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Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest

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Abstract

Seasonally dry tropical forests (SDTF) are a widely distributed vegetation type in the tropics, characterized by seasonal rainfall with several months of drought when they are subject to fire. This study is one of the first attempts to quantify above- and belowground biomass (AGB and BGB) and above- and belowground carbon (AGC and BGC) pools to calculate their recovery after fire, using a chronosequence approach (six forests that ranged form 1 to 29 years after fire and mature forest). We quantified AGB and AGC pools of trees, lianas, palms, and seedlings, and BGB and BGC pools (Oi, Oe, Oa soil horizons, and fine roots). Total AGC ranged from 0.05 to nearly 72 Mg C ha^{-1}, BGC from 21.6 to nearly 85 Mg C ha^{-1}, and total ecosystem carbon from 21.7 to 153.5 Mg C ha^{-1}; all these pools increased with forest age. Nearly 50% of the total ecosystem carbon was stored in the Oa horizon of mature forests, and up to 90% was stored in the Oa-horizon of early successional SDTF stands. The soils were shallow with a depth of $<$20 cm at the study site. To recover values similar to mature forests, BGC and BGB required $<$19 years with accumulation rates greater than 20 Mg C ha^{-1} yr^{-1}, while AGB required 80 years with accumulation rates nearly 2.5 Mg C ha^{-1} yr^{-1}. Total ecosystem biomass and carbon required 70 and 50 years, respectively, to recover values similar to mature forests. When belowground pools are not included in the calculation of total ecosystem biomass or carbon recovery, we estimated an overestimation of 10 and 30 years, respectively.

Keywords: biomass, carbon, carbon sequestration, chronosequence, fire, forest succession, seasonally dry tropical forests, soil carbon

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Introduction

Seasonally dry tropical forests (SDTF) are considered to be the most threatened of all major tropical forest types (Janzen, 1988; Bullock *et al*., 1995). These forests occur in tropical regions characterized by pronounced seasonality in rainfall, resulting in a well-define dry season (Murphy & Lugo, 1986a; Mooney *et al*., 1995). It has been estimated that 1 048 700 km^2 of SDTF remain in the tropics (Miles *et al*., 2006), which may represent 42% of the landmass covered by all tropical forests (Murphy & Lugo, 1986a). The original extent of SDTF is unknown (Murphy & Lugo, 1986a), and to our knowledge, there are no accurate estimates of the amount of carbon stored globally in these forests (Murphy & Lugo, 1986b). Reasons for the lack of estimates may be: (1) few studies have addressed both above- and belowground carbon (AGC and BGC) in SDTF, and (2) the proportion of mature and successional stands of SDTF globally is unknown.

The primary threats to SDTF result from natural fires, land use change, and escaped fires following slash and burn agriculture during the dry season (Murphy & Lugo, 1986a; Ellingson *et al*., 2000; Castellanos *et al*., 2001; Nepstad *et al*., 2001; Chazdon, 2003; Kauffman *et al*., 2003). These perturbations directly reduce biomass and carbon stored in these forests (Kauffman *et al*., 2003; van der Werf *et al*., 2003) and their soils (Castellanos *et al*., 2001; Desjardins *et al*., 2004; Powers, 2004). In addition, smoke generated from fires has a direct impact on the terrestrial surface energy budget and increases atmospheric temperatures (Wang & Christopher, 2006). Smoke from fires may also produce feedbacks on the evaporation processes, cloud formation, and precipitation patterns that could affect the hydrologic cycle at regional scales (Menon *et al*., 2002; Allen & Rincon, 2003). Finally, changes in forest biomass resulting from fires and the

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subsequent regrowth influence the net flux of carbon between forests and the atmosphere (Houghton, 2005).

Reviews of global forest biomass, carbon cycling, and storage have acknowledged the need for more information on carbon pools of tropical forests, especially in early successional stages (Pregitzer & Euskirchen, 2004; Houghton, 2005). In addition, quantification of changes in above- and belowground biomass (AGB and BGB) and carbon pools after fire is crucial to understand the effects of fire cycles in SDTF and their recovery. Miles *et al.* (2006) estimated that between 1998 and 2000 nearly 1 100 000 km^2 of SDTF in the world were affected by fire, and most of these areas were located in Africa and North and Central America.

Mature SDTF can store between 45 and 140 Mg C ha^{-1} (Murphy & Lugo, 1986b). Although fires represent an important disturbance in these regions, to our knowledge there are no studies that integrate AGC and BGC and AGB and BGB pools in forest recovery after fire events. For this study, we focused on SDTF of the northeastern Yucatan Peninsula, Mexico. These forests experience large-scale natural fires following hurricanes (Whigham *et al.*, 1991, 2003; Boose *et al.*, 2003) and anthropogenic fires by slash-and-burn agriculture (Gómez-Pompa, 1992; Gómez-Pompa *et al.*, 2003). As a result, the landscape of the Yucatan has shifted from a region of predominantly mature forest with scattered patches of successional forest, to a mosaic of secondary SDTF where mature forests are becoming scarce (Geoghegan *et al.*, 2001). Therefore, we used a forest chronosequence approach to infer SDTF biomass and carbon recovery after fire events. This approach is a recognized method to substitute space for time in tropical forest ecology (Aide *et al.*, 2000; Dewalt *et al.*, 2000, 2003; Ruiz *et al.*, 2005).

As a response to the lack of AGB, BGB, AGC and BGC recovery estimates for SDTF, our goal was to quantify these pools in successional and mature SDTF of the northeastern Yucatan Peninsula after severe fire events. We described trends and accumulation patterns for above- and belowground forest carbon and biomass pools to estimate recovery times to mature forest levels. We used a chronosequence approach by selecting an age sequence of forest stands after fire events and mature forests with similar soil, climate, and fire intensity. We sampled all standing vegetation including seedlings, palms, lianas, dead trees, and living trees, soils, and fine roots of 2 consecutive years.

Materials and methods

Study area

The study was conducted at El Eden Ecological Reserve, Quintana Roo, Mexico (Latitude 21°12′N, Longitude 87°11′W). It is located in the northeastern Yucatan Peninsula and south of the Yum-Balam Reserve. The Reserve has 2500 ha of protected landscape where 800 ha represent mature forest and the remaining area is secondary forest. The landscape is flat, with an elevation of 6 m above sea level, and occurs on limestone bedrock. Soils and climate are similar across the Reserve (see Gómez-Pompa *et al.*, 2003), as is the composition of the vascular flora, with a total of 404 species (Schultz, 2005). The soil is shallow (depth <20 cm), with mean soil organic matter of 40%, and a bulk density of 0.5 g cm^{-3}. Mean annual air temperature is 24.2 °C, and mean annual soil temperature at 10 cm depth is 23.2 °C. Annual precipitation is 1650 mm (years 1998–2005) most falling from June to December, and the dry season (<100 mm mol^{-1}) is from January to April.

Over the past four decades, severe fires have crossed portions of the Reserve following hurricanes and seasonal droughts (Allen *et al.*, 2003b; Boose *et al.*, 2003; Whigham *et al.*, 2003). These fires occurred during the dry seasons of 2002, 1999, 1995, 1989, and 1975 creating a chronosequence of five forests stands where we established our sampling plots. We observed that the standing vegetation was consumed during the fires of 1999, 1995, and 2002, and the bedrock was largely exposed due to the combustion of the organic soil (Allen *et al.*, 2003a). Additionally, control plots were established in sites of mature forests within the protected area of the Reserve with no evidence of fire, and no disturbance for more than 60 years. All the forest stands of the chronosequence and mature forests are located within a distance of 8 km. We assumed that any structural and functional differences among sites are related to the site age rather than their spatial location, because there is no slope or relief differences in the landscape, and soils and climate are similar across the Reserve (see Gómez-Pompa *et al.*, 2003). We know that ancient Maya used the Reserve 1500 years ago, but postcolonial land use has been minimal, with only selective tree harvesting in the late 1800s and early 1900s (Gómez-Pompa *et al.*, 2003). These sites have never been cultivated.

Plot design

During August of 2003, six forest stands were sampled using a nested plot design per forest stand (Fig. 1). The ages of the stands in 2003 were 1, 4, 8, 14, and 28 years, and mature forest. At each site, we randomly set one rectangular plot of 3000 m^2 to assess trees with a diameter at breast height (DBH) >30 cm (see 'Tree measurements'). Trees with DBH <30 but >10 cm were sampled in a central rectangular plot of 20×50 m^2 with a total area of 1000 m^2 inside the 3000 m^2 plot. Trees with DBH <10 cm but taller than 1.3 m were measured

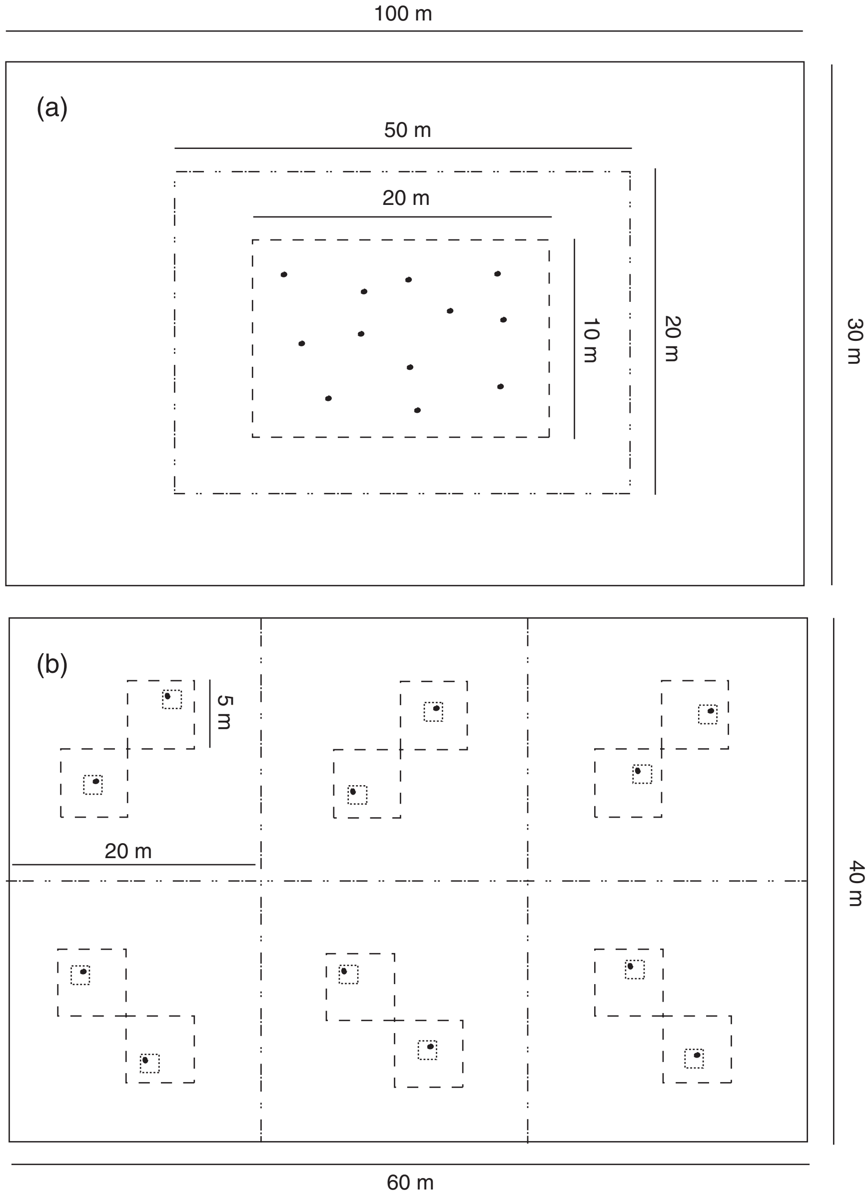

Fig. 1 Nested plots designs used for 2003 (a) and 2004 survey (b). We used the same allometric equations to calculate tree biomass to reduce error propagation associated with different plot design (see Chave *et al.*, 2004). Sampling design of plots for belowground pools (●) were not modify between years (see 'Materials and methods' for details). Plot diagrams are not to scale.

in a rectangular plot of $200\,\mathrm{m}^2$ within the central $1000\,\mathrm{m}^2$ plot. The Oi and Oe horizons were destructively sampled in 12 randomly located $0.5 \times 0.5\,\mathrm{m}^2$ microplots within the $3000\,\mathrm{m}^2$ plot. One soil sample of the Oa horizon was randomly collected in each microplot for root biomass and soil analysis (see 'Soil sampling' and 'Root sampling').

The nested plot design was modified in 2004 to better characterize the spatial variation of the forest. Two new plots were randomly established in each forest stand (see description of these plots below). This modification resulted in coverage of a larger area, and the ability to calculate standard error within each forest stand of the measured biomass and carbon pools (see Tables A1 and A2). We used the same allometric equations to calculate biomass of trees (Table 1) for the sampling years of 2003 and 2004. The use of the same equations reduce the error propagation associated with different plot design (see Chave *et al.*, 2004). The sampling plots for belowground pools were not modify, but we increase the number of replicates as we established new plots during 2004.

The forest stand ages in 2004 were 5, 9, 15, 29 years, and mature forest. The stand that burned in 2002 (1-year-old) was excluded for the 2004 sampling for logistical reasons. At each stand we randomly established two plots using a nested plot design (Fig. 1). In each plot, trees with DBH >30 cm were assessed within a rectangular area of 2400 m^2. This area was divided into six 20×20 m^2 plots in which we measured all trees with DBH <30 but >10 cm. Two 5×5 m^2 plots were established at the center of each 20×20 m^2 plot where we measured all trees, lianas and palms <10 cm but >1 cm in DBH (total area of 5×5 plots 300 m^2). Two subplots of 1×1 m^2 were established randomly inside each 5×5 m^2 plot to measure trees with a DBH <1 cm but taller than 1.3 m (total area of 1×1 plots 24 m^2). All seedlings <1.3 m in height were counted and harvested in two 1×1 m^2 subplots per forest stand. The Oi and Oe horizons (see 'Soil sampling') were destructively sampled in a 0.5×0.5 m^2 microplot randomly located inside each 1×1 m^2 plot. One sample of the Oa horizon was randomly collected in each microplot for fine root biomass and soil analysis in the same way as the previous year.

Measurements

We measured AGB, AGC, BGB, and BGC pools. AGC and AGB pools were defined as standing vegetation including seedlings, palms, lianas, dead trees and living trees. BGC and BGB pools include the soil horizons (Oi, Oe, and Oa) and fine roots with a diameter <3 mm (see 'Soil sampling' and 'Root sampling'). Total ecosystem biomass was defined as the sum of all components of AGB and BGB and total ecosystem carbon the sum of all components of AGC and BGC.

Tree measurements. DBH was measured at 1.30 m height of live and dead trees. When irregularities (e.g. bole irregularities, buttress roots) were present at this height, the measurement was taken 2 cm below the irregularity or 0.5 m above the highest point of the buttress (Condit *et al.*, 1998; Clark *et al.*, 2001a). During 2003, we measured tree heights and DBH of 994 trees total in all sites, and we developed regression models (tree height vs. DBH) for each site (Table 1). Thereafter, tree height was determined via these regression models. We used published allometric equations for biomass of all tree categories, palms, and lianas (Table 1), and the same equations were used for both sampling years.

Table 1 Equations used to determine tree height, and aboveground biomass for the forest sites

Parameter		Equation	CF	R^2
Height of trees (cm DBH)				
Site burned in 1999*	*(n = 134)*	$= 1.4371 \times \ln(x) + 1.7021$	1.02	0.86
Site burned in 1995*	*(n = 74)*	$= 1.9322 \times \ln(x) + 2.7364$	1.02	0.65
Site burned in 1989*	*(n = 561)*	$= 2.5233 \times \ln(x) + 2.3105$	1.02	0.85
Site burned in 1975*	*(n = 75)*	$= 2.9196 \times \ln(x) + 2.0294$	1.02	0.90
Mature forest*	*(n = 100)*	$= 2.8113 \times \ln(x) + 3.0073$	1.01	0.84
Biomass (Mg)				
Trees >10 cm DBH†		$= \exp(-2.173 + 0.868 \times \ln(D^2H) + (0.0939/2))$	None	0.90
Trees <10 cm DBH‡		$= (\exp(4.9375 + 1.0583 \times \ln(D^2))) \times 1.14/10^6$	1.14	0.93
Trees <1 cm DBH‡				
Wood		$= \exp(4.7472 + 1.0915 \times \ln(D^2))/10^6$	1.13	0.93
Leaves		$= \exp(3.0473 + 0.07778 \times \ln(D^2))/10^6$	1.45	0.71
Standing dead trees >10 cm DBH‡		$= \pi((D/2)^2)/\mathrm{H}(0.41)$	None	None
Seedlings*		$= (\text{number of seedlings} \times W_s)/10^6$	None	None
Dead trees <10 cm DBH‡		$= (\exp(4.6014 + 1.1204 \times \ln(D^2)))1.11/10^6$	1.11	0.95
Lianas§		$= \exp(0.298 + 1.027 \times \ln BA)$	None	0.87
Stem less palms*	*(n = 25)*	$= (\text{number of leaves} \times 148.84)/10^6$	None	None
Palms¶		$= (4.5 + (7.7 \times \mathrm{H}))/10^3$	None	0.90

Biomass is expressed as dry weight (Mg). *D*, diameter at breast height (cm); H, total tree height; W_s, average dry weight of seedlings at each site; *BA*, basal area (cm^2); DBH, diameter at breast height; CF, correction factor as per Sprugel (1983). Symbols after each parameter indicate source:
*This study.
†Cairns *et al.* (2003).
‡Hughes *et al.* (1999).
§DeWalt & Chave (2004).
¶Frangi & Lugo (1985).

Consistent with Clark *et al*. (2001a), Malhi *et al*. (2004), and Pregitzer & Euskirchen (2004), we used a conversion factor of 0.5 to estimate the carbon fraction in oven dry wood.

Soil sampling. We collected soil from the Oi, Oe, and Oa horizons according to Schoeneberger & Wysocki (2002) and we used the Soil Survey Staff (2003) soil horizon nomenclature. The Oi horizon is composed of slightly decomposed organic matter. The Oe horizon consists of moderately decomposed organic matter under the Oi horizon. The Oa horizon is the highly decomposed organic matter material formed below the Oi and Oe horizons and on top of the limestone bedrock. The material found in the Oe horizon was subdivided into Oe > 2 mm (material larger than 2 mm; partially decomposed litter) and Oe < 2 mm (material smaller than 2 mm; highly decomposed litter). The collected samples of the Oi and Oe horizons were weighed in the field and subsamples were taken to determine dry weight and the Oe < 2 mm fraction.

Root sampling. In each $0.5 \times 0.5\,\mathrm{m}^2$ microplot, we sampled fine roots (diameter < 3.0 mm) by inserting a 4.5 cm in diameter metal soil core vertically into the Oa horizon until we encountered the limestone bedrock (van Noordwijk, 1993). Fine roots were sorted by hand and rinsed free of soil and organic matter with deionized water. Subsamples of collected roots were taken to determine dry weight.

Laboratory analysis. All soil horizon samples were oven dried at 65 °C. Five samples of the Oi, Oe > 2 mm, Oe < 2 mm soil fractions, as well as roots were ground to pass through a 0.5 mm sieve. Oa-horizon samples (five per site) were sieved to remove roots > 3 mm in diameter and ground to pass through a 250 μm sieve. Organic carbon in the Oa-horizon samples was determined by acidification of 1 g of soil with 0.5 N HCl (Schumaher, 2002). Organic carbon in soil samples was determined by dry combustion using a Thermo Finnigan Flash EA1112 N/C analyzer. Carbon content per unit area for all fractions measured in this study was estimated using measurements of mass per area and percent carbon. Organic carbon in the Oa horizon was calculated based on soil bulk density and horizon thickness.

Statistical analyses

To evaluate relationships between biomass or carbon pools to forest age, we used three models: linear model $y = b_0 + b_1(A)$; logarithmic model $y = b_0 + (b_1\ln(A))$; and S-curve model $y = \mathrm{e}^{(b_0+(b_1/A))}$; where y was the measured pool (see Appendix A and Table 2 for measured pools used in the models); and A was the forest age. Only the model with the highest r^2 value for each measured pool is reported because all the models have the same number of parameters (Burnham & Anderson, 2002).

Table 2 Parameters, r^2 values, and P-values from models fitted to means of biomass and carbon pools from different successional stages in a seasonally dry tropical forest

Measured pool	Model	b_0	b_1	r^2	P-value
Biomass					
Total biomass	LIN	26.563	2.789	0.959	< 0.0001
	Richards	0.025	0.567	0.906	< 0.0001
Total AGB	Richards	0.027	0.840	0.974	< 0.0001
Trees > 30 cm	LIN	−3.317	0.393	0.803	< 0.0001
Trees 10–29.9 cm	LIN	−12.372	1.865	0.973	< 0.0001
Trees 5–9.9 cm	LOG	7.289	7.265	0.400	0.027
Trees < 1 cm	LIN	6.376	−0.116	0.375	0.034
Dead trees	LIN	−0.783	0.147	0.775	< 0.0001
Lianas	LIN	−2.410	0.032	0.915	0.003
Palms	LIN	−0.069	0.008	0.700	0.038
Seedlings	–	–	–	–	ns
Total BGB	S	3.264	−1.852	0.967	< 0.0001
	Richards	0.143	0.677	0.869	< 0.0001
Oi-horizon	S	2.334	−2.315	0.920	< 0.0001
Oe > 2 mm	LOG	0.198	0.627	0.866	< 0.0001
Oi < 2 mm	S	1.629	−1.744	0.704	0.001
Fine Roots	S	1.575	−1.131	0.531	0.007
Carbon					
Total Carbon	LOG	13.527	32.799	0.966	< 0.0001
	Richards	0.033	0.466	0.967	< 0.0001
Total AGC	S	4.007	−7.097	0.982	< 0.0001
	Richards	0.027	0.840	0.974	< 0.0001
Total BGC	S	4.338	−1.311	0.934	< 0.0001
	Richards	0.089	0.443	0.901	< 0.0001
Oi-horizon	S	1.506	−2.327	0.928	< 0.0001
Oe > 2 mm	LOG	−0.037	0.067	0.870	< 0.0001
Oe < 2 mm	S	0.610	−2.966	0.901	< 0.0001
Fine Roots	S	0.757	−1.089	0.501	0.010
Oa horizon (OC)	S	4.190	−1.237	0.905	< 0.0001
Carbon %					
Oi horizon	–	–	–	–	ns
Oe > 2 mm	S	3.680	−0.403	0.787	0.001
Oe < 2 mm	S	3.544	−0.839	0.661	0.004
Fine roots	–	–	–	–	ns
Oa horizon (OC)	S	3.222	−0.981	0.466	0.030

OC, Organic carbon; LIN, Linear model; S, S-curve model; LOG, Logarithmic model; AGC, aboveground carbon; BGC, belowground ca. For explanation about functions see 'Materials and methods.'

We calculated mean annual biomass and carbon accumulation curves for AGB, BGB, total ecosystem biomass, AGC, BGC, and total ecosystem carbon pools. Mean annual accumulation was defined as the biomass or carbon pool of each forest site divided by its age (i.e. years after fire event). In addition, we used a logistic growth equation, known as the Richards function (Cooper, 1983), to predict biomass and carbon based on the forest age and measured AGB, BGB, total ecosystem biomass, AGC, BGC, or total ecosystem carbon pools in these forests:

$$\text{Richards function:} Y = Y_{\max} \times (1 - \exp(-b_1 \times A))^{b_2},$$

where Y is the biomass or carbon pool at a given time following a severe fire event; $Y_{\max}$ is the potential maximum of the Y pool; and A is the forest age. In this model, we calculated $Y_{\max}$ as the average of Y pool in the mature forests at our study site (see Tables A1 and A2). We assumed that a Y pool was equivalent to a mature forest Y pool, when the Y pool reached 90% of the $Y_{\max}$ value. All statistical analyses were performed using procedures of SPSS statistical software (SPSS Inc., version 11.02, 2003).

Results

Biomass accumulation

Total ecosystem biomass increased with forest age ($P < 0.001$) from 4.2 to 174.8 Mg ha^{-1} (Table A1). Most AGB pools increased with forest age ($P < 0.05$) after the fire events, except for the biomass pool of seedlings (Table 2). Total AGB represented between 0.1 Mg ha^{-1} in the youngest site and 143.9 Mg ha^{-1} in the mature forests. Trees of the diameter class 10–30 cm DBH represented near 60% of the AGB in mature forests with a maximum of 86.1 Mg ha^{-1}, whereas trees >30 cm DBH contributed a maximum of 22.5 Mg ha^{-1} or 17% of AGB in mature forests. Biomass of trees with DBH < 1 cm varied from 0.7 to 10.8 Mg ha^{-1}, and trees with DBH > 1 to < 10 cm between 9.8 and 50.4 Mg ha^{-1} in the chronosequence. These DBH classes represented up to 50% of the AGB in forests younger than 29 years. Biomass stored in dead trees ranged between 0.3 and 6.6 Mg ha^{-1}. Lianas and palms had a maximum biomass of 1.4 and 0.49 Mg ha^{-1}; respectively (Table A1). Mean biomass of seedlings was 0.18 Mg ha^{-1}.

All BGB pools increased significantly ($P \leq 0.001$) with forest age (Table 2). Total BGB increased from 4.1 in the youngest site to 30.8 Mg ha^{-1} in the mature forest. The biomass in the Oi horizon increased from 0.9 to 10.9 Mg ha^{-1}. Biomass in the Oe <2 mm fraction increased from 0.9 to 7.7 Mg ha^{-1}, and biomass in the Oe >2 mm fraction from 0.8 to 7.8 Mg ha^{-1}. Similarly, biomass stored in fine roots increased from 1.5 to 7.8 Mg ha^{-1} with forest age (Table A1).

Mean annual AGB accumulation (Fig. 2a), mean annual BGB accumulation (Fig. 2b), and mean annual total biomass accumulation (Fig. 2c) decreased significantly ($P < 0.001$) with forest age. The 1-year-old site was excluded from the mean annual AGB and BGB accumulation calculations because accumulation rates increased during the first 5 years and thereafter followed a negative logarithmic relation (Fig. 2). Mean annual AGB accumulation ranged from 2.7 to 5.3 Mg ha^{-1} yr^{-1}, and was higher than mean annual BGB accumulation, which ranged between 0.5 and 4.1 Mg ha^{-1} yr^{-1}. Mean annual total biomass accumulation ranged from 2.7 to 9.6 Mg ha^{-1} yr^{-1}. Using ANCOVA, we found significant differences between the regression lines of mean annual total biomass accumulation with mean annual AGB accumulation ($F_{(1,19)} = 15.695$, $P = 0.001$). Similarly, we found differences between the regression lines of mean annual total biomass accumulation with mean annual BGB accumulation ($F_{(1,19)} = 15.3$, $P = 0.001$).

Forest total ecosystem biomass predicted by the Richards function (Fig. 3a) suggest that these forests require 70 years to reach 90% of the 148 Mg ha^{-1} of mean total ecosystem biomass found in mature forests. It require 80 years to reach 90% of the 124.4 Mg ha^{-1} for mean AGB found in mature forests, and only 14 years to reach 90% of the 23.6 Mg ha^{-1} for mean BGB of mature forests (Fig. 3a). Mean values for mature forests biomass pools were calculated from Table A1.

We compared percentage of total AGB with percentage of total BGB for the plots sampled during 2004 and found no significant differences (t-test after arcsine transformation) in the forest stand of 5 years, but %AGB was significantly higher ($P < 0.001$) than %BGB in the older forest stands (Fig. 4).

Carbon accumulation

Carbon percentages increased significantly ($P < 0.05$) with forest age in belowground pools of the Oa horizon, and the Oe < 2 mm and Oe < 2 mm fractions (Table 2). Organic carbon percentage ranged from 9.7% to 32.7%, from 15.7% to 42.3%, and from 26.7% to 42.3% in the Oa horizon, Oe < 2 mm and Oe > 2 mm fractions; respectively. No significant relationship with forest age was found for percent carbon in the Oi horizon (mean = 43.3%) and fine roots (mean = 44%).

All BGC pools increased significantly ($P < 0.001$) with forest age after fire. Total ecosystem carbon varied with forest age from 21.7 to 153.5 Mg C ha^{-1}, AGC from 0.05 to 72.0 Mg C ha^{-1}, and BGC from 21.6 to 85.2 Mg C ha^{-1} in the chronosequence (Table A2). Over 90% of the carbon in the BGC pool was stored as organic carbon

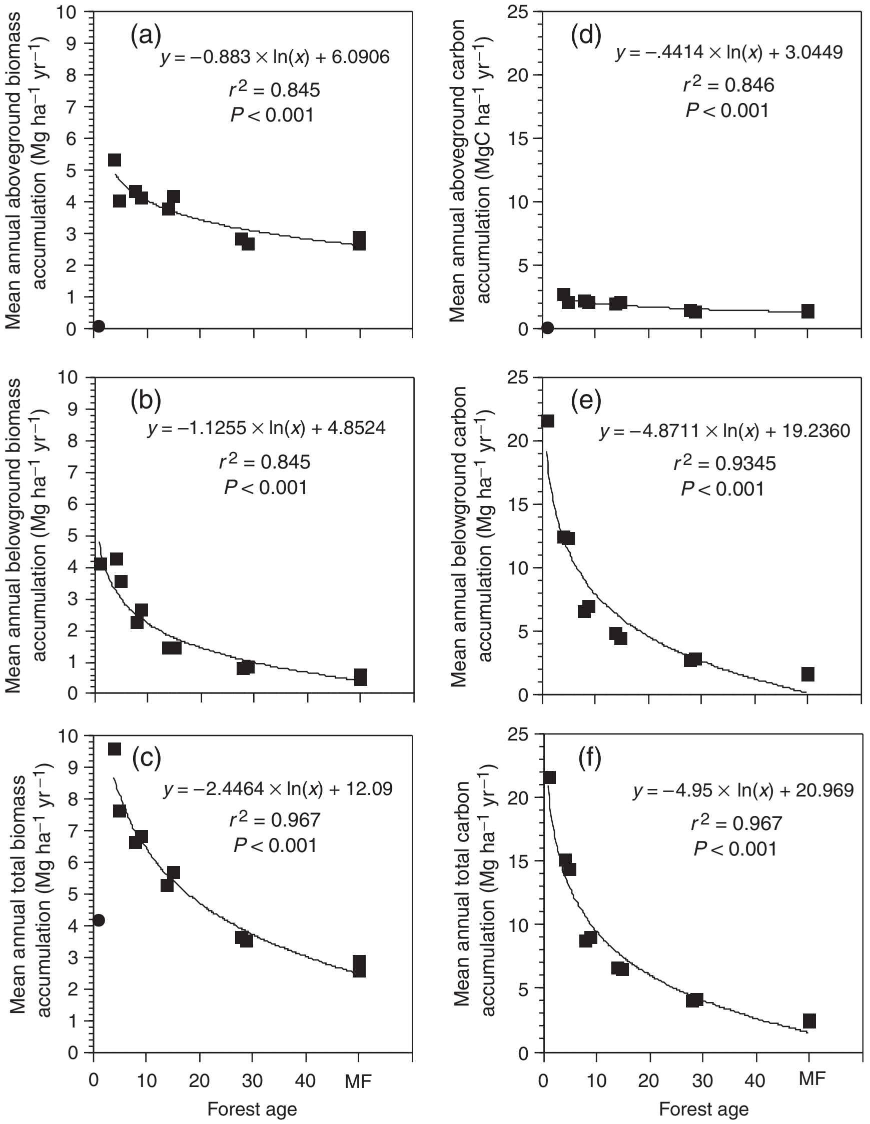

Fig. 2 Mean annual biomass and carbon accumulation curves. Negative logarithmic relationship between years after fire event, of mean annual aboveground biomass (a), mean annual belowground biomass (b), mean annual total biomass (c), mean annual aboveground carbon (d), mean annual belowground carbon (e), and mean annual total carbon (f) in the forest chronosequence. The mean annual accumulation is defined as the biomass or carbon pool of each forest site divided by its age (i.e. years after fire event).

in the Oa horizons with a range of 20.1 to 75.2 Mg C ha^{-1}. In the successional forest stands, carbon stored in the Oi horizon was always higher than the carbon stored in the total Oe horizon (sum of Oe $>$2 mm and Oe$<$2 mm fractions). However, in the mature forests the carbon in the total Oe horizon (mean = 5 Mg C ha^{-1}) exceeded the carbon stored in the Oi horizon (mean = 3.6 Mg C ha^{-1}).

Mean annual AGC accumulation (Fig. 2d), mean annual BGC accumulation (Fig. 2e), and mean annual total ecosystem carbon (Fig. 2f) decreased significantly ($P<0.001$) with forest age. The 1-year-old site was excluded from the mean annual AGC accumulation calculations because this accumulation rate increased during the first 5 years (Fig. 2). Contrary to the mean annual biomass accumulation models (Fig. 2a and b), mean annual AGC accumulation was lower in all cases, ranging from 2.7 to 1.4 Mg C ha^{-1} yr^{-1}, than mean annual BGC accumulation with values from 21.6 to 1.7 Mg C ha^{-1} yr^{-1}. Furthermore, an ANCOVA showed significant differences between slopes of mean annual total carbon accumulation and mean annual AGC accumulation ($F_{(1,18)} = 37.783$, $P<0.001$), but there were no significant differences between the slopes of mean annual total carbon accumulation and mean annual BGC accumulation ($F_{(1,20)} = 0.903$, $P = 0.353$).

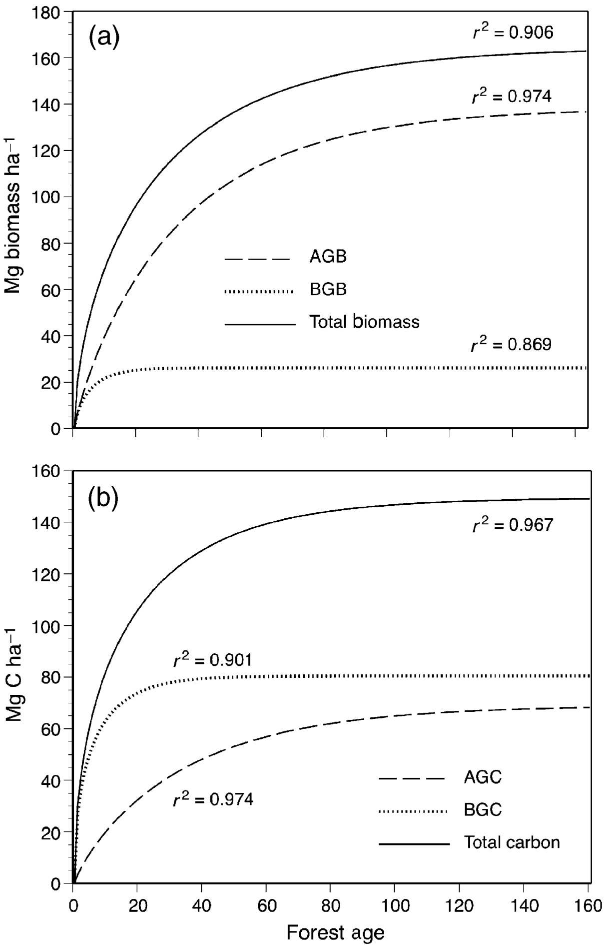

Fig. 3 Predicted aboveground biomass (AGB), belowground biomass (BGB), total biomass, aboveground carbon (AGC), belowground carbon (BGB) and total carbon accumulation using Richards function. R^2-values represent fit of the model with measured values from forest of different ages in a seasonally dry tropical forest at the Yucatan peninsula, Mexico (see Appendix A for measurements). The maximum potential values for each pool were defined as the average of each pool in the mature forests at our study site: AGB 138.2 Mg ha^{-1}, BGB 26.2 Mg ha^{-1}, total biomass 164.4 Mg ha^{-1}, AGC 69.1 Mg C ha^{-1}, BGC 80.4 Mg C ha^{-1}, total carbon 149.5 Mg C ha^{-1}.

Forest total ecosystem carbon predicted by the Richards function (Fig. 3b) suggest that these forests require 50 years to accumulate 90% of the 134.6 Mg C ha^{-1} of mean total ecosystem carbon found in mature forests. It require 80 years to reach 90% of the 62.2 Mg C ha^{-1} of mean AGC found in mature forests, but only 18 years to reach 90% of the 72.4 Mg C ha^{-1} for mean BGC of mature forests. Mean values for mature forests carbon pools were calculated from Table A2.

We compared the percentage AGC with the percentage of BGC for the plots sampled during 2004 (Fig. 4), and we found that BGC was significantly higher ($P < 0.001$) in forest stands from 5 to 29 years than AGC (*t*-test after arcsine transformation). Mature forests did not show significant differences between the percentage of AGC and BGC despite the shallow depth of the soil.

Discussion

Fire is an important disturbance for natural succession in SDTF (Vieira & Scariot, 2006), but extensive, recurrent fires may reduce the area of land covered by these forests (Miles *et al.*, 2006). Because local carbon stocks and fluxes depend upon forest age, estimating global carbon stocks and fluxes depends in part on understanding the differences across successional ages. One missing component for global carbon cycling models is the effect of disturbances and recovery in tropical forests. Thus, it is important to understand the recovery rates and stocks of SDTF after fire events. This study is the first attempt to report AGB and BGB and carbon stocks and recovery rates for SDTF of the northeastern Yucatan Peninsula.

AGB and AGC

Measurements of AGB of mature SDTF in our study site, ranging from 133.9 to 143.9 Mg ha^{-1}, fall within the global range of 23 to 273 Mg ha^{-1} for mature SDTF (Murphy & Lugo, 1986a; Martinez-Yrizar, 1995). However, the amount of AGC stored in mature forests at our study site fall in the low end when compared with other mature tropical forests with similar temperatures and precipitation (Table 3).

Our measurements were consistent with estimates from the southern part of the Yucatan Peninsula (Read & Lawrence, 2003, Table 3). However, the sites studied by Read & Lawrence (2003b) were abandoned agricultural sites, whereas our study sites were forests disturbed by severe fires and in a site that received higher annual precipitation (Table 3). Therefore, further research is needed to understand regional variation in AGC of the Yucatan Peninsula where differences in precipitation, soil depth, and the ability of vegetation to access nutrients and water exist (Campo & Vazquez-Yanes, 2004; Querejeta *et al.*, 2006). Additionally, forests at our study site may have been selectively logged during the late 1800s reducing the number of trees with DBH > 30 cm. Our results show that trees with DBH < 10 cm accounted for 25% of AGC or ~15 Mg C ha^{-1} in mature SDTF, and between 40% and 100% of AGC in early successional forest stands.

Lianas are an important component of AGB in tropical forests because they can have up to five times the leaf mass of trees of the same DBH (Gerwing & Lopes Farias, 2000; DeWalt & Chave, 2004) and they are

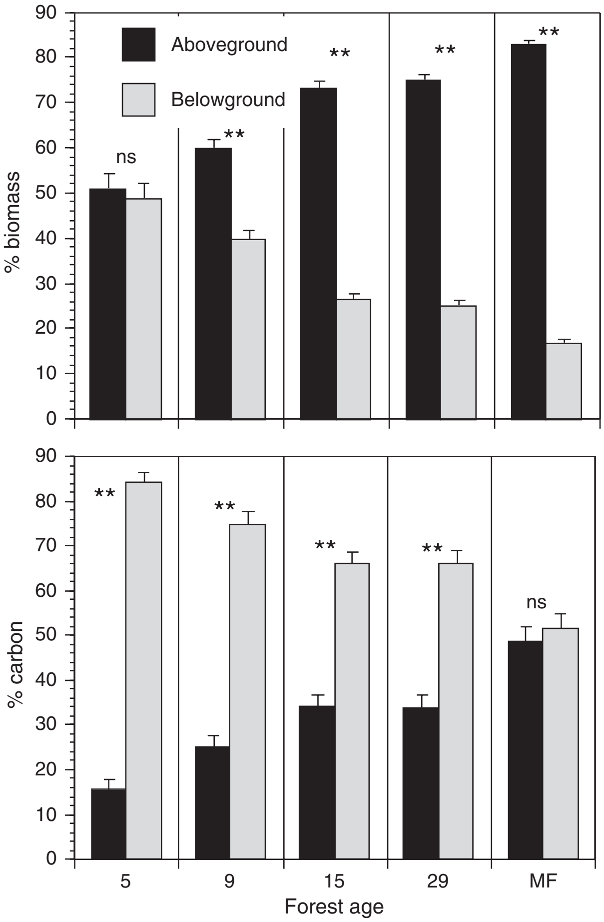

Fig. 4 Comparison of total aboveground biomass and carbon percentage including all diameter trees, palms, lianas, and seedling, and belowground biomass and carbon including as fine roots, Oi, Oe, and Oa horizons in forests of different ages. Aboveground carbon was estimated from aboveground biomass using a conversion factor of 0.5. Data were transformed (arcsin) to meet normality and an independent *t*-test was performed at the sites sampled during 2004. Note: ns, not significant; **$P < 0.0001$.

adapted to high-light environments (Dewalt *et al.*, 2000). Surprisingly, they were not present until 29 years after fire. Our estimates of liana biomass (1.2 Mg ha^{-1}) contrast with values up to 32.88 Mg ha^{-1} in successional forests, after agricultural abandonment, of southern Yucatan (Read & Lawrence, 2003). More research is needed in other SDTF in order to understand if a relationship exists between liana biomass and forest age or if previous land-use history has an effect on lianas establishment.

BGB and BGC

The Oi-horizon biomass ranged with forest age from 0.9 to 10.9 Mg ha^{-1}, and is comparable with reported global estimates of 3.2–12.3 Mg ha^{-1} of litter biomass in SDTF (Martinez-Yrizar, 1995). The biomass stored together in the Oe > 2 mm and the Oe < 2 mm contributed between 1.7 Mg ha^{-1} in the youngest stand and 15.5 Mg ha^{-1} in the mature forest. These values represented between 41% and 50% of the total BGB of these forests depending on forest age (Table A1). Our results showed the importance of the Oe horizon in BGB storage of SDTF and should be compared with future estimates of this horizon in other SDTF.

The 44% carbon in fine roots in our study was higher than the 37% reported in other SDTF (Jaramillo *et al.*, 2003b), and nearly 38% in evergreen Mexican forests (Jaramillo *et al.*, 2003a). This high carbon concentration in fine roots supports an active pool of mycorrhizal fungi, which are important in secondary succession for SDTF (Allen *et al.*, 1998, 2003a, 2005). The higher carbon content of fine roots might also be part of a long-term carbon storage that is advantageous for plants in systems with frequent fire disturbances (Langley *et al.*, 2002).

Fine root biomass ranged from 1.5 to 6.4 Mg ha^{-1} and it is consistent with estimates of forests growing on limestone bedrock in China (Muthukumar *et al.*, 2003), but are lower than the estimates of 17–31 Mg ha^{-1} for fine roots of mature SDTF of Chamela, Mexico (Castellanos *et al.*, 1991; Jaramillo *et al.*, 2003b). These last measurements correspond to a depth of 1 m into the soil, while our measurements are for the first 20 cm because of the nature of shallow soils. Our measures of fine roots underestimate this pool as many fine roots grow into small cracks into the limestone bedrock (R. Vargas, personal observation). It is important to include the contribution of roots deeper into the soil for complete BGC inventories as previous studies in tropical forest of the Amazon have reported roots up to 8 m deep in soils that account for large biomass stocks (Nepstad *et al.*, 1994).

Our results show that the limestone bedrock does not form a mineral soil and instead we found a shallow organic layer that increased with forest age. The organic carbon content in the Oa-horizon ranged from 20.1 to 75.2 Mg C ha^{-1} and represent > 90% of total BGC. Our measurements were lower than the 158 Mg C ha^{-1} global estimate of the top 1 m of mineral soil for tropical deciduous forests (Jobbagy & Jackson, 2000), but comparable with the range of 27.4 to ~98 Mg C ha^{-1} stored in the first 10–12 cm of mineral soil in mature SDTF of Venezuela and Mexico (Delaney *et al.*, 1997; Jaramillo *et al.*, 2003b).

Our results indicate that BGC of El Eden represent a large carbon pool with nearly 95% of the total ecosystem carbon in early successional stages and 51.4% in the mature forest. Previous studies of tropical forests with different precipitation have reported that mineral soils, at 1 m depth, contribute up to 51% of total ecosystem

Table 3 Aboveground carbon estimates of 41 mature tropical forests

Site	AGC ($Mg\,C\,ha^{-1}$)	MAT (°C)	Precipitation ($mm\,yr^{-1}$)	Reference
Puerto Rico, Guanica	22.5	25.1	860	Murphy & Lugo (1986b)
Puerto Rico, Pico del Este	23.8	19.0	5000	Weaver *et al.* (1986)
Puerto Rico, Guanica	26.5	25.1	860	Murphy & Lugo (1986a)
Mexico, Chamela	42.5	24.9	707	Martinez-Yrizar *et al.* (1992)
Mexico, Chamela	58.3	25.0	679	Jaramillo *et al.* (2003b)
Mexico, Arroyo Negro	63.6	25.0	1418	Read & Lawrence (2003)
Mexico, El Refugio	63.8	25.0	892	Read & Lawrence (2003)
Mexico, El Eden	69.1	24.2	1650	This study
Venezuela, Cerro El Coco	70.0	27.0	800	Delaney *et al.* (1997)
Panama, Barro Colorado	71.1	27.0	2600	DeWalt & Chave (2004)
Mexico, Nicolás Bravo	75.7	25.0	1144	Read & Lawrence (2003)
Costa Rica, La Selva	78.0	26.0	4000	Clark *et al.* (2002)
Puerto Rico, Colorado Forest	84.4	21.1	3725	Weaver & Murphy (1990)
Colombia, Magdalena terrace	89.9	27.5	3150	Chambers (1998) cited in Clark *et al.* (2001b)
Costa Rica, La Selva	95.5	25.8	4000	DeWalt & Chave (2004)
Mexico, La Pantera	112.5	25.0	1200	Cairns *et al.* (2003)
Jamaica, Blue Mt.	114.5	15.8	2230	Tanner (1985)
Puerto Rico, Palm forest	114.5	19.0	3725	Frangi & Lugo (1985)
Jamaica, Blue Mt.	115.0	15.3	2230	Tanner (1985)
Venezuela, San Carlos	118.7	26.2	3500	Klinge & Herrera (1983)
Jamaica, Blue Mt.	119.0	15.5	2230	Tanner (1985)
Venezuela, San Carlos	132.0	26.0	3550	Uhl & Jordan (1984)
Mexico, Los Tuxtlas	143.5	26.0	4000	Hughes *et al.* (1999)
Brazil, kilometer 41	144.0	26.7	2650	DeWalt & Chave (2004)
Venezuela, Caimital	148.0	26.0	1500	Delaney *et al.* (1997)
Brazil, Fazenda Gaviano	151.0	26.7	2300	Chambers (1998) cited in Clark *et al.* (2001b)
Jamaica, Blue Mt.	156.0	15.5	2230	Tanner (1985)
Venezuela, Mucuy	157.0	10.5	1968	Delaney *et al.* (1997)
Brazil, Fazenda Cabo Frio	157.5	26.7	2300	Chambers (1998) cited in Clark *et al.* (2001b)
Peru, Cashu	160.0	24.2	2165	DeWalt & Chave (2004)
Misiones, Argentina	162.9	27.5	3150	Vaccaro *et al.* (2003)
Colombia, Magdalena	162.9	27.5	3150	Folster *et al.* (1976) cited in Clark *et al.* (2001b)
Brazil, Vale do Rio Doce Reserve	167.3	22.2	1200	Rolim *et al.* (2005)
Brazil, Rondonia*	170.6	25.2	2300	Cummings *et al.* (2002)
Venezuela, Carbonera	173.0	15.0	1487	Delaney *et al.* (1997)
Venezuela, San Eusebio	174.0	13.8	1500	Grimm & Fassbender (1981)
Brazil, Manaus	175.0	25.5	2200	Malhi *et al.* (1999)
Brazil, Fazenda Dimona	178.0	26.7	2300	Chambers (1998) cited in Clark *et al.* (2001b)
Venezuela, Rio Grande	179.0	25.5	2850	Delaney *et al.* (1997)
Brazil, Fazenda Porto Alegre	200.5	26.7	2300	Chambers (1998) cited in Clark *et al.* (2001b)
Brazil, Egler Reserve	203.0	27.2	1171	Klinge & Rodrigue (1973)

AGC is aboveground carbon. Units of carbon were converted from biomass data under the assumption that plant biomass is 50% carbon. MAT, mean annual temperature.
*Average from 20 plots.

carbon in tropical wet forests (Hughes *et al.*, 1999), 63–72% in very dry tropical forests (Delaney *et al.*, 1997), and 54% in mature dry tropical forests (Jaramillo *et al.*, 2003b). The large amount of carbon stored in the Oa-horizon pool of these SDTF may require further attention with the increasing land use change in the Yucatan Peninsula (Geoghegan *et al.*, 2001).

Total ecosystem biomass and carbon

Total ecosystem biomass in SDTF at El Eden ranged from 4.2 to 102.6 $Mg\,ha^{-1}$ in secondary forest stands and from 156.4 to 174.8 $Mg\,ha^{-1}$ in mature forest stands. These results suggest that total biomass of mature SDTF in the Yucatan are in the high end of the estimates of other SDTF around the world which varied between 45 and 140 Mg ha^{-1} (Murphy & Lugo, 1986b).

Total ecosystem carbon in our study site ranged from 21.7 to 121.1 Mg C ha^{-1} in the secondary forests stands and from 145.9 to 153.5 Mg C ha^{-1} in the mature forest stands. Fewer studies of SDTF exist to compare these results because most studies concentrate on above- or belowground pools only, and the organic carbon in the soil profile is rarely included in the calculations of total ecosystem carbon. Total ecosystem carbon in mature SDTF of the world range from 45 to $\sim$140 Mg C ha^{-1} including the 1 m of soil (Murphy & Lugo, 1986b). These estimates of SDTF are comparable with total ecosystem carbon of mature tropical wet forests of Los Tuxltas, Mexico with $\sim$279 Mg C ha^{-1} including 1 m of soil (Hughes *et al*., 1999), and premontane moist forests of the Venezuelan Guayana with $\sim$432.4 Mg C ha^{-1} including 1 m of soil (Folster *et al*., 2001). These comparisons suggests that mature SDTF stores 54% of the carbon stored in mature wet tropical forests and only 35% of the carbon stored in mature premontane tropical forests.

It has been calculated that unmanaged SDTF in Mexico account for 2.3 Pg C and approximately 708 Tg C could result from biomass burning of these forests (Jaramillo *et al*., 2003b). However, the proportions of mature vs. successional SDTF in Mexico or globally remain unknown. It is important to understand the variation in carbon stored in early successional SDTF as these stands may have higher susceptibility to recurring fires (Whigham *et al*., 1991). Furthermore, for an accurate regional or global calculation of the carbon stored in SDTF it is critical to have a better estimate of the regional spatial heterogeneity of total ecosystem carbon (see Houghton, 2003; Malhi *et al*., 2006).

Carbon and biomass accumulation rates

We estimate that SDTF of the northeastern Yucatan require 70 years to recover 90% of total ecosystem biomass found in mature forests. They take 80 years to recover 90% of AGB but only 14 years for 90% of BGB values of mature forests. The shallow depth of the soils may explain the rapid recovery of BGB and BGC. The highest total ecosystem biomass mean annual accumulation rates occurred during the first 5 years after fire. This accumulation is mainly by storage of biomass in fine roots and the Oi horizon. Our estimates of AGB accumulation are comparable with the 55–95 years required to recover AGB levels equivalent to mature forests in SDTF of the Yucatan (Read & Lawrence, 2003), and the 73 years in wet tropical forests (Hughes *et al*., 1999). We have not found published BGB accumulation rates for other SDTF. Our results indicate that when estimates of BGB are included to the recovery rate of total ecosystem biomass, it reduces the required time by 10 years compared with using AGB estimates only for total ecosystem biomass.

In contrast with the 70 years to recover 90% of total ecosystem biomass of mature forests, only 50 years are require to recover 90% of total ecosystem carbon. Nearly 50% of total ecosystem carbon is stored in the BGC pool, and 90% of total BGC is acquired within 18 years. Our results suggest that most of the carbon sequestration of these forests is accounted for short term by rapid accumulation in BGC pools with rates of $\sim$20 Mg C ha^{-1} yr^{-1}, and long-term accumulations of both BGC and AGC pools with rates of $\sim$2.5 Mg C ha^{-1} yr^{-1}. Our results show that total ecosystem biomass accumulation is a component of both AGB and BGB accumulation, while total ecosystem carbon is mainly a function of BGC accumulation (see ANCOVA results). When estimates of BGC are included in the recovery rate of total ecosystem carbon, it reduces the required time by 30 years than if only AGC estimates are used. These results demonstrate the importance to include BGC pools in successional forests to better estimate SDTF carbon recovery or loss. Failure to calculate these pools may lead to differences in estimates of terrestrial carbon balance at regional or global scales (Houghton, 2003).

In forests of the Yucatan Peninsula soil resources are more limiting than sunlight, at least until a closed canopy develops (Campo & Vazquez-Yanes, 2004). Therefore, plants would be allocating as much fine roots as possible, in contrast with AGC, to establish a necessary resource base. Furthermore, because of the high soil moisture and temperatures, roots and litter would turn over rapidly, and contribute to increase soil carbon accumulation (Shang & Tiessen, 2003).

A critical factor that remains to be studied is how climate variability will affect tropical forests (Clark, 2007). One factor associated with climate variability is the return time and intensity of fire events that may be related to changes in precipitation patterns and to land use. If fire return time is reduced, carbon stored in these forests and their soils may be reduced as seen during land use change and fire events throughout the tropics (Nepstad *et al*., 2001; Shang & Tiessen, 2003; Powers, 2004). In addition, frequent fires could decrease soil fertility (Shang & Tiessen, 2003) and the mycorrhizal inoculum in the soil (Allen *et al*., 2003a, 2005). Changes in mycorrhizal inoculum may reduce the potential of forest regeneration by nutrient limitation (Campo & Vazquez-Yanes, 2004), and decrease the accumulation of stable carbon pools, such as glomalin (Rillig *et al*., 2001).

Conclusions

Total ecosystem biomass in our study site ranged from 4.2 to 174.8 Mg ha^{-1} while total ecosystem carbon ranged from 21.7 to 153.5 Mg ha^{-1}. Biomass and carbon pools in our study sites increase with forest age, but BGB and BGC had higher accumulation rates than AGB and AGC. BGC represented more than 90% in early successional forests to nearly 50% of total ecosystem carbon in mature forests. However, carbon stored in belowground fractions could rapidly be lost if forests are disturbed and the thin soil is lost by fire or erosion with a potential carbon loss between 120 and 150 Mg C ha^{-1} in a mature forest. Total ecosystem carbon inventories of mature and young stands of SDTF are needed to better estimate their role in the global carbon budget. In addition, further research is needed on how seasonally dry tropical forests may recover after different disturbances (e.g. hurricanes, deforestation) and what the effects of climate variability will be on their recovery processes.

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Appendix A

Table A1 Aboveground biomass (AGB) and belowground biomass (BGB) expressed as $\mathrm{Mg\,ha^{-1}}$ in secondary seasonal tropical forests of El Eden Reserve

Site age	Fine roots	Oe (<2 mm)	Oe (>2 mm)	Oi horizon	Seedlings	Palms	Lianas	Dead trees
1	1.5 ± 0.2	0.9 ± 0.2	0.8 ± 0.1	0.9 ± 0.1	0.06	0.0	0.0	0.0
4	3.8 ± 0.5	4.8 ± 1.1	2.0 ± 0.3	6.5 ± 0.9	na	na	0.0	0.7
5	3.0 ± 0.3	3.3 ± 0.4	3.0 ± 0.2	8.6 ± 0.4	0.2 ± 0.03	0.02 ± 0.01	0.0 ± 0.0	0.4 ± 0.1
8	5.1 ± 0.4	2.2 ± 0.4	3.8 ± 0.2	7.3 ± 0.8	na	na	0.0	0.9
9	7.8 ± 1.1	4.0 ± 0.4	3.0 ± 0.1	9.5 ± 0.4	0.4 ± 0.03	0.02 ± 0.01	0.0 ± 0.0	0.3 ± 0.1
14	4.2 ± 0.6	3.6 ± 0.4	3.9 ± 0.3	9.2 ± 0.5	na	na	0.0	1.1
15	4.7 ± 0.6	3.5 ± 0.4	4.2 ± 0.4	10.0 ± 0.4	0.2 ± 0.02	0.03 ± 0.01	0.0 ± 0.0	0.9 ± 0.2
28	3.7 ± 0.4	3.7 ± 0.4	6.7 ± 0.6	9.6 ± 0.5	na	na	na	1.1
29	2.7 ± 2.1	6.1 ± 0.4	5.5 ± 0.4	10.9 ± 0.6	0.2 ± 0.02	0.05 ± 0.03	1.0 ± 0.1	2.0 ± 0.7
MF	4.1 ± 0.6	6.0 ± 0.9	5.2 ± 1.0	7.2 ± 0.6	na	na	na	10.2
MF	6.4 ± 0.6	7.7 ± 0.5	7.8 ± 0.4	9.0 ± 0.5	0.1 ± 0.01	0.49 ± 0.08	1.4 ± 0.1	6.6 ± 3.3
MF	5.0 ± 0.6	6.1 ± 0.4	7.0 ± 0.3	7.1 ± 0.6	0.1 ± 0.01	0.22 ± 0.04	1.2 ± 0.2	5.0 ± 1.8

Trees

DBH (<1 cm)	DBH (<10 cm)	DBH (10–30 cm)	DBH (>30 cm)	Total AGB	Total BGB	Total biomass	MATBA ($\mathrm{Mg\,ha^{-1}\,yr^{-1}}$)
0.0	0.0	0.0	0.0	0.1	4.1 ± 0.2	4.2	4.2
10.8	9.8	0.0	0.0	21.3	17.1 ± 2.0	38.4	9.6
8.7 ± 1.5	10.8 ± 0.9	0.0 ± 0.0	0.0	20.2 ± 2.1	18.0 ± 0.5	38.1 ± 2.1	7.6
3.7	28.8	1.2	0.0	34.6	18.4 ± 0.7	53.0	6.6
5.4 ± 1.2	30.0 ± 2.0	1.2 ± 0.0	0.0	37.2 ± 2.3	24.3 ± 1.0	61.5 ± 2.7	6.8
6.0	40.3	5.5	0.0	53.0	20.9 ± 0.6	73.9	5.3
6.5 ± 0.8	50.4 ± 2.4	4.7 ± 0.7	0.0	62.8 ± 2.8	22.3 ± 0.9	85.1 ± 2.7	5.7
0.9	29.0	37.7	10.2	78.8	23.8 ± 0.9	102.6	3.7
1.2 ± 0.5	29.5 ± 2.3	43.4 ± 3.6	0.0	77.4 ± 4.4	25.2 ± 1.1	102.6 ± 4.7	3.5
0.7	25.1	79.8	18.0	133.9	22.5 ± 1.4	156.4	2.6
1.2 ± 0.7	35.2 ± 2.6	86.1 ± 2.3	12.8	143.9 ± 6.5	30.8 ± 0.9	174.8 ± 6.2	2.9
1.0 ± 0.7	24.2 ± 2.5	82.4 ± 8.4	22.5	136.7 ± 8.6	25.2 ± 0.8	161.9 ± 8.8	2.7

Mean ± 1 SE is given for components sampled within each plot, but not components that include a single or whole plot measures. Coarse forest floor woody debris found in the MF sites are not included in this table. Tree biomass is divided into diameter (DBH) classes (cm). 'na' represents data not analyzed for this study. 'Total AGB' is the sum of all aboveground components and 'Total BGB' the sum of all belowground components. 'Total biomass' is the sum of AGB and BGB. 'MATBA' represents mean annual total biomass accumulation and is defined as the Total biomass of each site divided by its age (i.e. years after fire event). Fine roots are defined as roots <3 mm in diameter. MF, mature forest.

Table A2 Aboveground carbon (AGC) and belowground carbon (BGC) (Mg C ha^{-1}) in secondary seasonal tropical forests of El Eden Reserve

Site (age)	Oa-horizon	Fine roots	Oe < 2 mm	Oe > 2 mm	Oi-horizon	Seedlings	Palms	Lianas	Dead trees
1	20.1 ± 1.62	0.7 ± 0.08	0.1 ± 0.03	0.2 ± 0.03	0.4 ± 0.05	0.06	0.0	0.0	0.0
4	43.9 ± 4.04	1.7 ± 0.24	1.0 ± 0.23	0.6 ± 0.08	2.7 ± 0.36	na	na	0.0	0.3
5	54.5 ± 7.23	1.3 ± 0.13	0.9 ± 0.1	1.1 ± 0.08	3.8 ± 0.16	0.1 ± 0.01	0.01 ± 0.006	0.0	0.2 ± 0.06
8	44.6 ± 5.21	2.2 ± 0.17	0.9 ± 0.06	1.6 ± 0.1	3.4 ± 0.38	na	na	0.0	0.45
9	52.2 ± 7.46	3.6 ± 0.49	1.6 ± 0.14	1.2 ± 0.06	4.3 ± 0.18	0.2 ± 0.02	0.01 ± 0.003	0.0	0.14 ± 0.04
14	59.1 ± 7.91	1.9 ± 0.25	1.0 ± 0.1	1.5 ± 0.11	3.8 ± 0.21	na	na	0.0	0.6
15	58.0 ± 8.09	2.1 ± 0.24	1.1 ± 0.14	1.5 ± 0.13	4.1 ± 0.18	0.1 ± 0.01	0.02 ± 0.001	0.0	0.44 ± 0.1
28	64.9 ± 4.66	1.6 ± 0.18	1.4 ± 0.13	2.7 ± 0.22	4.3 ± 0.22	na	na	na	0.6
29	72.4 ± 9.36	1.2 ± 0.09	2.0 ± 0.14	2.1 ± 0.17	4.6 ± 0.27	0.1 ± 0.01	0.03 ± 0.01	0.50 ± 0.05	1.0 ± 0.33
MF	69.5 ± 4.12	1.8 ± 0.26	2.4 ± 0.33	2.1 ± 0.34	3.2 ± 0.29	na	na	na	5.1
MF	64.7 ± 11.6	2.8 ± 0.27	2.5 ± 0.15	3.0 ± 0.14	4.0 ± 0.21	0.05 ± 0.01	0.43 ± 0.04	0.69 ± 0.06	3.3 ± 1.65
MF	75.2 ± 17.9	2.3 ± 0.27	2.0 ± 0.12	2.7 ± 0.12	3.2 ± 0.25	0.04 ± 0.001	0.12 ± 0.01	0.60 ± 0.08	2.5 ± 0.91

Trees							
DBH < 1 cm	DBH < 10 cm	DBH 10–30 cm	dbh > 30 cm	Total AGC	Total BGC	Total carbon	MATCA (Mg C $\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$)
0.0	0.0	0.0	0.0	0.05	21.6 ± 1.6	21.7	21.7
5.4	4.9	0.0	0.0	10.7	50.0 ± 4.2	60.7	15.2
4.4 ± 0.8	5.4 ± 0.5	0.0 ± 0.0	0.0	10.1 ± 1.1	61.6 ± 7.2	71.7 ± 6.9	14.3
1.9	14.4	0.6	0.0	17.3	52.7 ± 5.0	70.0	8.75
2.7 ± 0.6	15.0 ± 1.0	0.6 ± 0.0	0.0	18.6 ± 1.1	62.8 ± 7.6	81.4 ± 7.3	9.05
3.0	20.2	2.8	0.0	26.5	67.1 ± 7.8	93.6	6.69
6.5 ± 0.8	25.2 ± 1.2	2.3 ± 0.3	0.0	31.4 ± 1.4	66.7 ± 8.2	98.1 ± 8.4	6.54
0.5	14.5	18.9	5.1	39.4	74.8 ± 4.7	114.2	4.08
1.2 ± 0.5	14.8 ± 1.1	21.7 ± 1.8	0.0	38.7 ± 2.2	82.3 ± 9.5	121.0 ± 9.2	4.17
0.4	12.6	39.9	9.0	67.0	78.9 ± 3.9	145.9	2.43
1.2 ± 0.7	17.6 ± 1.3	43.0 ± 1.2	6.4	72.0 ± 3.3	77.1 ± 11.7	149.1 ± 9.9	2.48
1.0 ± 0.7	12.1 ± 1.2	41.2 ± 4.2	11.3	68.3 ± 4.3	85.2 ± 17.7	153.5 ± 19.2	2.56

Data were calculated by multiplying the dry weight times the percentage of carbon content at each component.

Mean ± 1 SE is given for components sampled within each plot, but not components that include a single or whole plot measures. Coarse forest floor woody debris found in the MF sites are not included in this table. Tree carbon is divided into diameter (DBH) classes (cm). ‘na’ represents data not analyzed for this study. ‘Total AGC’ is the sum of all aboveground components and ‘Total BGC’ the sum of all belowground components. ‘Total carbon’ is the sum of AGC and BGC. ‘MATCA’ represents mean annual total carbon accumulation and is defined as the total carbon of each site divided by its age (i.e. years after fire event). Fine roots are defined as roots < 3 mm in diameter. MF is mature forest, carbon in Oa horizon is organic carbon. We assumed a 0.5 conversion factor of dry wood to carbon for the AGC components.