



## Effects of Vegetation Thinning on Above- and Belowground Carbon in a Seasonally Dry Tropical Forest in Mexico

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### ABSTRACT

Mature tropical forests are disappearing and secondary forests are becoming more abundant, thus there is an increasing need to understand the ecology and management of secondary forests. In the Yucatan Peninsula, Mexico, seasonally dry tropical forests are subject to frequent fire, and early-successional stands are extremely dense. We applied vegetation thinning (removal of all stems < 2 cm in diameter) to hasten secondary succession and open the understory to reduce the fire ladder in an 11-yr-old stand. We quantified the effect of vegetation thinning on above- and belowground carbon over 5 yr. Aboveground carbon included all standing vegetation and belowground carbon included fine roots and organic carbon in the Oi, Oe, and Oa soil horizons. Trees with diameter of 2–10 cm and > 10 cm had higher carbon accumulation rates in thinned plots than in control plots. Carbon stored in the Oi-horizon and the Oe > 2 mm fraction remained significantly higher in thinned plots even 5 yr after treatment. Carbon in fine roots was significantly higher in thinned plots, and radiocarbon (<sup>14</sup>C) data suggest that fine roots in thinned plots were recently produced in comparison with fine roots in control plots. We did not find significant differences in total ecosystem carbon after 5 yr (126 ± 6 and 136 ± 8 Mg C/ha, respectively). These results suggest rapid carbon recovery and support the hypothesis that young tropical forests thinned to hasten succession and reduce the fire hazard may have only a short-term negative impact on carbon accumulation in vegetation and soils.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

**Key words:** carbon sequestration; fine roots; management; radiocarbon; Yucatan Peninsula.

TROPICAL FORESTS REPRESENT an important component of terrestrial carbon. These forests account for about 400 Pg of carbon, which represents nearly 37 percent of the carbon stored globally in forest ecosystems (Dixon *et al.* 1994). However, mature tropical forests are disappearing at an alarming rate and secondary forests are becoming more abundant by regeneration after logging, intense fires, and abandonment of agricultural lands (Chazdon 2003). It is crucial to understand current carbon stocks and sequestration potentials in tropical ecosystems for an accurate estimate of the global carbon balance (Houghton 2005). Furthermore, carbon management of tropical forests could reduce the cost of emissions limitations set by the Kyoto Protocol (Pfaff *et al.* 2000).

A crucial research question is how tropical forests will respond to future climate change (Clark 2007), and recent studies have reported a decelerating growth in tropical forest trees (Feeley *et al.* 2007, Chave *et al.* 2008). Thus, there is an increasing need to understand how different management approaches will influence carbon stocks in different tropical ecosystems. Most experimental research has been done to increase carbon sequestration by the establishment of silvicultural plantations and restoration of abandoned and degraded tropical lands (Silver *et al.* 2000), but there are fewer studies on management of early-successional stands (*e.g.*, Guariguata 1999).

Seasonally dry tropical forest (SDTF) cover an estimated area of over  $1.05 \times 10^6$  km<sup>2</sup> (Miles *et al.* 2006). However, they experience

exceptionally high rates of land-use change, with less than 10 percent of mature forest remaining in many areas (Murphy & Lugo 1986, Janzen 1988, Bullock *et al.* 1995). Thus, there is an increasing need to investigate different approaches to manage these forests to preserve habitat for many species (Putz *et al.* 2001, Ghazoul 2002) and their carbon sequestration potential (Jaramillo *et al.* 2003, Read & Lawrence 2003, Alvarez-Yepiz *et al.* 2008, Vargas *et al.* 2008).

The primary uses of these forests have been for shifting agriculture, selective logging, fruit tree plantations, and conversion to grasslands for grazing (Murphy & Lugo 1986). In SDTF of the Yucatan Peninsula, Mexico, the landscape is the result of a long history of disturbances forming a mosaic of different stages of secondary succession. The young stands are characterized by dense woody resprouts that provide ladder fuels that increase the flammability of early-successional forests. In contrast, mature forests appear to be more resistant to fire due to a large number of low-density hardwood species (Schultz 2005) and an open understory sparse in ladder fuels (Cochrane *et al.* 1999).

In this study, vegetation thinning was applied in an SDTF on the Yucatan Peninsula, Mexico in a densely resprouting forest following fire (11-yr old). Our goal was to reduce competition around remaining trees to enhance their growth, to open the forest understory to reduce the fire ladder, and thereby achieve a forest architecture more similar to a mature forest within a shorter time frame than natural self-thinning (Allen *et al.* 2003b, Vargas 2007). Thinning is a well-known mechanism to increase the size of individuals (*e.g.*, Yoda *et al.* 1963, White & Harper 1970, Gorham 1979) because it reallocates growing space within the stand to maximize dimensional growth of selected trees. Most research on forest thinning

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has been done to identify management guidelines to produce optimal stand growth, but recent studies have focused on the carbon implications of thinning (Garcia-Gonzalo *et al.* 2007, Hoover & Stout 2007).

The main objective of this research was to quantify the response of aboveground, belowground, and total ecosystem carbon stocks and carbon accumulation rates to thinning over 5 yr in a young SDTF. We asked the following questions: (1) How does thinning influence aboveground carbon (AGC) accumulation of the remaining trees? (2) What is the effect of the deposited thinned materials on belowground carbon (BGC) pools? (3) Tree density changes with thinning, so what is the effect of the treatment on carbon stored in fine roots and carbon used for fine root production? (4) What is the overall effect of vegetation thinning in total ecosystem carbon (AGC and BGC) after 5 yr? Question 3 is crucial for forest development but fine root dynamics in tropical forests is poorly understood. In addition, questions 2 and 3 are relevant for SDTF of the Yucatan Peninsula as most soils are shallow (< 50 cm) but may contain up to 50 percent of total ecosystem carbon in mature forests (Vargas *et al.* 2008). Finally, question 4 tests the conventional thinking that thinning a stand does not result in any net gain of biomass and carbon, since the increased growth is concentrated in a smaller number of stems. However, there is evidence that the choice of thinning method has the potential to alter carbon gains. Hoover and Stout (2007) reported that understory thinning was more effective than canopy thinning in improving carbon gain in a temperate forest. However, to date it is unclear how thinning affects AGC and BGC dynamics in SDTFs.

With these questions we tested the following hypotheses: (1) vegetation thinning would increase AGC accumulation in the remaining trees (Guariguata 1999); (2) carbon stocks would initially increase in belowground pools as a result of the thinned material deposited on the ground, but may experience high decomposition rates as expected for tropical forests (Trumbore 2000); (3) fine roots may experience high mortality after the treatment but may recover and store more carbon in the thinned plots following the treatment because they explore new space for water and nutrient uptake (Lopez *et al.* 1998, 2003; Hwang *et al.* 2007); and (4) total ecosystem carbon may be lower in the thinned plots because of AGC loss after the thinning treatment and the expected high decomposition rates of the thinned material. Finally, this study is an attempt to quantify the response of above- and belowground pools to understand the effect of vegetation thinning on total ecosystem carbon and to improve our knowledge of carbon management techniques.

## METHODS

**STUDY SITE.**—The study was conducted at El Eden Ecological Reserve (21°12.6' N, 87°10.93' W) in the northeast Yucatan Peninsula, Mexico. This site has a mean annual temperature of 24.2°C and annual precipitation of 1650 mm. The climate is typical of SDTF, with a pronounced dry season (< 100 mm/mo) in January–April (Giddings & Soto 2003). The soils in the Reserve are shallow

(< 20 cm) with *ca* 30 percent soil organic matter, pH 7.5, bulk density of 0.35 g/cm<sup>3</sup>, and overlaying limestone bedrock (Allen *et al.* 2003a, Vargas *et al.* 2008).

The vegetation of the Reserve is described in Schultz (2005), and is a mosaic of successional vegetation most recently disturbed by hurricanes and anthropogenic fires (Gómez-Pompa *et al.* 2003, Vargas & Allen 2008, Vargas *et al.* 2008). The experimental site had 53 tree species, with the 10 dominants including individuals of *Bursera simaruba* (L.) Sarg., *Dendropanax arboreus* (L.) Decne. & Planch., *Ficus cotinifolia* Kunth., *Guettarda combsii* Urb., *Jatropha gaudieri* Greenm., *Lonchocarpus castilloi* Standl., *Lonchocarpus rugosus* Benth., *Nectandra salicifolia* Kunth, *Piscidia piscipula* (L.) Sarg., and *Vitex gaudieri* Greenm. These species accounted for 90 percent of the individuals at the experimental site (Vargas 2007).

The experimental plots were located within a forest stand burned during a severe wildfire in 1989. The site was divided into a grid of 20 plots, with 10 treatments and 10 controls in a randomized, blocked, replicated design. Each plot was 20 × 20 m with a 5-m aisle between plots. Tree height, basal area, and density of all tree size classes were measured in all plots at the beginning of the experiment and no significant differences (GLM procedure,  $P > 0.05$ ) were found among treatment and control plots (Fig. 1). A thinning treatment was applied in July 2000 to the treatment plots by cutting all trees with a dbh < 2 cm, regardless of species (Vargas 2007). Cut trees were counted in 5 × 5 m sub samples of each plot and all the cut vegetation was left where it fell and allowed to decompose on site. The remaining 10 plots were left uncut and used as control plots. We will refer to these plots as thinned and control throughout the text. After the thinning in 2000 no further treatment was applied.

**MEASUREMENTS.**—For this study we sampled six thinned and six control plots during August of 2003, 2004, and 2005. We defined AGC pools as the carbon retained in standing vegetation including dead and living trees. BGC pools were defined as the carbon retained in the soil profile including fine roots, litter, and soil organic matter. Total ecosystem carbon was defined as the sum of all the AGC and BGC pools.

**TREE MEASUREMENTS.**—We measured aboveground components using a nested plot design. Within each 20 × 20 m plot we measured all trees with dbh > 10 cm. We established two 5 × 5 m plots inside each 20 × 20 m plot, in which we measured all trees < 10 cm but > 1 cm dbh. Within each 5 × 5 m plot we established two subplots of 1 × 1 m to measure all trees with a dbh < 1 cm but > 1.3 m in height. All seedlings < 1.3 m in height were counted and harvested in all 1 × 1 m plots. Tree height of standing trees (> 1 cm dbh) was determined via regression models (tree height vs. diam.) developed from measurements of 561 trees in the thinned and control plots during 2003 (Table 1). Biomass of trees was calculated using published allometric equations (Table 1). For trees > 10 cm dbh we used equations developed in nearby forests of the Yucatan Peninsula (Cairns *et al.* 2003), while for trees < 10 cm we used equations developed from tropical forests of Veracruz, Mexico (Hughes *et al.* 1999). Consistent with Clark *et al.* (2001) and

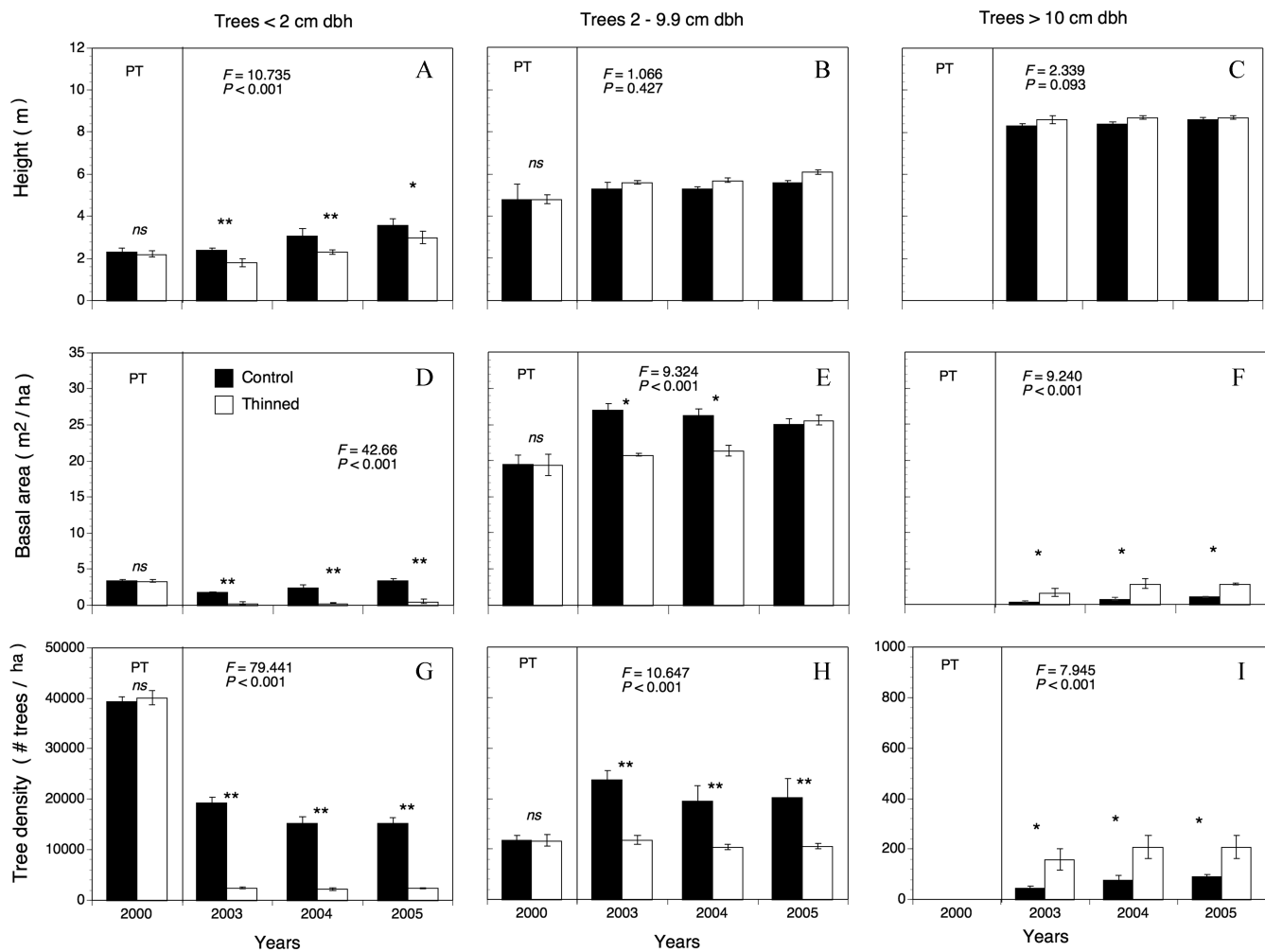


FIGURE 1. Tree height (A–C), basal area (D–F), and tree density (G–I) in the control and thinned plots in a seasonally dry tropical forest following a selective vegetation treatment. Values represent means  $\pm$  SE. We did not find significant differences between control and thinned plots at the onset of the experiment (pre-treatment). PT = pre-treatment. \* $P < 0.05$ , \*\* $P < 0.01$  represent significant differences of *post-hoc* tests between treatments after thinning.

Vargas *et al.* (2008) we used a conversion factor of 0.5 to estimate the carbon fraction in oven dry wood.

**SOIL SAMPLING.**—To measure BGC pools we collected samples in the Oi (litter) and Oe (decomposed litter) horizons in two areas of  $0.5 \times 0.5$  m of each control and thinned plot. The material found in the Oe horizon was subdivided into Oe  $> 2$  mm (material  $> 2$  mm; partially decomposed litter) and Oe  $< 2$  mm (material  $< 2$  mm; highly decomposed litter). The samples from the Oi and Oe horizons were oven-dried at  $65^{\circ}\text{C}$  to determine dry weight. At the center of each  $0.5 \times 0.5$  m plot we collected samples of the Oa-soil horizon (including fine roots) by inserting a 4.5-cm-diam. metal soil corer until we encountered the limestone bedrock (usually  $< 10$  cm in depth). All cores taken within the same  $20 \times 20$  m plot were combined. Soil samples were air-dried and transported to the University of California, Riverside where they were stored at  $-20^{\circ}\text{C}$  prior to laboratory analysis. Fine roots

( $< 2.0$  mm in diameter) from cores were sorted by hand and rinsed free of organic matter with deionized water and oven-dried at  $65^{\circ}\text{C}$  to determine dry weight. With this sampling protocol our cores only intercepted fine roots at the depth of the cores, averaging  $< 10$  cm depth, but not large roots that typically penetrate the limestone bedrock. Sampling these larger roots was not possible for this research, as major disturbances would be required to sample roots in bedrock during consecutive years.

**LABORATORY ANALYSES.**—Soil samples from all horizons (Oa, Oe, and Oi horizons) and fine roots were ground to pass through a  $250\text{ }\mu\text{m}$  sieve and oven-dried at  $65^{\circ}\text{C}$  for 72 h. Sub samples from the Oa horizon (1 g) were treated with 0.5 N HCl to remove carbonates and then analyzed for total organic carbon (Schumacher 2002). Carbon percentage was determined by dry combustion using a Thermo Finnigan Flash EA1112 N/C analyzer (Milan, Italy). Carbon content per unit area for all fractions measured in this study

TABLE 1. Equations used to determine tree height and biomass in control and thinned plots in a seasonally dry tropical forest.

Parameter	Equation	CF	R <sup>2</sup>
Height of trees (cm)			
(1) Thinned and Control plots*	$= 2.5233 \times \ln(D) + 2.3105$	1.02	0.85
Biomass (Mg)			
(2) Trees > 10 cm dbh**	$= \exp(-2.173 + 0.868 \times \ln[D^2H] + [0.0939/2])$	none	0.9
(3) Trees < 10 cm dbh***	$= (\exp[4.9375 + 1.0583 \times \ln(D^2)]) \times 1.14/10^6$	1.14	0.93
(4) Wood in trees < 1 cm dbh***	$= \exp(4.7472 + 1.0915 \times \ln[D^2])/10^6$	1.13	0.93
(5) Leaves in trees < 1 cm dbh***	$= \exp(3.0473 + 0.07778 \times \ln[D^2])/10^6$	1.45	0.71
(6) Standing dead trees > 10 cm dbh***	$= \pi ([D/2]^2)/H(0.41)$	none	none
(7) Dead trees < 10 cm dbh***	$= (\exp[4.6014 + 1.1204 \times \ln(D^2)])1.11/10^6$	1.11	0.95

Notes: Symbols after each parameter indicate source: \*this study, \*\*Cairns *et al.* (2003), \*\*\*Hughes *et al.* (1999). Biomass is expressed as dry weight (Mg). Definitions of symbols: D = diameter at breast height (cm), H = total tree height (m), BA = basal area (cm<sup>2</sup>), dbh (diameter at breast height), CF = correction factor as per Sprugel (1983).

was estimated using measurements of mass per area and percent carbon, and organic carbon in the Oa-horizon was calculated based on soil bulk density and horizon thickness (Schoeneberger & Wysocki 2002).

Radiocarbon <sup>14</sup>C was used to estimate the mean age of carbon in fine roots in the thinned and control plots to test for potential changes in fine root radiocarbon age after thinning. This technique was applied to answer question 3 to identify differences in fine root production. Soil cores were collected from three control and three thinned plots during 2005. Fine roots (< 2.0 mm in diam.) from cores were sorted by hand and rinsed free of organic matter with deionized water, but we did not discriminate between live and dead roots. After an acid–base–acid treatment (Gaudinski *et al.* 2001), root samples were oven-dried at 60°C and then ground. Samples were converted to graphite according to Xu *et al.* (2007) and measured for radiocarbon using accelerator mass spectrometry (AMS) at the UC Irvine W. M. Keck Carbon Cycle AMS facility (see Trumbore *et al.* 2006). To estimate the mean age of carbon in fine roots we assumed that all structural carbon in the root grew in a single year and the average age of the root was determined by comparing the  $\Delta^{14}\text{C}$  of the structural carbon of the roots to the record of  $\Delta^{14}\text{C}$  of CO<sub>2</sub> in the atmosphere (Gaudinski *et al.* 2001, Trumbore *et al.* 2006). We used the  $\Delta^{14}\text{C}$  record for tropical latitudes (30°N–30°S) reported by Levin and Kromer (2004) and updated by X. Xu (pers. comm.).

STATISTICAL ANALYSES.—Data sets were tested for normality, arcsine-transformed when needed, and analyzed using the GLM procedure for pretreatment comparisons, and repeated measures GLM procedure to show differences on each variable over time after the treatment. Potential block interactions were statistically tested, but were not significant for any measured variable ( $P > 0.05$ ). *Post-hoc* tests were performed with a *t*-test between groups (control and thinned) at each time. Annual carbon accumulation rates were calculated using the slope generated by linear regressions, and analysis

of covariance (ANCOVA) was used to test differences in slopes between treatments. All statistical analyses were performed using SPSS statistical software (SPSS Inc., v13.0, 2006).

## RESULTS

TREE BASAL AREA, DENSITY, AND HEIGHT.—The trees cut during the thinning in July 2000 were on average nearly 2-m tall whereas the remaining trees were nearly 4-m tall. Total tree basal area was reduced by *ca* 17 percent from nearly 23.0 to nearly 19.0 m<sup>2</sup>/ha after thinning all trees < 2 cm dbh. Nearly 40,000 trees/ha were cut during the treatment, and nearly 11,000 trees/ha with dbh > 2 cm remained reducing about 78 percent of the individuals.

We found an overall significant difference ( $P < 0.001$ ) in basal area between the control and thinned plots during the 3 yr of measurements. Basal area for trees with dbh < 2 cm was significantly ( $P < 0.001$ ) higher in the control plots from 2003 to 2005 (Fig. 1A), mainly because of the high number (> 15,000 trees/ha) of trees in this category (Fig. 1B). Although we observed resprouting of trees < 2 cm in the thinned plots, these were significantly lower ( $P < 0.001$ ) in number and height than trees of the same category in the control plots (Fig. 1B, C).

Five years after the treatment, we observed a recovery of basal area of trees with dbh 2–10 cm in the thinned plots (Fig. 1A). The density of trees of this category was significantly lower ( $P < 0.001$ ) in the thinned than in the control plots (nearly 10,000 and 20,000 stems/ha, respectively; Fig. 1B). Therefore, trees of this category responded to the treatment by having greater dbh but similar height compared to trees in the control plots.

Trees > 10 cm dbh were highly responsive to the treatment. These trees had significantly larger ( $P < 0.001$ ) basal area in the thinned plots from 2003 to 2005 than in the control plots. Trees > 10 cm were significantly ( $P < 0.001$ ) more abundant in the thinned plots, but not significantly taller (Fig. 1).

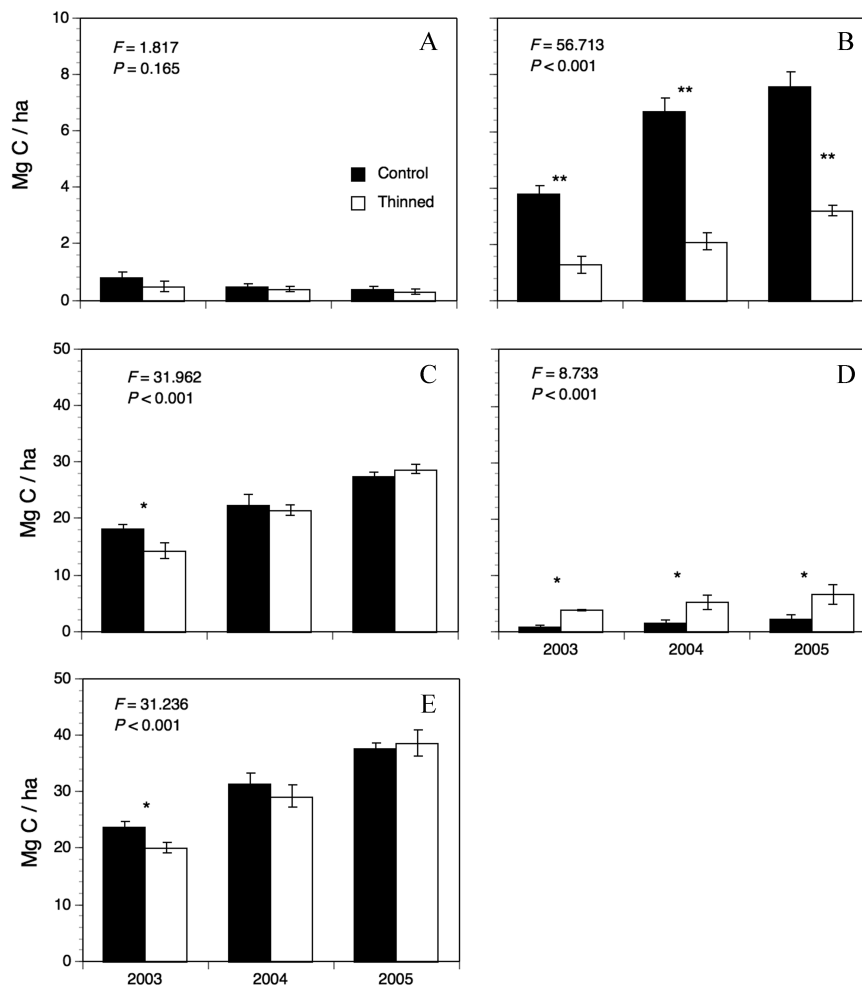


FIGURE 2. Aboveground carbon of trees with dbh < 2 cm (A), 2–10 cm (B), > 10 cm (C); and total aboveground carbon (sum of all tree diameter classes). (D) Values represent means  $\pm$  SE in Mg C/ha in thinned and control plots. We did not find significant differences between control and thinned plots at the onset of the experiment (pre-treatment). PT = pre-treatment. There were no trees > 10 cm dbh at the onset of the experiment. \* $P$  < 0.05, \*\* $P$  < 0.05 represent significant differences of *post-hoc* tests between treatments after thinning.

**ABOVEGROUND CARBON.**—We found a significantly larger ( $P$  < 0.001) carbon pool in trees < 2 cm dbh in the control plots between 2003 and 2005 (Fig. 2A), and significantly lower ( $P$  < 0.001) carbon accumulation rates in thinned than control plots (0.9 and 1.9 Mg C/ha/yr, respectively).

We found overall differences in carbon stored in trees 2–10 cm dbh ( $P$  < 0.001); however, the differences were accentuated with significantly lower ( $P$  < 0.05) carbon in the thinned plots 3 yr after the treatment, but no significant differences thereafter (Fig. 2B). Carbon accumulation rates were significantly higher ( $P$  < 0.001) in the thinned than control plots with rates of 7.1 and 4.6 Mg C/ha/yr, respectively, between 2003 and 2005. Carbon stored in this size category (2–10 cm dbh) of trees represented nearly 70 percent of the AGC in control and thinned plots.

Trees with dbh > 10 cm were responsive to the treatment with significantly greater carbon stored in the thinned plots, and

a maximum difference of nearly 4.3 Mg C/ha 5 yr after treatment (Fig. 2C). Higher accumulation rates ( $P$  < 0.001) were observed in the thinned than in the control plots (1.3 and 0.7 Mg C/ha/yr, respectively), between 2003 and 2005.

We calculated that the thinning treatment reduced total AGC from 16.2 to 11.5 Mg C/ha in 2000 based on our count of cut trees and equation (3) in Table 1. We found overall total AGC significant differences ( $P$  < 0.001) between the control and thinned plots. Total AGC remained significantly lower ( $P$  < 0.05) in the thinned plots after 3 yr, but we did not find significant differences thereafter (Fig. 2D). Five years after the treatment AGC accounted for 37.8 and 38.7 Mg C/ha in the control and thinned plots, respectively. We found significantly higher ( $P$  < 0.001) total AGC accumulation rates of the thinned than the control plots (9.2 and 6.9 Mg C/ha/yr, respectively) between 2003 and 2005. In addition, the net gain in total AGC in 5 yr was 21.6 Mg C/ha for the control plots and 27.2 Mg C/ha for the thinned plots.

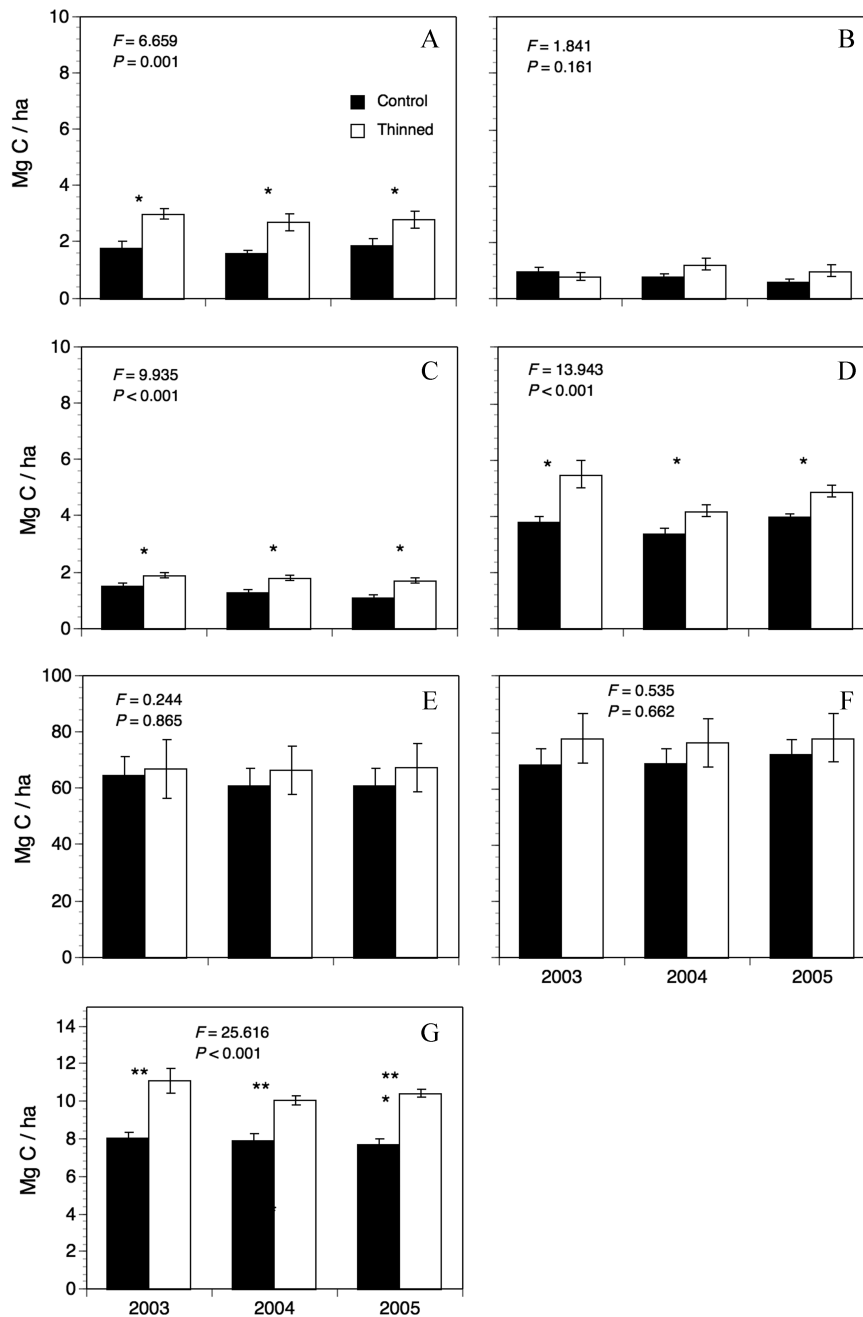


FIGURE 3. Belowground carbon of (A) fine roots, (B) Oe < 2 mm fraction, (C) Oe > 2 mm fraction, (D) Oi-horizon, (E) Oa-horizon, (F) total belowground carbon (sum all belowground pools), and (G) belowground carbon without Oa-horizon pool. Values represent means  $\pm$  SE in Mg C/ha in thinned and control plots. Belowground carbon was not measured at the onset of the experiment. \* $P < 0.05$ , \*\* $P < 0.05$ , \*\*\* $P < 0.001$  represent significant differences of *post-hoc* tests between treatments after thinning.

**BELOWGROUND CARBON.**—Carbon stored in fine roots was significantly higher ( $P < 0.001$ ) up to 5 yr in the thinned plots than in the control plots with an average of 2.1 and 1.1 Mg C/ha, respectively (Fig. 3A). The carbon stored in fine roots of the thinned plots may come from recently produced fine roots after the treatment as suggested by the radiocarbon measurements.  $\Delta^{14}\text{C}$  of structural carbon of fine roots in the thinned plots was significantly

lower ( $P = 0.023$ ) than in the control plots ( $\Delta^{14}\text{C} = 81.2 \pm 4.3$  and  $94.8 \pm 5.8$ , respectively). The mean radiocarbon age of fine roots ranged from 3 yr in the thinned plots to 6 yr in the control plots.

We did not find significant differences in the carbon stored in the Oe < 2 mm fraction (Fig. 3B), but carbon stored in the Oe > 2 mm fraction was significantly greater ( $P < 0.001$ ) in the thinned

plots up to 5 yr (Fig. 3C). We did not find differences in carbon accumulation rates in either of the Oi fractions.

Carbon stored in the Oi-horizon remained significantly higher ( $P < 0.001$ ) in the thinned plots even 5 yr after the treatment (Fig. 3D). We found a significant decrease ( $P < 0.001$ ) of carbon stored in the Oi-horizon of the thinned plots at a rate of  $-0.2 \text{ Mg C/ha/yr}$  during 2003–2005, and an accumulation of the carbon stored in the Oi-horizon of the control plots of  $0.1 \text{ Mg C/ha/yr}$  in the same time period.

We did not find significant differences in the carbon stored in the Oa-horizon (Fig. 3E), nor were there differences in carbon accumulation rates in this horizon between the control and thinned plots. Total BGC was not significantly different between the thinned and control plots, most likely as a result of the high carbon content and variation of the Oa-horizon (Fig. 3F). The Oa horizon contained nearly  $60 \text{ Mg C/ha}$  with about 28 percent of organic carbon at an average depth of 6 cm. However, with the Oa-horizon pool excluded from the analysis we found significantly ( $P < 0.001$ ) higher BGC in the remaining pools in the thinned plots (Fig. 3G).

**TOTAL ECOSYSTEM CARBON.**—Total AGC in these forests represented nearly 23 percent of total ecosystem carbon in 2003, 30 percent in 2004, and 35 percent in 2005. Conversely, total BGC represented nearly 77 percent of total ecosystem carbon in 2003, 70 percent in 2004, and 65 percent in 2005. We did not find significant differences in total ecosystem carbon with values of  $126 \pm 6 \text{ Mg C/ha}$  in the control plots and  $136 \pm 8 \text{ Mg C/ha}$  in the thinned plots 5 yr after the treatment, indicating that the thinned plots were able to recover their carbon stocks in spite of the thinning treatment. Noteworthy, the Oa-horizon represented nearly 60 percent of total ecosystem carbon at our study site, with large variation (Fig. 3E).

## DISCUSSION

**ABOVEGROUND CARBON.**—This research is one of the few studies to apply vegetation thinning in an early-successional tropical forest (e.g., Guariguata 1999, Andresen *et al.* 2005). Our goal was to open the canopy to allow the larger trees to increase their size and trunk diameter growth while reducing the flammable fire ladder. The experimental treatment reduced 14 percent of total tree basal area, which represented  $4.7 \text{ Mg C/ha}$  in the thinned plots, and we assessed the carbon consequences of thinning-induced changes in stand structure over 5 yr. We observed greater AGC accumulation rates of all trees  $> 2 \text{ cm}$  in the thinned plots with more carbon stored in trees  $> 10 \text{ cm dbh}$  than in the control plots. Five years after the treatment, we were able to create a less dense forest in the thinned plots, but one with similar total basal area and AGC as the control plots.

Our results support hypothesis 1 but because of higher AGC accumulation rates they challenge hypothesis 4 as we did not find differences in total ecosystem carbon. The carbon accumulation rates in the thinned plots are comparable to the increase in carbon sequestration found in thinned plots in a Pennsylvania Allegheny hardwood stand in the U.S. (Hoover & Stout 2007). Plots thinned

from below (small diameter understory stems) had greater carbon accumulation after 25 yr compared to controls than plots receiving middle or top thinning (Hoover & Stout 2007). Our thinning treatment is comparable to the plots thinned from below by Hoover and Stout (2007), and our results support the hypothesis that changes in stand structure can affect carbon storage. We postulate that recovery rates may differ with stand age at the time of thinning treatment, site history, and vegetation type. Thus, more research is needed on the carbon implications of thinning management in natural successional stands in tropical forests.

We observed that, after opening the canopy, the remaining trees rapidly filled in the canopy gaps with increased leaf area (Vargas 2007) and significantly increased their stem growth as has been observed elsewhere (Haggar & Ewel 1995). Additionally, thinning reduced competition from small-diameter trees, which may have been using belowground resources, especially water (Haggar & Ewel 1997). The fact that total AGC was similar in thinned and control plots by 2004, 4 yr after thinning, indicates the more rapid growth rate of the thinned forest, and was shown by our calculations of carbon accumulation rates. The increased carbon accumulation of individuals and the stand following thinning in an early-to-mid seral stand would be expected (Clark 1990), and our increased biomass accumulation of  $1.3 \text{ MgC/ha}$  for trees  $> 10 \text{ cm dbh}$  were well within the expected estimates of increased production of  $1.1\text{--}1.5 \text{ MgC/ha}$  following thinning (Dewar 1993).

Designing carbon management approaches to increase AGC is crucial because SDTF in the Yucatan peninsula requires nearly 80 yr to recover AGC levels (nearly  $70 \text{ MgC/ha}$ ) equivalent to mature forests (Read & Lawrence 2003, Vargas *et al.* 2008). Additionally, thinning may not only increase AGC accumulation of the remaining trees, but it also creates a less dense forest reducing the fire ladder. In contrast to early-successional stands, mature tropical forests are characterized by an open understory and a reduced fire ladder that may increase resistance to fire (Allen *et al.* 2003b, Ray *et al.* 2005). For example, the tree density of stems  $< 10 \text{ cm}$  in mature forests at El Eden Ecological Reserve is nearly 11,000 trees/ha (Vargas 2007), while in the thinned and control plots it was 12,500 and 35,000 trees/ha, respectively (5 yr after treatment).

**BELOWGROUND.**—A chronosequence study, comparing stands of SDTF at our study site, showed that 18 yr are required to recover BGC levels similar to mature forests (*ca*  $80 \text{ MgC/ha}$ ) in these shallow organic soils (Vargas *et al.* 2008). Therefore, prior to the thinning treatment, our 11-yr-old forest (in 2000) had accumulated about 50 percent of BGC levels of mature forests. In addition, most of the BGC is stored in the Oa-horizon and the remaining pools represent only 15 percent of total BGC.

Our results do not support hypothesis 2 as we expected higher decomposition rates in tropical forests and therefore find similar values of BGC between the control and thinned plots 5 yr after the treatment. We found higher carbon stocks in the Oi-horizon of the thinned plots probably as a direct result of the remaining debris (e.g., stems  $< 2 \text{ cm}$  in diameter) even after 5 yr of the treatment. We found that the rate of accumulation of Oi-horizon in thinned plots decreased during the 3 yr, while the rate increased

for control plots. However, our results show that the coarse materials deposited after the treatment may have lower turnover rates than litter alone and could contribute to BGC for a longer period of time. High decomposition rates are expected in tropical forests (Trumbore 2000), and it has been reported that litter inputs from hurricane disturbances disappear in less than 1 yr (Ostertag *et al.* 2003). Noteworthy, we found higher carbon stocks in the Oe > 2 mm fraction of the thinned plots, which suggests that part of the deposited materials have likely decomposed into a more stable carbon pool, but long-term observations (> 10 yr) are needed to show the possible contribution of material deposited after the thinning to more stable carbon pools in the Oa-horizon (Lal *et al.* 2004). We did not measure litterfall, but an alternative explanation is that higher carbon in the Oi-horizon may be a result of changes in forest canopy of the thinned plots in comparison with the control plots (Vargas 2007), which could cause possible differences in litter input. Thus, changes in forest structure after thinning may influence decomposition rates of deposited materials and litterfall input by increasing the leaf area (Vargas 2007).

Our results support hypothesis 3 as a significantly higher carbon pool was found in fine roots of the thinned plots up to 5 yr after the treatment. Fine root mortality has been observed after vegetation thinning (Hwang *et al.* 2007), so it is likely that root mortality occurred immediately after the thinning treatment. However, our results are comparable to other studies where fine root biomass and production is higher in the thinned than in the control plots (Lopez *et al.* 1998, 2003; Hwang *et al.* 2007). We postulate that less competition from small trees may have favored the colonization of small pockets of soil by newly formed fine roots (Hodge 2004) of the remaining trees in the thinned plots as soil is a limited resource in this karstic ecosystem (Vargas *et al.* 2008). This hypothesis is supported by our observations of younger radiocarbon-dates in structural carbon of fine roots in the thinned plots. Radiocarbon dating of fine roots may be interpreted as: (1) the mean age of carbon in fine roots of the thinned plots is younger than the mean age of carbon in fine roots of the control plots; or (2) plants in the thinned plots use recent carbon to produce fine root tissues (Gaudinski *et al.* 2001, Trumbore *et al.* 2006). Both interpretations suggest that changes in forest aboveground structure by vegetation thinning influenced fine root dynamics. Our research is one of the few studies that have measured radiocarbon in fine roots of tropical forests and supports the observations that recently fix carbon is used to produce new fine roots (Trumbore *et al.* 2006).

Our fine root results are relevant because investment in carbon to fine root production could enhance water and nutrient uptake and support arbuscular mycorrhizae fungi (Allen 1991), which in turn benefit tree growth (Allen *et al.* 2003a, 2005). We observed more carbon stored in fine roots of the thinned plots, but our sampling underestimates total BGC because we only sampled fine roots and not larger coarse roots that penetrate into the limestone bedrock and have access to pockets of deeper soil and water (Querejeta *et al.* 2006). Finally, it is important to recognize that the thinning treatment appears to have increased the flux of carbon to belowground as fine root production, but this does not mean that it increased the partitioning of total carbon to belowground (flux to belowground

as a fraction of total flux). Understanding how carbon is allocated in forest ecosystems is crucial to understand forest ecosystem carbon cycling (Litton *et al.* 2007).

**TOTAL ECOSYSTEM CARBON.**—Our results do not support hypothesis 4 and challenge the conventional thinking that thinning a stand does not result in any net gain of carbon. Five years after the treatment, total ecosystem carbon did not differ significantly by treatment with  $136 \pm 8$  and  $126 \pm 6$  Mg C/ha in the thinned and control plots, respectively. These results suggest the fast recovery potential of these forests after vegetation thinning. We do not know if this trend will continue in subsequent years because the site was severely impacted by hurricane Wilma during October 2005 and modified forest structure and forest carbon dynamics (Vargas & Allen 2008).

In early-successional SDTF of the Yucatan most of the carbon is stored belowground (Vargas *et al.* 2008). In our study, we observed that AGC represented 23–35 percent of total ecosystem carbon but BGC represented 65–77 percent. Total ecosystem carbon may be underestimated by not accounting for large roots embedded in the limestone bedrock. A previous study in a mature SDTF reported that carbon stored in roots (including fine roots and roots > 20 mm) represented 4.7 percent of total ecosystem carbon (Jaramillo *et al.* 2003). Our results show that fine roots represented 0.9 and 1.5 percent of total ecosystem carbon in the control and thinned plots, respectively. Thus, based on the former study, we suggest that our estimates of carbon stored in roots may underestimate total ecosystem carbon by nearly 3 percent. More studies are needed in SDTF to better understand the contribution of AGC and BGC pools and their responses to different management practices to test the outcomes of our study.

**CONCLUSIONS.**—Our results suggest that thinning a young SDTF to hasten succession and reduce the fire hazard may have only a short-term negative impact on carbon accumulation in vegetation and soils. This study showed the response of AGC and BGC pools in an 11-yr-old SDTF after thinning as a practice to open the forest understory, hasten secondary succession, and reduce the fire ladder (Allen *et al.* 2003b, Ray *et al.* 2005).

Our results suggest higher AGC accumulation rates, higher fine root biomass, and no differences in BGC and total ecosystem carbon between the thinned plots and the control plots over 5 yr following the treatment. No difference in BGC is explained by the large (> 50%) contribution of this component to total ecosystem carbon. However, the relatively high rate of fine root recovery following thinning suggests that plants have the ability to produce fine roots when soil space is available as it is a limited resource in the Yucatan Peninsula. The fine root response shows the importance of studying the impact of aboveground management on belowground processes to understand feedbacks that will influence forest regeneration and carbon balance (Houghton 2003). However, a complete inventory of the coarse roots embedded in the limestone is needed for a full ecosystem carbon inventory.

This thinning approach was not designed to restore the high diversity found in mature SDTF, but the treatment did not reduce



the number of species present in the thinned plots in comparison with the control plots (Vargas 2007). Additional studies on the diversity changes in this forest are forthcoming. The treatment presented in this study could be improved by preserving endangered species present in the stand (e.g., *V. gaumeri*), species also present in mature forest, or species with important economic value. However, we have been able to show that thinning is a beneficial practice in the long term from the standpoint of carbon accumulation, mediated through both aboveground and belowground responses to a reduction in the forest density. Finally, secondary SDTF may be especially economically attractive for carbon markets (Olschewski & Benitez 2005), but may require management to enhance carbon accumulation rates.

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## LITERATURE CITED

- ALLEN, E. B., M. F. ALLEN, L. EGERTON-WARBURTON, L. CORKIDI, AND A. GÓMEZ-POMPA. 2003a. Impacts of early- and late-seral mycorrhizae during restoration in seasonal tropical forest, Mexico. *Ecol. Appl.* 13: 1701–1717.
- ALLEN, E. B., H. A. VIOLI, M. F. ALLEN, AND A. GÓMEZ-POMPA. 2003b. Restoration of tropical seasonal forest in Quintana Roo. In A. Gómez-Pompa, M. F. Allen, S. L. Fedick, and J. J. Jiménez-Osornio (Eds.), *The Lowland Maya area: Three millennia at the human-wildland interface*, pp. 587–598. Haworth Press, Binghamton, New York.
- ALLEN, M. F. 1991. *The ecology of mycorrhizae*. Cambridge University Press, Cambridge; New York.
- ALLEN, M. F., E. B. ALLEN, AND A. GÓMEZ-POMPA. 2005. Effects of mycorrhizae and nontarget organisms on restoration of a seasonal tropical forest in Quintana Roo, Mexico: Factors limiting tree establishment. *Restor. Ecol.* 13: 325–333.
- ALVAREZ-YEPÍZ, J. C., A. MARTÍNEZ-YRIZAR, A. BURQUEZ, AND C. LINDQUIST. 2008. Variation in vegetation structure and soil properties related to land use history of old-growth and secondary tropical dry forests in northwestern Mexico. *For. Ecol. Manage.* 256: 355–366.
- ANDRESEN, E., L. PEDROZA-ESPINO, E. B. ALLEN, AND D. R. PÉREZ-SALICRUP. 2005. Effects of selective vegetation thinning on seed removal in secondary forest succession. *Biotropica* 37: 145–148.
- BULLOCK, S. H., H. A. MOONEY, AND E. MEDINA. 1995. *Seasonally dry tropical forests*. Cambridge University Press, Cambridge, UK; New York, New York.
- CAIRNS, M. A., I. OLMSTED, J. GRANADOS, AND J. ARGAEZ. 2003. Composition and aboveground tree biomass of a dry semi-evergreen forest on Mexico's Yucatan Peninsula. *For. Ecol. Manage.* 186: 125–132.
- CHAVE, J., R. CONDIT, H. C. MULLER-LANDAU, S. C. THOMAS, P. S. ASHTON, S. BUNYAVEJCHEWIN, L. L. CO, H. S. DATTARAJA, S. J. DAVIES, S. ESUFALI, C. E. N. EWANGO, K. J. FEELEY, R. B. FOSTER, N. GUNATILLEKE, S. GUNATILLEKE, P. HALL, T. B. HART, C. HERNÁNDEZ, S. P. HUBBELL, A. ITOH, S. KIRATIPRAYOON, J. V. LAFRANKIE, S. LOO DE LAO, J.-R. MAKANA, M. N. S. NOOR, A. R. KASSIM, C. SAMPER, R. SUKUMAR, H. S. SURESH, S. TAN, J. THOMPSON, M. D. C. TONGCO, R. VALENCIA, M. VALLEJO, G. VILLA, T. YAMAKURA, J. K. ZIMMERMAN, AND E. C. LOSOS. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biol.* 6: e45.
- CHAZDON, R. L. 2003. Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6: 51–71.
- CLARK, D. A. 2007. Detecting tropical forests' responses to global climatic and atmospheric change: Current challenges and a way forward. *Biotropica* 39: 4–19.
- CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, AND J. NI. 2001. Measuring net primary production in forests: Concepts and field methods. *Ecol. Appl.* 11: 356–370.
- CLARK, J. S. 1990. Integration of ecological levels: Individual plant-growth, population mortality and ecosystem processes. *J. Ecol.* 78: 275–299.
- COCHRANE, M. A., A. ALENCAR, M. D. SCHULZE, C. M. SOUZA, D. C. NEPSTAD, P. LEFEBVRE, AND E. A. DAVIDSON. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284: 1832–1835.
- DEWAR, R. C. 1993. A mechanistic analysis of self-thinning in terms of the carbon balance of trees. *Ann. Bot.* 71: 147–159.
- DIXON, R. K., S. BROWN, R. A. HOUGHTON, A. M. SOLOMON, M. C. TREXLER, AND J. WISNIEWSKI. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263: 185–190.
- FEELEY, K. J., S. J. WRIGHT, M. N. N. SUPARDI, A. R. KASSIM, AND S. J. DAVIES. 2007. Decelerating growth in tropical forest trees. *Ecol. Letts.* 10: 461–469.
- GARCIA-GONZALO, J., H. PELTOLA, E. BRICENO-ELIZONDO, AND S. KELLOMAKI. 2007. Changed thinning regimes may increase carbon stock under climate change: A case study from a Finnish boreal forest. *Clim. Change* 81: 431–454.
- GAUDINSKI, J. B., S. E. TRUMBORE, E. A. DAVIDSON, A. C. COOK, D. MARKEWITZ, AND D. D. RICHTER. 2001. The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. *Oecologia* 129: 420–429.
- GHAZOUL, J. 2002. Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodivers. Conserv.* 11: 521–541.
- GIDDINGS, L., AND M. SOTO. 2003. Rhythms of precipitation in the Yucatan Peninsula. In A. Gómez-Pompa, M. F. Allen, S. L. Fedick, and J. J. Jiménez-Osornio (Eds.), *The Lowland Maya area: Three millennia at the human-wildland interface*, pp. 77–90. Haworth Press, Binghamton, New York.
- GÓMEZ-POMPA, A., M. F. ALLEN, S. L. FEDICK, AND J. J. JIMÉNEZ-OSORNIO. 2003. *The Lowland Maya area: Three millennia at the human-wildland interface*. Haworth Press, Binghamton, New York.
- GORHAM, E. 1979. Shoot height, weight and standing crop in relation to density of monospecific plant stands. *Nature* 279: 148–150.
- GUARIGUATA, M. R. 1999. Early response of selected tree species to liberation thinning in a young secondary forest in Northeastern Costa Rica. *For. Ecol. Manage.* 124: 255–261.
- HAGGAR, J. P., AND J. J. EWEL. 1995. Establishment, resource acquisition, and early productivity as determined by biomass allocation patterns of three tropical tree species. *For. Sci.* 41: 689–708.
- HAGGAR, J. P., AND J. J. EWEL. 1997. Primary productivity and resource partitioning in model tropical ecosystems. *Ecology* 78: 1211–1221.
- HODGE, A. 2004. The plastic plant: Root responses to heterogeneous supplies of nutrients. *New Phytol.* 162: 9–24.

- HOOVER, C., AND S. STOUT. 2007. The carbon consequences of thinning techniques: Stand structure makes a difference. *J. Forest.* 105: 266–270.
- HOUGHTON, R. A. 2003. Why are estimates of the terrestrial carbon balance so different? *Global Change Biol.* 9: 500–509.
- HOUGHTON, R. A. 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biol.* 11: 945–958.
- HUGHES, R. F., J. B. KAUFFMAN, AND V. J. JARAMILLO. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80: 1892–1907.
- HWANG, J., Y. SON, C. KIM, M. J. YI, Z. S. KIM, W. K. LEE, AND S. K. HONG. 2007. Fine root dynamics in thinned and limed pitch pine and Japanese larch plantations. *J. Plant Nutr.* 30: 1821–1839.
- JANZEN, D. H. 1988. Tropical dry forests: The most endangered major tropical ecosystem. In E. O. Wilson (Ed.). *Biodiversity*, pp. 130–137. National Academy of Sciences/Smithsonian Institution, Washington, DC.
- JARAMILLO, V. J., J. B. KAUFFMAN, L. RENTERIA-RODRIGUEZ, D. L. CUMMINGS, AND L. J. ELLINGSON. 2003. Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. *Ecosystems* 6: 609–629.
- LAL, R., M. GRIFFIN, J. APT, L. LAVE, AND M. G. MORGAN. 2004. Ecology—Managing soil carbon. *Science* 304: 393.
- LEVIN, I., AND B. KROMER. 2004. The tropospheric (CO<sub>2</sub>)-C-14 level in mid-latitudes of the Northern Hemisphere (1959–2003). *Radiocarbon* 46: 1261–1272.
- LITTON, C. M., J. W. RAICH, AND M. G. RYAN. 2007. Carbon allocation in forest ecosystems. *Global Change Biol.* 13: 2089–2109.
- LOPEZ, B., S. SABATE, AND C. GRACIA. 1998. Fine roots dynamics in a Mediterranean forest: Effects of drought and stem density. *Tree Physiol.* 18: 601–606.
- LOPEZ, B. C., S. SABATE, AND C. A. GRACIA. 2003. Thinning effects on carbon allocation to fine roots in a *Quercus ilex* forest. *Tree Physiol.* 23: 1217–1224.
- MILES, L., A. C. NEWTON, R. S. DEFRIES, C. RAVILIOUS, I. MAY, S. BLYTH, V. KAPO, AND J. E. GORDON. 2006. A global overview of the conservation status of tropical dry forests. *J. Biogeogr.* 33: 491–505.
- MURPHY, P. G., AND A. E. LUGO. 1986. Ecology of tropical dry forest. *Annu. Rev. Ecol. Syst.* 17: 67–88.
- OLSCHEWSKI, R., AND P. C. BENITEZ. 2005. Secondary forests as temporary carbon sinks? The economic impact of accounting methods on reforestation projects in the tropics. *Ecol. Econ.* 55: 380–394.
- OSTERTAG, R., F. N. SCATENA, AND W. L. SILVER. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. *Ecosystems* 6: 261–273.
- PPAFF, A. S. P., S. KERR, R. F. HUGHES, S. LIU, G. A. SANCHEZ-AZOFEIFA, D. SCHIMEL, J. TOSI, AND V. WATSON. 2000. The Kyoto protocol and payments for tropical forest: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. *Ecol. Econ.* 35: 203–221.
- PUTZ, F. E., G. M. BLATE, K. H. REDFORD, R. FIMBEL, AND J. ROBINSON. 2001. Tropical forest management and conservation of biodiversity: An overview. *Conserv. Biol.* 15: 7–20.
- QUEREJETA, J. I., H. ESTRADA-MEDINA, M. F. ALLEN, J. J. JIMENEZ-OSORNIO, AND R. RUENES. 2006. Utilization of bedrock water by *Brosimum ali-castrum* trees growing on shallow soil atop limestone in a dry tropical climate. *Plant Soil* 287: 187–197.
- RAY, D., D. NEPSTAD, AND P. MOUTINHO. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecol. Appl.* 15: 1664–1678.
- READ, L., AND D. LAWRENCE. 2003. Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecol. Appl.* 13: 85–97.
- SCHOENEBERGER, P. J., AND D. A. WYSOCKI (Eds.). 2002. Field book for describing and sampling soils. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, New England.
- SCHULTZ, G. P. 2005. Vascular flora of the El Eden Ecological Reserve, Quintana Roo, Mexico. *J. Torrey Bot. Soc.* 132: 311–322.
- SCHUMAHER, B. A. 2002. Methods for the determination of total organic carbon (TOC) in soils and sediments. United States Environmental Protection Agency, Ecological Risk Assessment Support Center.
- SILVER, W. L., R. OSTERTAG, AND A. E. LUGO. 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restor. Ecol.* 8: 394–407.
- SPRUGEL, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64: 209–210.
- TRUMBORE, S. 2000. Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecol. Appl.* 10: 399–411.
- TRUMBORE, S., E. S. DA COSTA, D. C. NEPSTAD, P. B. DE CAMARGO, L. MARTINELLI, D. RAY, T. RESTOM, AND W. SILVER. 2006. Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biol.* 12: 217–229.
- VARGAS, R. 2007. Carbon dynamics in a seasonally dry tropical forest. PhD Dissertation. University of California, Riverside, California.
- VARGAS, R., AND M. F. ALLEN. 2008. Diel patterns of soil respiration in a tropical forest after hurricane Wilma. *J. Geophys. Res.* 113: G03021.
- VARGAS, R., M. F. ALLEN, AND E. B. ALLEN. 2008. Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. *Global Change Biol.* 14: 109–124.
- WHITE, J., AND J. L. HARPER. 1970. Correlated changes in plant size and number in plant populations. *J. Ecol.* 58: 467–485.
- XU, X. M., S. E. TRUMBORE, S. H. ZHENG, J. R. SOUTON, K. E. MCDUFFEE, M. LUTTGREN, AND J. C. LIU. 2007. Modifying a sealed tube zinc reduction method for preparation of AMS graphite targets: Reducing background and attaining high precision. *Nucl. Instrum. Methods Phys. Res.* 259: 320–329.
- YODA, K., T. KIRA, H. OGAWA, AND H. HOZUMI. 1963. Self-thinning in over crowded pure stands under cultivated and natural conditions. *Journal-Institute of Polytechnics, Series D (Biology)*, pp. 107–129. Osaka City University, Japan.