., 2003). In this karstic upland, high seasonal and yearly variation in precipitation combined with calcareous and highly permeable lithosol-redzina soils (Whigham et al., 1990) result in few permanent sources of surface water (White and Darwin, 1995).

Live aboveground biomass, forest floor litter and soil were sampled at 36 sites on several farms at each ejido. The sites included montañas ($n = 8$) and secondary forest in the fallow state following cultivation (aged 2–25 yr, $n = 28$, Table 1). Montañas are areas of mature forest that were probably disturbed by selective logging from 1930 to 1960 (Klepeis, 2000) but have never been cleared in recent history. Brown and Lugo (1982, 1990) assert that secondary tropical dry forest can attain a biomass similar to mature forest after 50 years of regrowth following cultivation. In the Yucatán, however, recovery from shifting cultivation may take 55–95 yr (Read and Lawrence, 2003). It is unclear how fast the forests would recover from selective logging.

Secondary forests had experienced one to four cycles of shifting cultivation with a fallow period of 2–15 years. Only patches cultivated for maize and those which have not received chemical inputs (fertilizer, pesticide, or herbicide) were included. Woody debris required more intensive sampling, as it is highly variable at small spatial scales (Eaton and Lawrence, 2006). Focusing on El Refugio, woody debris was sampled at 23 forested sites: 3 young, 8 middle-aged and 6 old secondary forests, and 6 montañas (Table 1).

2.2. Forest components

Read and Lawrence (2003) estimated aboveground biomass >1 cm DBH (diameter at breast height) in ER, NB and AN using stand inventories from 500-m^2 plots and regression equations for trees (Martínez-Yrizar et al., 1992), palms (Hughes et al., 1999) and lianas (Gerwing and Lopes Farias, 2000). We converted these biomass data to carbon stocks using a carbon value of 45% (Woomer and Palm, 1998). Mean annual aboveground biomass carbon accumulation rate was estimated by dividing aboveground biomass by secondary forest age.

Coarse woody debris (diameter ≥10 cm) was inventoried in two randomly located 16-m radius plots per site (1608 m^2 total). For all coarse woody debris, the length, diameter to the nearest cm, and decay class were recorded (Harmon et al., 1986; Pyle and Brown, 1998; for details see Eaton and Lawrence, 2006). Mass of coarse woody debris was calculated for each site using volume and density by decay class (after Harmon and Sexton, 1996). Coarse woody debris volume included standing dead wood and was corrected for hollow sections in fallen logs (after Clark et al., 2001). Samples from 62 cross sections of coarse woody debris were dried at 60 °C to a constant weight, ground to a fine powder using a Wiley Mill and analyzed for percent carbon using a Carlo Erba NA 2500 Elemental Analyzer. Because percent carbon did not differ significantly by decomposition class, carbon stocks were determined from mass and mean percent carbon, 46.84%.

Stocks of fine woody debris were measured in eight 1-m^2 quadrats within each coarse woody debris plot (total 16 m^2 per site). Fine woody debris ≥1.8 cm and ≤10 cm diameter was collected and weighed. Sub-samples were dried at 60 °C to determine dry mass of fine woody debris. This was converted to a carbon stock using the mean percent carbon value for coarse woody debris, 46.84%.

Fine litter on the forest floor (including wood <1.8 cm in diameter) was collected from four 1-m^2 quadrats in each of the 36 aboveground biomass sampling sites (Table 1). Our estimate of forest floor litter mass represents a minimum value for a pool that fluctuates seasonally. The collection was made at the end of the wet season (November-December 1999), seven to eight months after peak litter fall. Carbon stocks were calculated from the dry mass and corresponding carbon value, determined by dry combustion.

We sampled the top 15 cm of soil by compositing 8 cores (2.5 cm diameter) at four locations, 8 m from the center point along orthogonal axes, for a total of 32 cores per plot. In addition, at each plot, one hole was dug to sample at a depth of 45–55 cm and 90–100 cm. Lawrence and Foster (2002) reported on soil texture and organic matter in the top 15 cm; here we report a new analysis of carbon content in the surface soils and soils at depth. Soils were sieved (<2 mm), air dried and stored in Ziploc bags.

Because of the predominance of calcium carbonate in the soil, we determined percent organic carbon as the difference between total and inorganic soil carbon (Ellert et al., 2001; Schumacher,

Table 1
Live aboveground biomass, forest floor litter, soil, coarse woody debris and fine woody debris sampling sites in the SYPR.

Town	Site name	Age[a]	# of cultivation-fallow cycles	LAB, FFL, Soil[b]	CWD, FWD[c]
AN	Antonio	4	4	X	
AN	Gilberto	5	1	X	
AN	Fermin	5	2	X	
AN	Gilberto	7	2	X	
AN	Antonio	8	2	X	
AN	Fermin	9	3	X	
AN	Fermin	15	2	X	
AN	Antonio	18	2	X	
AN	Antonio	Montaña	0	X	
AN	Jose	Montaña	0	X	
ER	Hermelindo	2	1	X	X
ER	Juventino	3	2	X	X
ER	Juan	4	2	X	
ER	Hermelindo	5	1	X	X
ER	Raphael	5	1		X
ER	Juan	5	3		X
ER	Cornelio	7	2		X
ER	Domingo	7	2		X
ER	Cornelio	8	1		X
ER	Juan	8	1	X	
ER	Rufino	8	1	X	
ER	Raphael	9	1		X
ER	Juventino	10	1	X	X
ER	Juventino	10	3		X
ER	Cornelio	11	2		X
ER	Hermelindo	12	1	X	X
ER	Juan	12	1	X	X
ER	Juventino	12	1	X	
ER	Domingo	13	2		X
ER	Raphael	14	1		X
ER	Juan	16	1		X
ER	Camino Principal	Montaña	0	X	
ER	Claudio	Montaña	0		X
ER	Cornelio	Montaña	0		X
ER	Domingo	Montaña	0		X
ER	Juan	Montaña	0		X
ER	Juventino	Montaña	0		X
ER	Raphael	Montaña	0		X
ER	Roberto	Montaña	0	X	
ER	Victor	Montaña	0	X	
NB	Agustin	3	3	X	
NB	Enrique	5	2	X	
NB	Pedro	5	2	X	
NB	Agustin	6	2	X	
NB	Benito	8	2	X	
NB	Pedro	16	2	X	
NB	Benito	18	1	X	
NB	Pedro	24	1	X	
NB	Agustin	25	1	X	
NB	Enrique	25	1	X	
NB	Calakmulita	Montaña	0	X	
NB	NB1	Montaña	0	X	
NB	NB2	Montaña	0	X	

[a] Age of successional forest in January 1999.
[b] LAB, FFL and soil were sampled in January 1999.
[c] CWD and FWD were sampled in May 2002.

2002). Percent total C was determined by combusting untreated soil samples (as above, for coarse woody debris). Then, sub-samples were placed in a muffle furnace at 500°C for 6 h to release organic carbon. This treated sub-sample was then combusted to determine the mass of inorganic C remaining. Mass of inorganic C was divided by the original mass of soil that entered the muffle furnace to yield the concentration of inorganic C. This method corrects for the mass loss of organic matter and structural soil water due to combustion. Percent organic carbon was calculated by subtracting the corrected percent inorganic carbon from the percent total carbon. The traditional method of rinsing with acid to release inorganic C prior to analysis was complicated by fungal growth between sequential rinses. Thus, we adopted this alternative approach, which yielded results that were not significantly different from the traditional method (t-test, $n = 20$, n.s.).

Soil organic carbon stocks were calculated by multiplying bulk density by percent organic carbon for each centimeter of depth (Woomer et al., 2001) and summing over the depth of soil for each site (usually at least 100 cm, but as shallow as 63 cm in a few cases). Organic carbon content for 0–15 cm, 45–55 cm and 90–100 cm was determined directly. For the remainder of the profile, percent organic carbon for each centimeter of depth was estimated from exponential regressions developed for each of the 36 stands (after Walker and Desanker, 2004). The midpoint of each depth class (0–15 cm, 45–55 cm and 90–100 cm) was used to predict percent carbon. Where the soil profile did not extend to 100 cm, the deepest 10 cm was sampled and its midpoint used in regressions. Soil bulk density was calculated for each site using organic matter, clay content and silt content (Rawls, 1983) of samples 0–15 cm deep. Bulk density estimates ranged from 0.54–1.01 g/cm^3, with a mean of 0.83 $\pm$ 0.08 (standard deviation). These estimates are similar to other estimates from the region: 0.5 g/cm^3 in Yucatán state to the north (Campo and Vázques-Yanes, 2004) and 0.56–1.25 g/cm^3 in Guatemala to the south (Popenoe, 1957). We assumed conservatively that bulk density did not increase with depth, which results in a lower bound on soil carbon.

2.3. Statistical analyses

Carbon stocks in each of the five forest components were initially examined as a function of soil texture, forest age, number of prior cultivation-fallow cycles, and location along the precipitation gradient. Soil texture was not a significant factor and was subsequently dropped from the model. Analysis of covariance (ANCOVA) was used to account for a negative correlation between two of the three potential drivers of carbon stocks: number of prior cultivation-fallow cycles and forest age. Age and cycles were treated as continuous variables to test for a linear response in either; they were treated as categorical variables to test for a non-linear response. In either case, region was treated as a fixed categorical factor. In addition to the class of montañas, deforested lands were classified into three categories: young (1–5 yr), middle (6–11 yr) and old (12–25 yr) secondary forest. When treating age as a continuous variable, we set an age of 75 years for montaña, based on the mean rate of biomass recovery following shifting cultivation in the Yuctan (Read and Lawrence, 2003). Sensitivity analysis suggested little difference in results for montaña age from 50–200 years (see also Lawrence et al., 2007).

Pairwise comparisons and Tukey's honest significant difference (Tukey HSD) test were used to determine differences among means following a significant ANCOVA or ANOVA, respectively. Live aboveground biomass was square root transformed in order to meet the assumptions of ANOVA (Sokal and Rohlf, 1995). The back-transformed means were presented with 95% confidence limits. Neither raw nor transformed coarse or fine woody debris data met the assumptions of ANOVA, so woody debris results should be interpreted with caution. Where ANCOVA showed significant effects of the number of cultivation-fallow cycles, we followed up by excluding montaña, to focus on the effects in secondary forest. From this set of analyses, we reported marginal means for one, two, and three or more cycles, where forest age is assumed to be 9.8 years. For montañas, we reported arithmetic means.

The effects of age on secondary forest carbon stocks were further analyzed by regression with best-fit models. These analyses provided finer resolution of carbon dynamics with forest age but they do not account specifically for region or cycles. Coarse and fine woody debris were analyzed using a similar ANCOVA without the regional component, as woody debris was sampled at one area only. Age-class-specific coarse and fine woody debris means (derived in El Refugio) were used for all regions to estimate combined aboveground and soil carbon stocks. Tests were carried out using SPSSv.11.5 (2002).

3. Results

3.1. Live aboveground biomass

The carbon stocks in live aboveground biomass ranged from 4.8 Mg ha^{-1} in a three year old secondary forest to 73.5 Mg ha^{-1} in montaña. Age, region and the number of cultivation-fallow cycles all significantly affected the carbon stocks in live aboveground biomass (complete ANCOVA, $p < 0.001$). Aboveground live biomass carbon declined with the number of cultivation-fallow cycles (Fig. 3a, ANCOVA history effect $p = 0.025$); decreasing ca. 64% from one to three or four cycles. Forests in the northern-most ejido (El Refugio) held significantly less live aboveground biomass carbon than those in the central ejido (Nicolás Bravo, $p = 0.011$) but did not differ significantly from those in the ejido furthest south (Arroyo Negro, $p = 0.416$).

After 24–25 years following one cycle of cultivation, secondary forest held ca. 62% of the live aboveground biomass carbon in montañas (mean of 37.7 versus 60.9 Mg ha^{-1}), accumulating carbon at an average rate of 1.2 Mg ha^{-1} yr^{-1} (Fig. 1a). Without adjusting for number of cycles, mean annual carbon accumulation rate declined significantly with forest age (up to 5.8 Mg ha^{-1} yr^{-1} in a 5 year old forest, and1–2 Mg ha^{-1} yr^{-1} in 25 year old forest, Fig. 2). Modeled as a function of age, carbon accumulation rate shows a 66% decline from 2 to 25 years, most of which (42%) occurs between 2 and 10 years. This estimate is conservative, as the younger sites tended to have experienced more cycles, and thus their measured accumulation rate was relatively low compared to that of the older sites.

3.2. Forest floor litter

Forest floor litter carbon ranged from 0.5 to 4.4 Mg ha^{-1} at the end of the wet season. It increased logarithmically with age in secondary forests from ca. 1.5 Mg ha^{-1} in 2-year old forest to ca. 2.8 Mg ha^{-1} after 15 years (Fig. 1b). Stocks in the oldest secondary forests were smaller but did not significantly differ from stocks in montaña (3.4 Mg ha^{-1}, two-way ANOVA, Tukey HSD, $p \leq 0.160$). Forest floor litter carbon was lower in El Refugio than in Nicolás Bravo (two-way ANOVA, Tukey HSD, $p = 0.026$) and Arroyo Negro (Tukey HSD, $p = 0.009$) but did not significantly differ between the latter. Despite a significant 20% decline in litter production following two cycles cultivation (Lawrence et al., 2007), forest floor litter stocks did not decline significantly with the number of prior cycles (ANCOVA history effect $p > 0.05$, Fig. 3b).

3.3. Woody debris

Coarse woody debris carbon stocks were highly variable and ranged from 0.4 to 24.3 Mg ha^{-1}. These stocks were almost three times as large in montaña (14.8 Mg ha^{-1}) as in secondary forest (5.1 Mg ha^{-1}) (ANOVA, $p = 0.005$). Fields currently under cultivation (age 0) do have significantly higher coarse woody debris stocks than the secondary forests that succeed them (Eaton and Lawrence, 2006), indicating early, rapid change with age not captured by looking at secondary forests alone (Fig. 1e). Coarse woody debris carbon declined by ca. 85% from the first to the third cultivation-fallow cycle (ANCOVA history effect $p = 0.056$, Fig. 3e). The number of cycles was not a significant factor in predicting the carbon stocks of fine woody debris (Fig. 3d). These stocks ranged from 1.3 to 3.0 Mg ha^{-1}. Fine woody debris stocks declined initially with age if current fields were included (Fig. 1d). Among forests, stocks tended to be higher in montaña and young secondary forests and lower in older secondary forest, but ANCOVA revealed no significant differences.

3.4. Soil

Estimated soil organic carbon in the top 1 m of soil was very high, ranging from 155–394 Mg ha^{-1}. Soil organic carbon tended to be high in the youngest forests, lower in middle-aged forest and

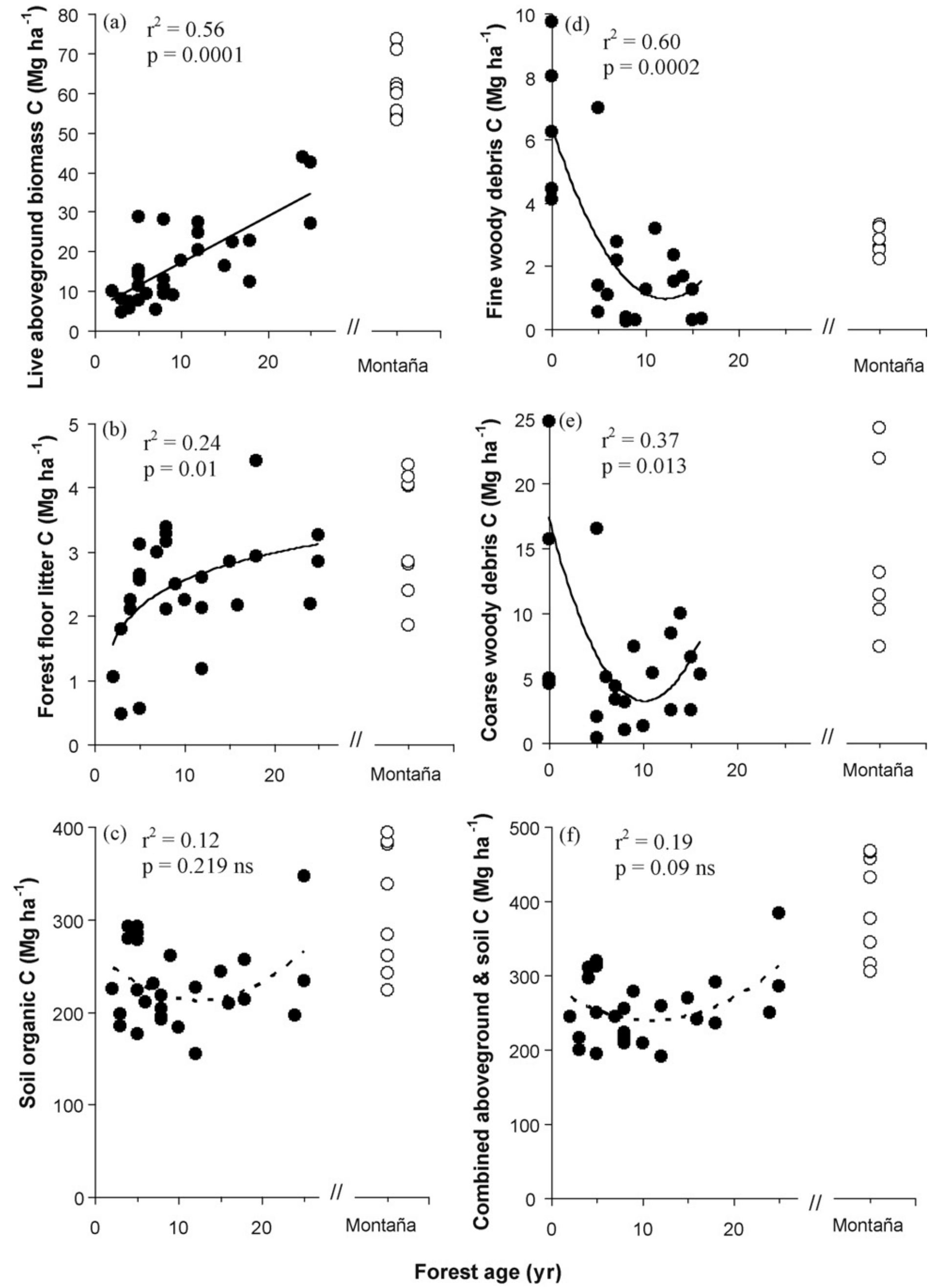

Fig. 1. Carbon in all forest components as a function of secondary forest age. Live aboveground biomass (a) includes all stems >1 cm DBH. Forest floor litter (b) includes leaves, reproductive parts and small branches up to 1.8 cm in diameter. Soil organic C (c) was determined to 1 m. Fine woody debris (d) includes dead wood between 1.8 and 10 cm in diameter. Coarse woody debris (e) includes dead wood >10 cm in diameter. Combined aboveground and soil C (f) was determined by adding all components within a stand; for stands in Nicolás Bravo (NB) and Arroyo Negro (AN) where woody debris was not measured, mean values per age class (generated in El Refugio, ER) were added to individual stand values. Solid lines are the best-fit regressions between forest age and individual carbon pools. Dashed lines indicate non-significant trends that were highly significant if montañas were included ($r^2 = 0.30$–0.55).

high again in older secondary forest (Fig. 1c). Montañas, with a mean of 322 Mg ha^{-1} (Table 2) had significantly more soil organic carbon than all secondary forest (two-way ANOVA, Tukey HSD, $p < 0.05$), but they had only 17% more soil carbon than the three oldest secondary forests, 24–25 years old. Soil organic carbon was significantly lower in El Refugio, the site with the least precipitation, than in Arroyo Negro, the site with the most precipitation (two-way ANOVA, $p = 0.006$). The number of cultivation-fallow cycles did not significantly affect soil organic carbon stocks (ANCOVA, $p > 0.05$, Fig. 3c).

3.5. Combined aboveground and soil organic carbon pools

The combined aboveground and soil carbon stocks of forests in the SYPR varied more with age than across the region (Table 3), ranging from 192 Mg ha^{-1} in a twelve year old secondary forest of El Refugio to 469 Mg ha^{-1} in a montaña of Arroyo Negro. Combined aboveground and soil carbon stocks were largest in montañas (mean 396 Mg ha^{-1}), followed by young and old secondary forests (Fig. 1f). As for soil carbon, combined stocks tended to be lowest in middle-aged secondary forests. Mean combined aboveground and

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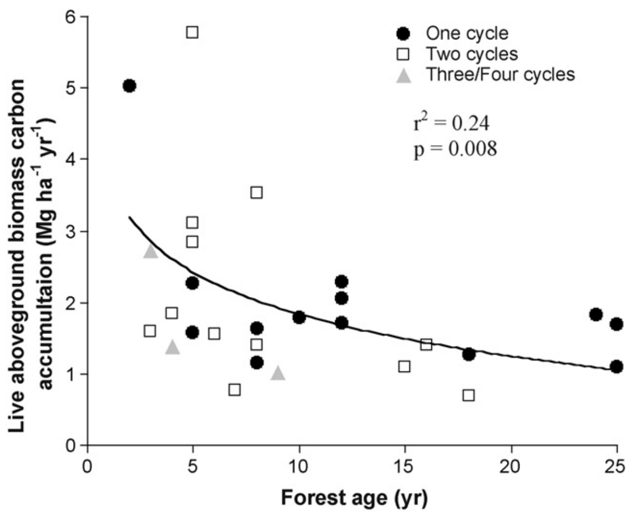

Fig. 2. Accumulation rate of carbon (Mg C ha^{-1} yr^{-1}) in live aboveground biomass as a function of forest age in the southern Yucatán region. All secondary forest sites are included.

soil carbon stocks for the oldest three secondary forests (306.8 Mg ha^{-1}) were 22% lower than stocks in montañas.

Soil organic carbon dominated combined aboveground and soil stocks for each age class, comprising a mean of 79% of stocks in montañas and 91% of stocks in younger forests (Fig. 4). Combined aboveground and soil carbon stocks tended to increase along the precipitation gradient. El Refugio, in the drier north, had the lowest carbon stocks (mean of 226 Mg ha^{-1} in secondary forests). The largest stocks, 18% higher, were in Arroyo Negro (mean of 276 Mg ha^{-1} in secondary forest). The first cultivation-fallow cycle reduced the combined carbon stock almost 36%, but further cycles had no significant effect (Fig. 3f).

4. Discussion

Age was the main predictor of carbon stocks for all but one forest component, including soil carbon, the dominant pool. The number of prior cultivation-fallow cycles was also important as it significantly affected both coarse woody debris and live aboveground biomass, the second largest and most dynamic pool. In contrast with results from wetter tropical forests, live aboveground biomass carbon declined with repeated cultivation over the first three to four cycles in the dry forests of the southern Yucatán (Fig. 3a). With fallow periods in the range of those observed here (2–15 years), two to four cycles of shifting cultivation in Brazil and Bolivia had no significant effect on live biomass carbon (Hughes et al., 2000b; Steininger, 2000). Lawrence (2005), working in Indonesia on long-fallow (20 yr) shifting cultivation, did observe a decline in biomass increment from four to ten cycles, but it did not differ between one and four cycles. Working in the Amazon, Zarin et al. (2005) also found carbon accumulation to be reduced by half after 5 burns (not always 'cycles' as defined here).

For farmers, the decline in aboveground biomass and woody debris result in fewer nutrient inputs to cultivation, potentially limiting productivity in the short term. In the long term, reductions in these carbon stocks mean lower inputs to soil organic matter from decomposition of uncombusted material following each successive burn. In addition, because litter production is positively correlated with aboveground biomass (Lawrence, 2005b), litter inputs to soil organic matter are also likely to decline. Lower soil organic matter may reduce the rate of nutrient supply, further limiting crop productivity and feeding back on biomass accumulation during the fallow period. For policy makers at regional to international scales, a projected reduction in the soil C pool during future cultivation cycles marks a significant loss of sequestered carbon and, because of feedbacks on nutrient cycling, of future sequestration potential.

Estimates of carbon stocks in live aboveground biomass for montañas (57.3–68.1 Mg ha^{-1}) are similar to those found by Cairns et al. (2000) for Quintana Roo and Campeche (59.9 Mg ha^{-1}). Jaramillo et al. (2003) also calculated similar carbon stocks (58.3 Mg ha^{-1}) in a drier forest of Chamela in Jalisco, Mexico (679 mm/yr). We derived much higher C stocks (86.4 Mg ha^{-1}) in aboveground biomass using data from Urquiza-Haas et al. (2007) who worked in the states of Campeche and Yucatán, just adjacent to the SYPR. Despite small variations, the overall magnitude of potential losses associated with land-use should be similar for the major areas of dry forest in Mexico. Although potential losses are similar for dry forests, they seem to recover these losses quickly. After 25 years, secondary forest in the SYPR contained 62% of the

Table 2
Estimated carbon stock (Mg ha^{-1}) by forest component, age class and study area (El Refugio, ER, ca. 890 mm/yr; Nicolás Bravo, NB, ca. 1150 mm/yr; Arroyo Negro, AN, ca. 1400 mm/yr; and the average for the Southern Yucatán Peninsular Region, SYPR).

Forest carbon (Mg ha^{-1})	Region	Young (1–5 years)			Middle (6–11 years)			Old (12–25 years)			Montaña		
		Estimate	+	–	Estimate	+	–	Estimate	+	–	Estimate	+	–
LAB[Aa]	ER	8.1	4.8	3.7	11.8	6.8	5.2	22.3	9.0	7.5	57.4	4.2	4.2
	NB	22.1	10.6	8.5	13.2	9.3	6.9	30.3	7.8	6.9	68.1	4.2	4.2
	AN	14.5	8.8	6.7	17.6	9.6	7.5	17.8	10.6	8.2	57.3	5.1	5.1
	SYPR	14.3	5.1	4.3	14.1	4.8	4.1	23.2	5.1	4.6	60.9	2.6	2.6
CWD[B]	ER/SYPR	6.3	2.9	2.9	3.9	1.8	1.8	5.9	2.0	2.0	14.8	2.0	2.0
FWD[Bb]	ER/SYPR	3.0	0.8	0.8	1.4	0.5	0.5	1.2	0.6	0.6	2.8	0.6	0.6
FFL[B]	ER	1.4	0.4	0.4	2.5	0.4	0.4	2.0	0.4	0.4	2.5	0.4	0.4
	NB	1.9	0.4	0.4	3.3	0.8	0.8	3.0	0.3	0.3	3.6	0.4	0.4
	AN	2.7	0.4	0.4	3.0	0.4	0.4	2.9	0.5	0.5	4.1	0.5	0.5
	SYPR	2.0	0.2	0.2	2.9	0.3	0.3	2.6	0.3	0.3	3.4	0.3	0.3
Soil[B]	ER	219.5	22.9	22.9	189.7	26.4	26.4	190.6	32.4	32.4	294.9	26.4	26.4
	NB	233.3	26.4	26.4	207.2	32.4	32.4	248.7	20.5	20.5	282.0	26.4	26.4
	AN	286.0	26.4	26.4	236.6	26.4	26.4	228.4	32.4	32.4	388.8	32.4	32.4
	SYPR	246.3	14.6	14.6	211.2	16.5	16.5	222.6	16.7	16.7	321.9	16.5	16.5

Estimates are based on estimated marginal mean plus or minus, the confidence limit[A] or standard error[B].
[a] Estimates of live aboveground biomass in secondary forest assume 1.21 cultivation-fallow cycles. Montaña estimates are arithmetic means.
[b] Estimates of fine woody debris in secondary forest assume 1.31 cultivation-fallow cycles. Montaña estimates are arithmetic means.

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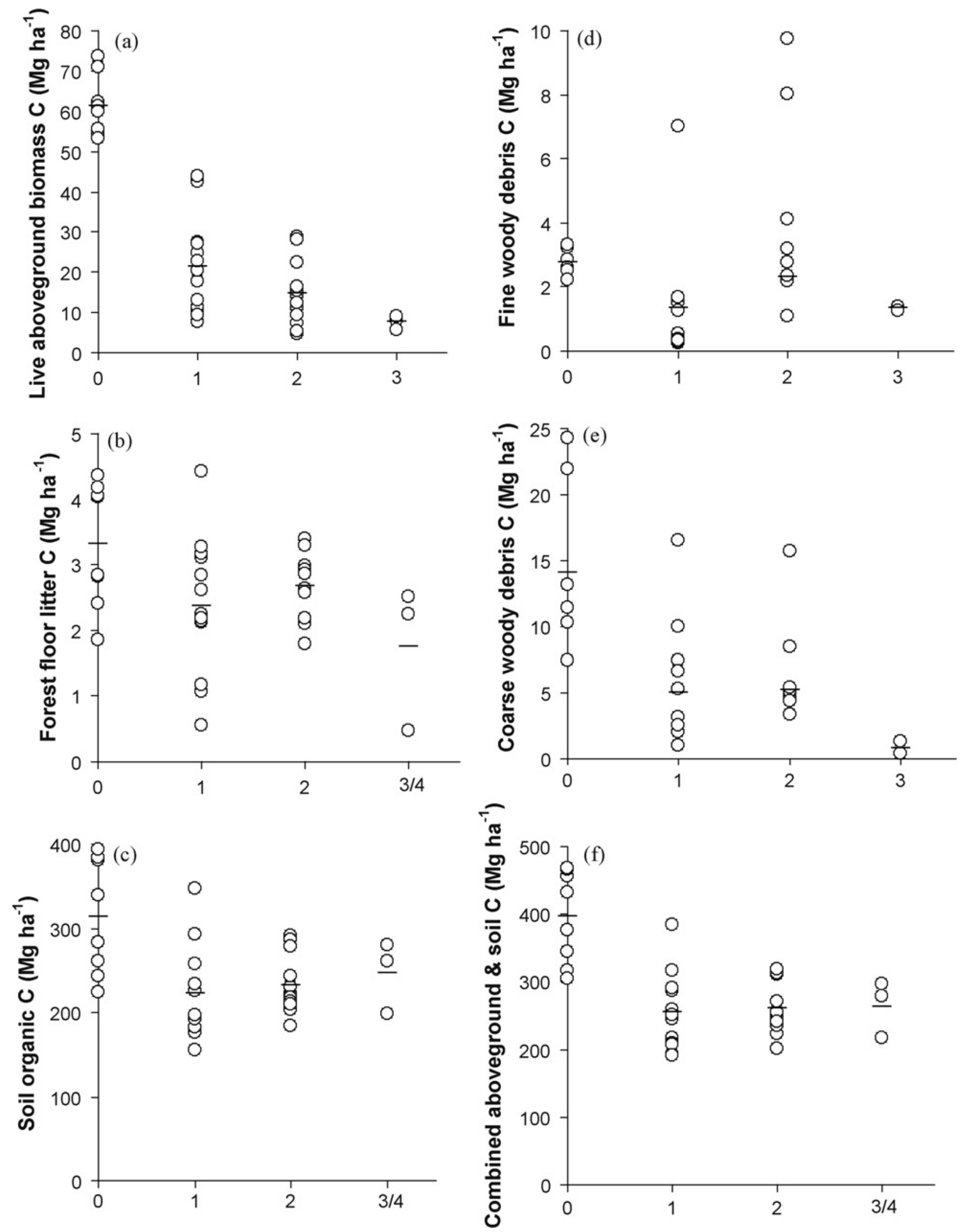

Fig. 3. Carbon as a function of the number of prior cultivation-fallow cycles in (a) live aboveground biomass ($p < 0.05$), (b) forest floor litter, (c) soil, (d) fine woody debris, (e) coarse woody debris ($p < 0.05$), and (f) combined soil and aboveground pools. Horizontal lines represent the marginal mean (except for montañas, with arithmetic mean). The circles represent site-specific data; "0" prior cultivation-fallow cycles are montañas.

live aboveground biomass found in mature forests, whereas a wet tropical forest in the Amazon only contained 50% (Gehring et al., 2005). We note, however, that recovery slowed with each cycle in the dry forests of the Yucatán.

As expected, forest floor litter carbon increased with age, consistent with both an increase in litter production (Lawrence, 2005) and a decline in decomposition rate with forest age (Xuluc-Tolosa et al., 2003). Carbon in fine woody debris (1.8–10 cm in

Table 3
Combined aboveground and soil carbon stocks (Mg ha^{-1}) for several forest areas in Mexico (derived from the sum of all components at a given site). Means for the areas in this study represent the average of the sum, rather than the sum of the average component values (as calculated from Table 2).

Location	2–5 yr	6–11 yr	12–25 yr	Montaña	PPT (mm/yr)	Source
Chamela, Jalisco	–	–	–	141	679	Jaramillo et al., 2003[a]
El Refugio, Campeche	238	211	225	372	890	This study
Nicolas Bravo, Quintana Roo	262	223	291	371	1150	This study
Arroyo Negro, Campeche	308	259	253	468	1400	This study
Los Tuxtlas, Veracruz	297	–	314	405	4700	Hughes et al., 1999, 2000a

[a] Maximum soil depth was 60 cm. This study also included root biomass carbon.

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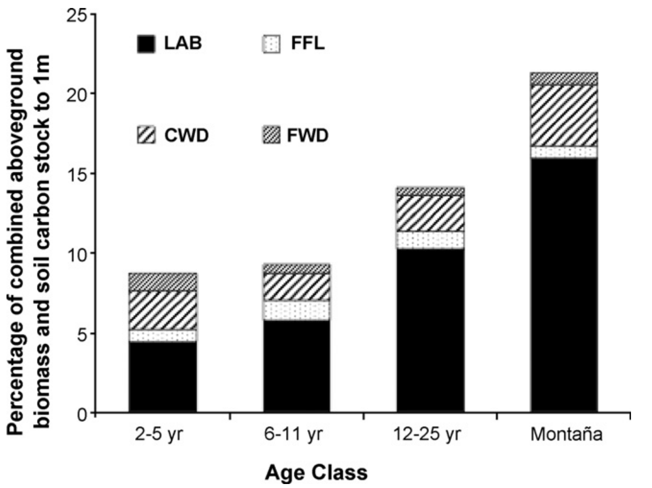

Fig. 4. Aboveground carbon pools in relation to combined aboveground and soil carbon stock (to 1 m soil depth) by age class. Mean stocks in live aboveground biomass (LAB), forest floor litter (FFL), coarse woody debris (CWD) and fine woody debris (FWD) were calculated by region, except for CWD and FWD, which were measured only in El Refugio. Regional means were then averaged to yield one value for each age class. These values were then summed to determine the distribution of carbon between soil and aboveground stocks as a function of age class.

diameter), which should be related to live biomass, did not respond as predicted. A shift in the source of fine woody debris may explain why stocks did not change significantly with age. In young secondary forest, much of the stock is derived from incomplete biomass burning. In this case, the actual source of FWD is the previous forest. In older secondary forest, most FWD is derived from thinning of stems and branch fall, rather than the burn that initiated forest regeneration. Initial stocks derived from burning the previous forest are soon lost, as fine woody debris decomposes twice as fast as coarse woody debris (Eaton and Lawrence, 2006). They are replaced with stocks generated by the current forest.

The carbon pool in coarse woody debris is both sizeable and dynamic on multiple timescales. As a percent of total aboveground biomass carbon, coarse woody debris carbon decreased from approximately 30% in young secondary forest to 18% in montaña. These values are consistent with estimates of 10–20% in mature forests of North and South America (Turner et al., 1995; Delaney et al., 1998) but less than the 27–29% estimate for mature forest at Chamela (Jaramillo et al., 2003) and the 25% estimate for a mature rainforest in Costa Rica (derived from Clark et al., 2001).

In secondary forests, change in coarse woody debris is greater from cycle to cycle than from one age class to the next. The effectiveness of the burn prior to cultivation influences pool size during the first cycle of regrowth. Compared to aboveground biomass stocks in montaña, stocks of biomass that would create coarse woody debris are generally much smaller before the burn initiating the second cycle (Fig. 1a). Thus, even if the intensity of the burn is the same, inputs of coarse woody debris decrease each time an area is slashed and burned. Inputs in addition to those derived from the burn itself are few (Eaton and Lawrence, 2006). Trees can reach 10 cm DBH (the minimum cut-off for coarse woody debris) within 8–10 years, but these rapidly growing trees are not likely to die or suffer large branch mortality at this age, unless an escaped or wild fire moves through the stand. Relatively little difference in stocks of young and old secondary forests suggests that decomposition of coarse woody debris slows with time. Both live aboveground biomass and coarse woody debris carbon are dynamic through the course of succession following deforestation and also through the course of subsequent disturbance and succession. Models depicting carbon fluxes due to land-use change at decadal time scales must account for this dynamic shift.

Estimates of soil organic carbon stocks in the SYPR are among the highest reported for mature tropical forests (to 1 m). They are two to five times larger than the 76 Mg ha^{-1} of soil carbon quantified by Jaramillo et al. (2003) for soils to 60 cm in Chamela. Even scaled to 100 cm, soil stocks in southwestern Mexico are less than half those observed in southeastern Mexico. Litter inputs are 28% higher in the Yucatán (6.8 versus 5.3 Mg ha^{-1} yr^{-1} in montaña; Lawrence, 2005 and Martínez-Yrizar and Sarukhan, 1990). However, total rainfall is also somewhat higher, so mineralization of soil organic carbon is likely to be faster, not slower. The major difference between these dry forests appears to be soil type. Although both sites have shallow upland soils, Chamela soils are sandy typic ustorthents derived from rhyolite (Jaramillo et al., 2003), while soils in the SYPR area are highly organic lithosol/redzina soils derived from limestone (Whigham et al., 1990).

The calcareous soils of the Yucatán impede decomposition and organic carbon turnover (Shang and Tiessen, 2003). Comparing shifting cultivation systems, Shang and Tiessen (1997, 1998) found one tenth as much soil organic carbon in a region of Brazil with a similar climate as they found in the soils of the Yucatán. Working in dry secondary forests on limestone-derived soils in Puerto Rico, Lugo et al. (1986) found 77–90 Mg of carbon stored in the top 25 cm of soil. Scaled to 1 m, this is the same order of magnitude as found in the Yucatán. The soils of a dry tropical forest in Venezuela have also demonstrated a high capacity for binding organic carbon, with stocks similar to ours (233 Mg ha^{-1} to 1 m, Delaney et al., 1997).

The conversion of forest to cropland and the resulting decrease of soil carbon is well documented, however the recovery of soil carbon following return to secondary forest is less well studied (reviewed in Murty et al., 2002). In post-agricultural soils of dry forests in Puerto Rico, organic carbon increased with time since abandonment, reaching mature forest levels after 30 years (Lugo et al., 1986). Our study broadly agrees, demonstrating that a 25-year fallow period can replenish soil carbon stocks to within 90% of mature forest levels. However, the data suggest a decline in soil organic carbon stocks during the first 5–10 years of regrowth, followed by an increase (also seen globally in secondary forests, e.g. Pregitizer and Euskirchen, 2004). The current fallow period in the Yucatán is often less than 12 years (Turner et al., 2001), half the time needed to recover 90% of mature forest levels. Thus, regional soil carbon stocks defined by current management are probably reduced by substantially more than 10%, perhaps by as much as 30% (Fig. 1c). Lower soil carbon stocks in young secondary forests are most likely due to reduced organic matter inputs (Raich, 1983; Powers, 2004), higher rates of decomposition (Xuluc-Tolosa et al., 2003) and a breakdown of the protective capacity of the soil (Shang and Tiessen, 2003).

Fortunately for local and national stakeholders, despite loss during the first cycle following forest conversion, soil carbon did not decline further with each cultivation-fallow cycle in the Yucatán. As shown by Powers (2004), initial loss of soil carbon occurs rapidly, while recovery and further loss are slower processes. High capacity for carbon fixation may protect the soils from continued losses with each cycle, as suggested by research on soil carbon dynamics following cultivation in allophane-rich soils (Hughes et al., 1999) and clay-rich versus sandy soils (Lugo et al., 1986). However, a demonstrated loss of inputs from live above-ground biomass and coarse woody debris is likely to result in continued losses of soil carbon in the future.

The percent of combined aboveground and soil carbon in soil (87%) is high for dry forest compared to the value of ca. 50% in

Mexican wet forest (Hughes et al., 1999, 2000a). In two mature Venezuelan dry forests, Delaney et al. (1997) found the soil component comprised 68% of the total ecosystem carbon in the drier of the two (800 mm/yr) and only 41% in the wetter (1500 mm/yr). A similar precipitation increase in this study, from ca. 890–1400 mm/yr, did not lessen the contribution of soil carbon. Because soil bulk density often increases with depth, and we assumed constant bulk density, we may have underestimated soil carbon stocks. If so, soils would constitute an even larger proportion of combined aboveground and soil carbon to 1 m.

Large soil carbon stocks dominated the prediction of combined aboveground and soil carbon stocks. Because age was a main predictor of all forest components, it is not surprising that it was the sole significant predictor of combined aboveground and soil carbon stocks. Significant variation in non-soil carbon stocks due to precipitation or the number of prior cultivation-fallow cycles was overshadowed by the influence of soil organic carbon on combined aboveground and soil carbon stock estimates.

Combined aboveground and soil carbon stocks, calculated for mature forest in each area (Table 3) are closer than might be predicted based on the precipitation gradient, but they are within the range observed for other forests in Mexico. Because soil carbon represents a larger proportion of the total, changes in ecosystem carbon stocks following land-use are not driven primarily by losses in aboveground biomass, as found in previous studies (e.g. Kauffman et al., 1995; Trumbore et al., 1995; Hughes et al., 2000a). Although carbon stocks are thought to recover quickly following one cycle of disturbance (Lugo et al., 1986; Brown and Lugo, 1990), current land-use practices, with fallow periods of less than 12 years, prevent full recovery in the southern Yucatán during the first cycle. The rate of recovery in subsequent cycles is slower still. Adaptive management will be required as the implications become clear for farmers and other stakeholders from the regional to the international level.

5. Conclusion

Forest age was the dominant influence on the size and distribution of forest carbon stocks. Monotonic increase occurred only for live biomass and forest floor litter stocks, whereas woody debris and soil tended to show an initial decline before increasing with forest age. Current fallow practices limit combined aboveground and soil carbon recovery to less than 66% of montaña (mature forest) levels. With no effect of repeated cultivation, but continued conversion for agriculture, the region will continue to be a net source of carbon to the atmosphere. Assuming a fallow length of 6–11 years, each hectare of mature dry tropical forest converted to shifting cultivation could mean a net loss of 162 Mg of carbon. This flux would be exacerbated if carbon recovery declines with repeated cultivation. The onset of cultivation depressed carbon stocks in the three largest carbon pools: soil organic carbon, live aboveground biomass and coarse woody debris. Repeated shifting cultivation further depressed carbon stocks in live aboveground biomass and coarse woody debris and carbon fluxes in litter. Additional cycles of shifting cultivation may limit future recovery of ecosystem carbon through a decrease in organic matter inputs to the soil.

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