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Woody debris stocks and fluxes during succession in a dry tropical forest

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Abstract

In Southern Mexico, shifting cultivation is creating a mosaic of agricultural lands, secondary forests, and disturbed mature forests (montañas). Increased land-use change, due to population and market pressures has changed the structure and function of these forests. This study investigates the stocks and fluxes of woody debris during the course of secondary succession. We inventoried fine ($\geq$1.8 cm to $\leq$10 cm diameter) and coarse woody debris ($\geq$10 cm diameter) stocks in 28 stands. In a subset of montañas and secondary forest fallows, we monitored inputs and decomposition over a 2-year period. Total woody debris stocks were largest in montañas (37.46 Mg/ha) and in the first year after clearing (milpa, 51.62 Mg/ha). Woody debris was 22% of the total aboveground biomass in montañas and 88% in milpas. Although stocks were highly variable in secondary forest, coarse woody debris stocks were roughly three times larger than fine woody debris stocks. Coarse woody debris stocks decreased following cultivation for 10–15 years, until inputs exceeded losses to decomposition. Inputs were higher in montaña (0.91 Mg ha^{-1} year^{-1}) than in secondary forest (0.11 Mg ha^{-1} year^{-1}). Coarse woody debris inputs were higher during the dry season, while fine woody debris inputs tended to be higher during the wet season. Decomposition varied significantly among tree species, with decomposition rate constants from 0.124 to 0.643 year^{-1} for coarse woody debris and 0.368–0.857 year^{-1} for fine woody debris. In young forests, when woody debris stocks are largest, cultivation history is the most important factor in predicting stocks of woody debris. As forest age increases woody debris processes, both inputs and decomposition, become increasingly important factors in regulating woody debris stocks, and therefore age is a better predictor of woody debris stocks in older forests.

Keywords: Woody debris; Decomposition; Dry tropical forest; Secondary forest; Shifting cultivation; Yucatán peninsula; Mexico

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1. Introduction

Dry tropical forests account for approximately 5% of carbon in vegetation and soils of terrestrial ecosystems throughout the world (Houghton and Skole, 1990). In the late 20th century, secondary forests comprised 40% of the total forested area in the tropics (Brown and Lugo, 1990). Current estimates of degraded and secondary forest in the tropics range up to 60% of total forested area (International Tropical Timber Organization, 2002). The conversion of forest to agricultural land is the primary cause of land-use change in Mexico (Cairns et al., 2000) and the tropical Americas (Brown and Lugo, 1990). In the tropical southern states of Mexico, the area of agroecosystems increased 64% between 1977 and 1992 (Cairns et al., 2000). In 2000, at least 12% of land in the Southern Yucatán Peninsular Region (SYPR) had been deforested and were either in cultivation or secondary forest (Vester et al., in preparation). The timing and magnitude of carbon fluxes associated with this deforestation are poorly understood (Cairns et al., 2000). Sparse literature on woody debris (WD), especially in the tropics (Chambers et al., 2000), suggests woody debris dynamics have been understudied despite their importance in the structure and function of forest ecosystems (Franklin et al., 1987) and the carbon cycle.

Woody debris is understood as a short-term nutrient sink and as a long-term source of energy and nutrients (McFee and Stone, 1966; Larsen et al., 1978; Triska and Cromack, 1980; Harmon et al., 1986). Studies have focused on the role of decomposition in the carbon cycle (Hughes et al., 1999; Chambers et al., 2000) or on local changes in mass and nutrients of woody debris over time (McFee and Stone, 1966; Graham and Cromack, 1982; Arthur and Fahey, 1990; Means et al., 1992; Brown et al., 1996). Brown et al. (1996) and Chambers et al. (2000) found that the decomposition rate of woody debris

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increases slightly with precipitation and with temperature. Arthur and Fahey (1990) found that woody debris contains 5% of the phosphorus, 7% of the nitrogen, 16% of the potassium, 12% of the calcium, 17% of the magnesium, and 9% of the sodium present in above and belowground biomass of a subalpine fir forest in Colorado. These works clarify some aspects of the role of woody litter in ecosystems, yet fail to explain how land-use history affects the biogeochemical processes that control woody debris. According to Lawrence and Foster (2002) cultivation history, forest age, and land management practices are the major stand level factors affecting ecosystem processes in the SYPR. The impact of these factors on woody debris remains to be considered.

Researchers have long neglected the dynamics of woody debris because of the slow but variable rate of decomposition, the stochastic nature of inputs, and logistical difficulties in measuring debris stocks (Currie and Nadelhoffer, 2002). These problems are compounded in a disturbed landscape consisting of many forest ‘‘types’’ differing primarily by forest age, but also due to management practices. Sampling intensively to address several of these challenges, we studied woody debris in a chronosequence of sites in El Refugio, Campeche, Mexico.

Shifting cultivation is a method of agriculture used throughout the world to enhance site fertility when fertilizers are not available or affordable. Shifting cultivation is the dominant agricultural practice in the SYPR. Starting annually in March, farmers clear an area of forest cutting down all vegetation in a 1–2 ha plot using machetes and chainsaws. Farmers then wait 3–6 weeks for the downed vegetation to dry before burning the plot. The resulting landscape includes many stumps, logs, and larger branches not destroyed in the fire. Corn is then hand planted in these fields, locally known as milpas, using a 2 m long stick to make a small hole (2 cm wide by 6 cm deep) in the ground. A few kernels of corn are dropped in each hole and then the hole is covered. The corn plants are usually located less than a half meter apart. The farmers periodically weed their milpas but do not use any pesticide, herbicide, or fertilizer on the corn plants. All harvesting is done by hand and then the milpa is left fallow. After a fallow period of 3–15 years the process repeats itself. This full cycle from initial clearing of the forest to the second clearing is considered one shifting cultivation cycle (or swidden cycle).

Our goal was to understand the patterns and drivers of woody debris stocks and fluxes in the dry forests of southern Mexico. The two primary objectives were to (1) determine how forest age and cultivation history affect stocks and fluxes of woody debris and (2) determine what percent of total aboveground biomass is in the form of woody debris and how that changes during succession. We investigated woody debris stocks, inputs, and decomposition over a 2-year period.

We expected the number of shifting cultivation cycles experienced by a stand to be the main factor affecting the size of aboveground woody debris stocks (Fig. 1). The magnitude and shape of the curve for this model is based on preliminary data from 20 sites, while the effect of cultivation is an a priori guess. The burn prior to each cultivation period combusts some proportion of the existing woody debris stocks. We hypothesized that stocks of woody debris would be large immediately following cultivation and would decrease with age until the rate of woody debris inputs surpasses the rate of decomposition. Despite few coarse woody debris inputs into secondary forest younger than 11-years old, we still expected coarse woody debris (CWD) to be a larger percentage of woody debris stocks than fine woody debris (FWD) because much CWD was not combusted in the pre-cultivation burn. We hypothesized that forest age would be the primary factor affecting woody debris inputs. Mature forest, with high biomass, should input the most woody debris. Young successional forest in the process of thinning may also have high inputs of woody debris. We expected decomposition to be slow with complex dynamics related to microbial and fungal colonization rates and seasonality.

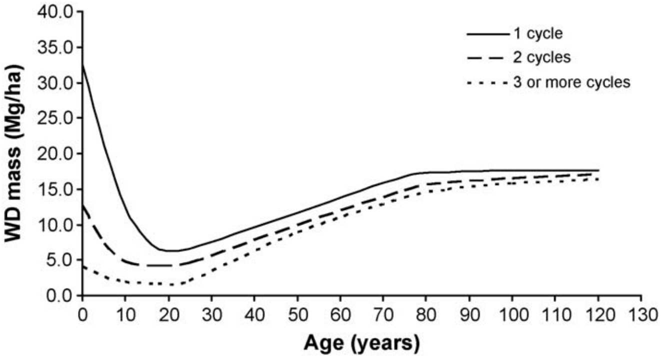

Fig. 1. Hypothesized stock of woody debris (Mg/ha) in secondary forest as a function of age and number of prior shifting cultivation cycles.

2. Methods

2.1. Study site

El Refugio (18°49′N, 89°27′W), with a mean annual rainfall of approximately 900 mm, is in the north-central area of the Southern Yucatán Peninsular Region in the state of Campeche. With a mean annual temperature of ca. 25 °C (Whigham et al., 1990), the Holdridge life zone system classifies this region as a dry tropical forest (Holdridge et al., 1971). Miranda (1958) classified these forests as Selva mediana subperennifolia (medium-statured semi-evergreen forest). Mean canopy height in mature forests with a history of selective logging was 12 m; 90% of trees >10 cm dbh were <23 m (Vester et al., in preparation). High seasonal and yearly variation in precipitation combined with shallow, calcareous, and highly permeable rendzina soils (Whigham et al., 1990) result in few permanent sources of surface water (White and Darwin, 1995). The dry period in El Refugio (<50 mm of precipitation per month) begins between November and January and lasts 5–7 months, and peak rainfall occurs in September or October (Lawrence and Foster, 2002).

2.2. Stocks of woody debris

As much as possible, we conformed to methods set forth by Harmon et al. (1986) and Harmon and Sexton (1996). In

Table 1
Equations used to calculate the stocks of coarse woody debris

Parameter	Equation	R^2	Source
Volume of CWD	$V = L \times [(A_b + n \times A_m + A_t)/(n + 2)]$	–	Harmon and Sexton (1996)
Diameter at height	$d_{ht} = 1.59 \times \text{dbh} \times (\text{ht}^{-0.091})$	0.87–0.99	Chambers et al. (2000)
Hollow volume	$V = \pi \times r^2 \times (\text{ht}/3)$	–	Clark et al. (2002)

V, volume; L, length; A_b, area at base; n, number of cross-sectional areas measured (not including the areas at the base and top); A_m, area of middle; A_t, area at top; d_{ht}, diameter at height; dbh, diameter at breast height; ht, height; r, radius.

May–June 2002 and 2003, woody debris was intensively sampled on six farmers' land. We sampled five sites per farmer including a current agricultural field (milpa), three secondary forest fallows (acahuals) of different ages (young, middle, and old, or 1–5 years, 6–11 years and 12–16 years, respectively), and a mature forest where selective timber extraction ended in the early 1960s (montaña). A total of 28 sites were sampled; not all parcels included all land-cover types. We selected parcels whose age and number of prior shifting cultivation cycles had been determined through interviews.

Coarse woody debris (diameter ≥10 cm) was sampled in two 16 m radius circular plots totaling 0.16 ha per site. Only one plot was sampled at two sites because the size or shape of the site did not allow for two 16 m radius circular plots. The center point of each plot was randomly located within a stand such that the plot was at least 10 m from the edge of the land-use unit. In an anthropogenic, fire-dominated, low-stature forest, sampling a minimum length of coarse woody debris (1.5 m set by Harmon and Sexton, 1996) would have grossly underestimated the mass of woody debris. Under shifting cultivation in the southern Yucatán, intentional slash fires occur every 3–15 years and unintentional fires may occur more often. Such anthropogenic disturbance disproportionately reduces the length to mass ratio of woody debris. Thus, all woody debris, with a diameter ≥10 cm, regardless of length, was considered to be CWD and was included in the surveys.

Each piece of coarse woody debris was numbered, marked with spray paint, and measured for length. Diameter (to the nearest cm) was measured approximately every meter of length. A decay class was assigned, ranging from 1 to 5 (Harmon et al., 1986; Pyle and Brown, 1998). Class 1 consisted of coarse woody debris in the least decayed state, with extensive and firm bark, and twigs and leaves still attached. Class 2 woody debris was still solid, had extensive bark that may have been peeling or burned, and generally lacked fine twigs and leaves. Class 3 debris was typified by the absence of bark, occasional spongy surface, firmness when pressure was applied by foot, and solid branch stubs. Class 4 debris lacked bark and branches, the outer surface may have been case-hardened, and the inner wood was spongy or powdered. Debris in decay class 5 lacked shape and was predominantly powdered wood. All coarse woody debris that had undergone a burn was classified as decay class 2, because firm bark, twigs, and leaves were no longer present. A few pieces that had been heavily burned were assigned to decay class 3.

Mass of coarse woody debris was calculated by decay class, using volume and density. Volume was calculated using a modified version of Newton's formula (Table 1) (Harmon and Sexton, 1996). Standing dead wood volume was calculated as the base of a cone, or frustum, using an equation by Chambers et al. (2000) for the upper diameter of the tree. The volume of hollow sections in fallen logs was calculated as the volume of a cone (Clark et al., 2002) and subtracted from the total volume for the corresponding decay class.

To determine density, cross-sections of 181 pieces of coarse woody debris, covering a range of species and decomposition classes, were collected from sites on one parcel and classified. These sites ranged in age from 0 (milpa) to 13 years. Field samples were dried at 60 °C until they achieved a constant weight and then stored in plastic bags until volume could be determined. Samples were vacuum-sealed in plastic to prevent the absorption of water (Grove, 2001), and then submersed to determine volume by displacement. Density (g cm^{-3}) was calculated by dividing the oven-dried weight by volume for 2–79 woody debris cross-sections per decay class (Table 2). Class 1 was not encountered in our surveys as all samples had undergone a burn or showed other indications of decomposition. Class 5 was rarely encountered and thus had fewer samples. Mean class-specific density was multiplied by the volume of coarse woody debris for each decay class to arrive at the mass of coarse woody debris for each class. All classes were summed and scaled to 1 ha to yield total coarse woody debris density (Mg/ha) for each site.

FWD was defines as all woody debris with a diameter ≥1.8 cm and ≤10 cm and a length greater than 1.8 cm. Stocks of fine woody debris were measured in eight 1 m^2 quadrats within each coarse woody debris plot. The eight 1 m^2 quadrats were arrayed 8 m from the central point in both the primary and secondary directions. All fine woody debris within these quadrats was collected and weighed. A sub-sample of fine woody debris was taken at each site to determine the conversion rate from field moist to oven dry. These sub-samples were stored in a cool place and later dried at 60 °C to constant weight.

Table 2
Density of coarse woody debris by decomposition class used to calculate mass from volume

Decomposition class	Density (g cm^{-3})		
	Mean ± 1 S.E.	Range	No. of samples
1	–	–	–
2	0.74 ± 0.03 A	0.22–1.33	79
3	0.78 ± 0.04 A	0.29–1.41	35
4	0.62 ± 0.06 B	0.15–1.18	22
5	0.36 ± 0.19 B	0.28–0.41	2
Average	0.73 ± 0.02	0.15–1.41	138

Significant differences among decay classes are indicated by different letters.

Stocks of woody debris were compared with total aboveground biomass. Total aboveground biomass included woody debris (this study) plus forest floor litter (Lawrence and Foster, 2002) and live aboveground biomass (Read and Lawrence, 2003b). Because we have not sampled aboveground biomass in milpas, we estimated it based on data from Hughes et al. (2000).

2.3. Inputs of woody debris

Inputs of coarse and fine woody debris were monitored over a 2-year period. Beginning in January 2003, we inventoried coarse woody debris inputs approximately every 6 months in the same plots used for coarse woody debris stock measurements using the same method as the initial inventory, recording only new (unmarked) pieces. Inputs of fine woody debris were estimated using 11 m radius plots (380 m^2) at six sites on one farmer's land: one 6-year old site, two 10-year old sites, one 13-year old site, and two montaña sites. We weighed and removed all fine woody debris from each input plot every 6 months, subsampling for wet–dry mass conversions. Annual inputs rates were calculated by dividing dry mass inputs for approximately 1 year (two sampling periods) by the number of days sampled and then standardizing to 365 days. We report the mean of rates for 2 consecutive years.

2.4. Decomposition of woody debris

In a 13-year old acahual, over a 1.5-year period, we investigated the decomposition of four common secondary forest species: *Lonchocarpus castilloi*, *Lysiloma bahamensis*, *Piscidia communis*, *Bursera simaruba* (common names: Machiche, Tzalam, Jabin, Chacah rojo). To ensure that time of tree death (thus woody debris origin) was known, all samples for the decomposition study were taken from a single milpa cut and burned from secondary forest in April/May 2002. Most fine woody debris <3–4 cm was consumed by the fire and not much coarse woody debris >12 cm was present in the milpa. Our experiment included two diameter classes: 11–13 cm (coarse) and 5–7 cm (fine). Harmon and Sexton (1996) suggest a length to diameter ratio of 10:1, thus our samples were 6 ± 1 cm × 60 cm and 12 ± 1 cm × 120 cm. For each size class, we set out three paired samples for each species within 3 m of each other. Length, diameter, decay class, and mass were measured on all samples every 6 months. In addition, a cross-section from the middle of one of the paired samples per size class and species was harvested to determine changes in water content. Variation in decomposition rates due to microclimate was minimized by positioning all samples completely in contact with the ground within several meters of each other (Boddy and Watkinson, 1995). Other confounding factors such as precipitation, temperature, substrate, and organisms (Harmon et al., 1986) should not vary systematically on such a small spatial scale (<3 m × 3 m).

2.5. Statistical analyses

Forest of similar age, and therefore structure, were combined into five age categories: milpa, young, middle, and old secondary forest fallows, and montaña. We used age class rather than age itself as there was no accurate estimate of the age of montaña and farmers may have been inaccurate in remembering the age of their fallows. Number of prior shifting cultivation cycles was usually treated as a continuous variable. For woody debris inputs, we treated cultivation history as a categorical variable with two groups: montañas (never cleared in recent history) and secondary forest fallows (one or more cycles).

Analysis of variance (ANOVA) was used to determine the broad effects of age class and number of prior shifting cultivation cycles on total stocks of woody debris (CWD + FWD). Subsequently, we used analysis of covariance (ANCOVA) to account for the influence of number of prior shifting cultivation cycles while further investigating age effects in secondary forest. Age class was assigned as a fixed factor and the number of prior shifting cultivation cycles was assigned as a covariate. Montañas were not included in this analysis. The numerical difference between zero and one prior cycle (the same as that between one and two prior cycles) does not adequately capture the fundamental difference in land-use history. The mechanics of ANCOVA could distort or obscure real differences if montañas were included. Coarse and fine woody debris stocks were log transformed to meet the assumptions of ANCOVA (Sokal and Rohlf, 1995). Due to the necessity of removing the effect of the covariate, we did not use a nonparametric test despite FWD stocks not meeting the assumptions of ANCOVA even with data transformation.

The effect of forest type (montaña versus secondary forest) and time on coarse and fine woody debris inputs were analyzed by repeated measures ANOVA. Input data on coarse and fine woody debris could not be transformed to meet the equality of variances assumption of ANOVA and results should be interpreted with caution. A repeated measures ANOVA was also used to analyze the effects of species and time on percent dry mass remaining in the decomposition study. The two size classes in the decomposition study were analyzed separately to eliminate confounding effects due to differences in microbial and fungal colonization rates. Decomposition rate constants (*k*-values) by species and size class were calculated as the slope of a linear regression of the natural log transformed percent mass remaining versus time (Olson, 1963).

Estimated marginal means are reported for all models. Post hoc tests involved a pair-wise contrast when ANCOVA or repeated measures ANOVA yielded significant results ($p < 0.05$). A Tukey's honestly significant difference (Tukey HSD) test was used to test among means following a significant ANOVA ($p < 0.05$). Back-transformed means are presented with 95% confidence limits, rather than standard error, as back-transformed standard error values would be misleading (Sokal and Rohlf, 1995). All statistics were carried out using SPSSv.11.5 (2002).

3. Results

3.1. Total stocks of woody debris

The total stock of woody debris ranged from a low of 2.77 Mg/ha, in an 8-year old secondary forest fallow during the

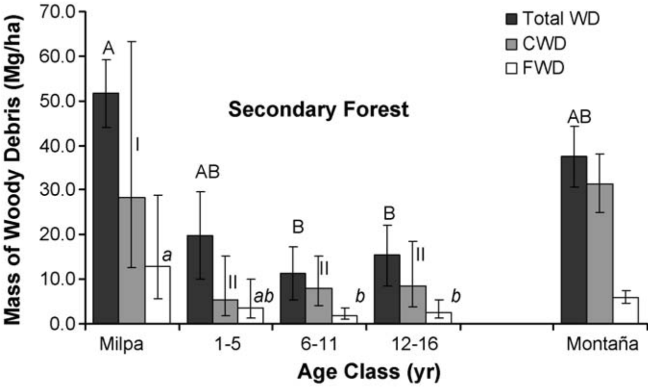

Fig. 2. Total, coarse, and fine woody debris stocks (Mg/ha) as a function of age class in El Refugio. Total woody debris bars represent estimated marginal means ± 1 S.E. (ANOVA, $p = 0.002$). CWD and FWD bars for secondary forests show estimated marginal means (ANCOVA, $p \leq 0.05$) with error bars representing upper and lower 95% confidence limits, assuming 1.55 shifting cultivation cycles. The montaña bar shows the arithmetic mean ± 1 S.E. Significant differences among age classes within a woody debris category are indicated by different letters. Montaña sites for CWD and FWD were not included in the ANCOVA analysis, as it would be incorrect to adjust these means for the covariate, and therefore do not have letters indicating significant differences. Fine woody debris data did not conform to the assumptions of ANCOVA even with transformation.

first shifting cultivation cycle, to a high of 94.92 Mg/ha in a milpa that had been cleared from montaña. Coarse woody debris stocks accounted for nearly 75% of total woody debris stocks over all age classes. Woody debris stocks declined from milpa (mean of 51.62 Mg/ha) to 1–5-year old forest (19.88 Mg/ha) to 6–10-year old forest (11.38 Mg/ha). Stocks tended to increase after 11 years (Fig. 2). Stocks of woody debris in montañas and milpas were not significantly different. As a proportion of the mean, the range of woody debris stocks was greatest in secondary forests. The proportion of total aboveground biomass in woody debris declined with forest age, from 88% in milpas to 22% in montañas (Fig. 3).

Total woody debris stocks declined as the number of prior shifting cultivation cycles increased (Fig. 4). Montañas (cultivated zero times) had significantly greater stocks than areas cultivated three times (ANOVA, $p = 0.002$). Number of prior shifting cultivation cycles also modified the relationship between forest age and woody debris mass. For sites having experienced one or two cycles woody debris stocks decreased with age for ca. 8–12 years, after which stocks increased (Fig. 5). The initial stocks, however, were half as great at the beginning of the second cycle (ca. 33.53 versus 77.83 Mg/ha).

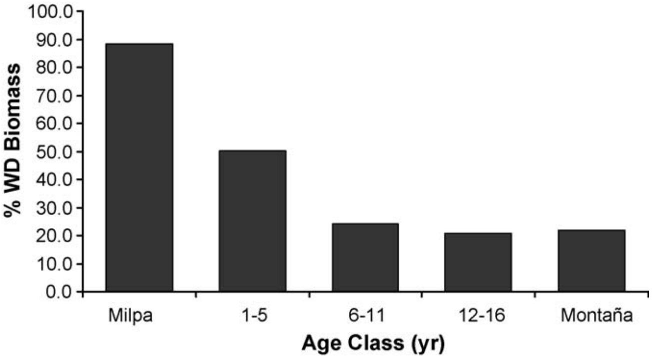

Fig. 3. Woody debris biomass as a percentage of total aboveground biomass (including live aboveground biomass + coarse woody debris + fine woody debris + forest floor litter).

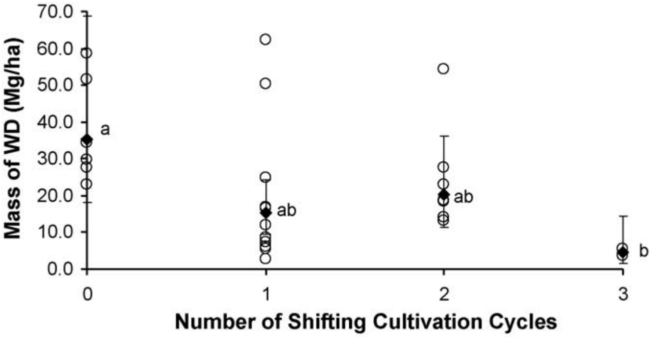

Fig. 4. Woody debris stocks (Mg/ha) as a function of the number of shifting cultivation cycles. Solid symbols are estimated marginal means with error bars representing upper and lower 95% confidence limits (ANOVA, $p = 0.002$). Significant differences are indicated by different letters. Sites with "0" prior cycles are montañas.

3.2. Coarse versus fine woody debris

Both age class ($p = 0.047$) and number of shifting cultivation cycles ($p = 0.038$) significantly affected the stocks of coarse woody debris (ANCOVA, $p = 0.02$). Pair-wise contrasts among means indicated that milpas, with 28.34 Mg/ha, had significantly greater stocks of coarse woody debris than secondary forest fallows, with 5.35–8.61 Mg/ha (Fig. 2). Among secondary forest fallows, age did not significantly influence CWD stocks. Stocks were much lower in secondary forest than in montañas (31.50 Mg/ha). Not accounting for forest age, mean CWD stocks declined by 35% from the first to the second cycle and by 87% from the second to the third (data not shown).

The number of shifting cultivation cycles was only marginally significant ($p = 0.088$) in predicting the stocks of

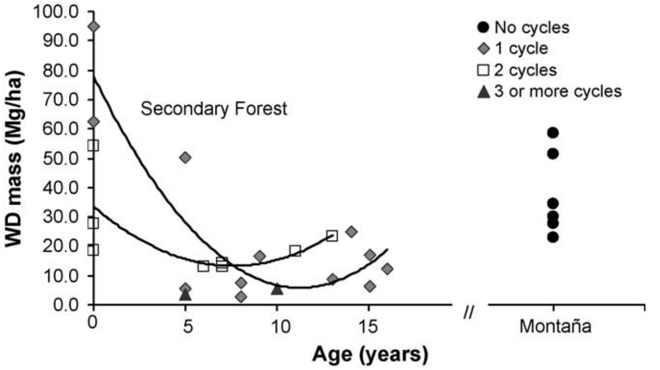

Fig. 5. Woody debris stocks (Mg/ha) as a function of age by number of shifting cultivation cycles. Best-fit regressions show that trends with age depend on the number of prior shifting cultivation cycles (one cycle, $p = 0.001$, $R^2 = 0.775$; two cycles, $p = 0.197$, $R^2 = 0.478$; only two sites had three prior cycles, no model fit).

fine woody debris in secondary forest, even though the ANCOVA model was significant ($p = 0.007$). Milpas had significantly higher fine woody debris stocks than secondary forests >6 years old (ANCOVA, $p \leq 0.008$) (Fig. 2). The mass of fine woody debris stocks decreased from 12.81 Mg/ha in milpas to 3.53 Mg/ha in the youngest secondary forest. Fine woody debris further declined to 1.85 Mg/ha in older secondary forests before increasing to 5.96 Mg/ha in montañas. It is important to note that although FWD stocks decreased initially after cultivation, this study was designed as a chronosequence, using forests of different ages to infer forest development through time.

3.3. Inputs of woody debris

Coarse woody debris inputs to montaña were greater than inputs to secondary forest fallows (repeated measures ANOVA, effect of forest type, $p = 0.002$) (Fig. 6a). Inputs to montañas ranged from 0.038 to 1.186 Mg/ha over 6 months with a mean annual rate of 0.91 Mg ha^{-1} year^{-1}. Inputs in secondary forests ranged from 0.005 to 0.075 Mg/ha over 6 months with a mean annual rate of 0.11 Mg ha^{-1} year^{-1}. Coarse woody debris inputs during the dry season (from January to June) were 7–31-fold higher than during the wet season (from June to January, pair-wise contrasts, $p < 0.05$). In contrast, fine woody debris inputs were high from June to January and low from January to June, however, the seasonal effect was not significant ($p = 0.436$) (Fig. 6b). Fine woody debris inputs did not differ significantly by forest type (0.88 versus 0.51 Mg ha^{-1} year^{-1} in montaña versus secondary forest, $p = 0.357$). In montaña, the annual rate of coarse woody debris inputs was very close to that of fine woody debris. In secondary forest fallows, fine woody debris inputs were about five times as large as inputs of coarse woody debris.

3.4. Decomposition of woody debris

Bursera simaruba decomposed faster than *Lonchocarpus castilloi*, *Lysiloma bahamensis*, and *Piscidia communis* for both coarse and fine woody debris (repeated measures ANOVA, $p < 0.001$). For coarse woody debris, the latter species had 80% of the original mass remaining after 1.5 years while *Bursera simaruba* had only 40% remaining (Fig. 7a). The decomposition rate constants (k-values) of coarse woody debris varied by over a factor of 5 among species. *Bursera simaruba* had a rate three to five times higher than other species (Table 3).

The onset of fine woody debris decomposition was delayed compared to that of coarse woody debris. After 154 days

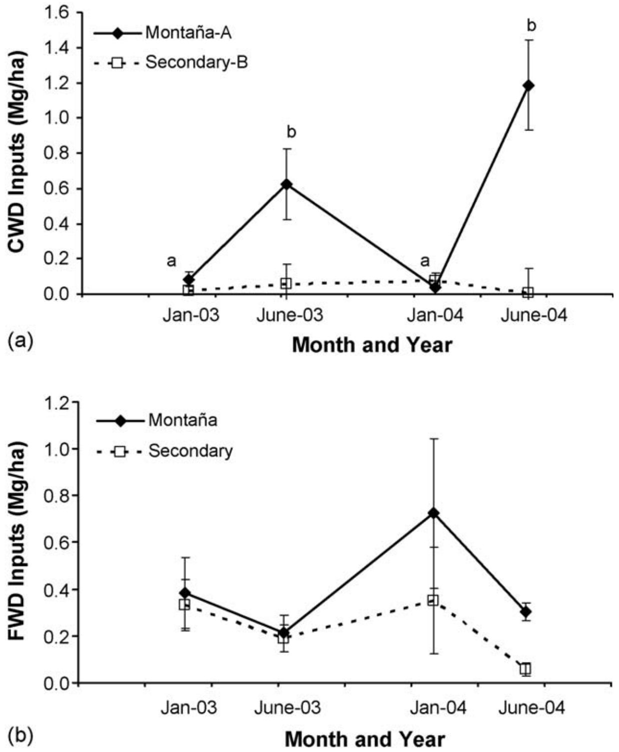

Fig. 6. (a) Coarse and (b) fine woody debris inputs in El Refugio. Coarse woody debris estimated marginal means (±1 S.E.) were higher in montaña and varied through time (repeated measures ANOVA, effect of forest type $p = 0.002$, time effect $p < 0.001$). Fine woody debris estimated marginal means (±1 S.E.) did not vary significantly with time or between mature and secondary forest (repeated measures ANOVA, effect of forest type $p = 0.357$, time effect $p = 0.436$). Significant differences over time are indicated by different letters. The study was initiated in June 2002, 154 days prior to the first sampling for inputs.

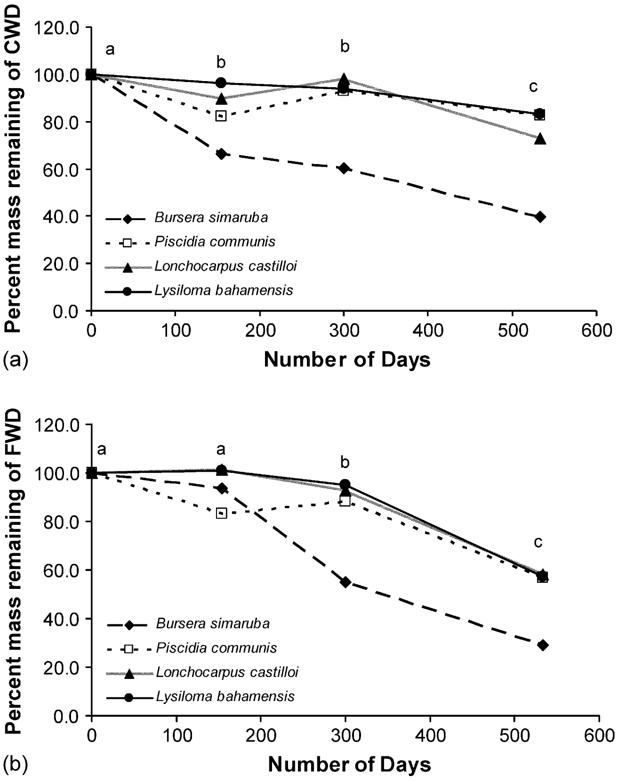

Fig. 7. Decomposition of (a) coarse and (b) fine woody debris in four tree species. Coarse and fine woody debris estimated marginal means of percent mass remaining declined significantly with time and more quickly in *Bursera simaruba* (repeated measures ANOVA, species effect $p < 0.001$, time effect $p < 0.001$). Original size of coarse woody debris pieces were 12 ± 1 cm × 120 cm, while the original size of fine woody debris pieces were 6 ± 1 cm × 60 cm. Significant differences over time are indicated by different letters.

Table 3
Decomposition rate constant (k, year^{-1}) by species and size class

	Latin name			
	Bursera simaruba	*Lonchocarpus castilloi*	*Lysiloma bahamensis*	*Piscidia communis*
CWD				
$k \pm$ S.E. (year^{-1})	0.643 ± 0.066	0.214 ± 0.066	0.124 ± 0.085	0.131 ± 0.066
Mean diameter (cm)	12.93	12.51	12.97	12.37
n	17	9	12	12
FWD				
$k \pm$ S.E. (year^{-1})	0.857 ± 0.073	0.368 ± 0.066	0.377 ± 0.073	0.403 ± 0.066
Mean diameter (cm)	5.66	6.44	6.46	6.15
n	17	17	17	17

Lonchocarpus castilloi and *Lysiloma bahamensis* had 100% of their mass remaining, whereas no species of coarse woody debris had 100% of its mass remaining after 154 days. The decomposition rate of fine woody debris significantly varied among species (repeated measures ANOVA, $p < 0.001$). The decay rate for *Bursera simaruba* (0.857 year^{-1}) was twice the rate calculated for the other three species (0.368–0.403 year^{-1}). With 30% mass remaining for *Bursera simaruba*, and 60% mass remaining for the other three species, fine woody debris had a greater percent loss than coarse woody debris after approximately 1.5 years (Fig. 7a and b). Within species, the decay rates for fine woody debris were higher than the rates for coarse woody debris (Table 3).

4. Discussion

4.1. Stocks of woody debris

Coarse and fine woody debris stocks in milpas and young secondary forests are a function of the number of times an area has been burned rather than age alone. The intensity of the burn, and its dependence on weather and management, is another important factor for further study. Stocks of coarse woody debris in milpas were often much larger than the stocks of coarse woody debris in the forest prior to slash, burn, and cultivation, as indicated by stocks in montañas and older fallows (Fig. 2). These stocks declined with each cycle of cultivation because the secondary forests that regenerate after the initial clearing contain few large diameter (>10 cm) trees (Read and Lawrence, 2003b). When they are then cut and burned, little coarse woody debris is produced, but a lot of fine woody debris is produced (Fig. 2). The stock of coarse woody debris can only increase once trees with a dbh > 10 cm are common, as in montañas. Although coarse woody debris inputs begin to appear after 8–10 years, trees >10 cm are likely to be vigorous and to contribute little woody debris through mortality. For the first 8–11 years, decomposition of the initial post-burn stocks tends to diminish coarse woody debris stocks until inputs from large trees begin to balance losses from decomposition. The large fine woody debris stocks in milpas (Fig. 2) are most likely due to incomplete slash and burn. Subsequent stocks are the balance of decomposition and inputs of fine woody debris from branch fall in younger secondary forest and branch fall and tree mortality associated with thinning in older secondary forest.

Woody debris stocks are highly variable in forests (Grove, 2001). Stocks of coarse woody debris in montañas of El Refugio (31.50 Mg/ha) were similar to those of a relatively undisturbed forest in the northern Yucatán peninsula (33.3 Mg/ha, Harmon et al., 1995), ca. 400 km to the northeast of El Refugio. Lower coarse woody debris stocks in El Refugio may reflect a history of logging that selectively removed the largest trees over the past 40–100 years (Klepeis, 2000). However, precipitation was also modestly lower in our study area (900 versus 1100 mm/year), which may naturally reduce forest stature and thus CWD inputs. Stocks in El Refugio were larger than in dry tropical forests of Venezuela (4.8 and 6.6 Mg/ha) that receive 800 and 1500 mm/year (Delaney et al., 1998). As expected, coarse woody debris was much larger (52.8 Mg/ha) in an old-growth rainforest of Costa Rica (Clark et al., 2002).

Few studies are available for comparison of the distribution of woody debris stocks and fluxes over the course of forest succession. Mattson et al. (1987) reported very large stocks of coarse and fine woody debris in a temperate forest of North Carolina immediately following clear-cutting, but a rapid decline in the first 7 years. Grove (2001), working in Australian lowland tropical rainforest, found the largest volume of coarse woody debris in old-growth forest and the smallest in secondary forest disturbed by logging. Because fire was not an integral part of these ecosystems, comparisons with this study are difficult.

As suggested by Brown and Lugo (1990), the relative contribution of coarse woody debris to total aboveground biomass declined with forest age in El Refugio. Woody debris in montañas accounted for just over 22% of the total aboveground biomass, slightly higher than the 13.5% found in the northern Yucatán (after Harmon et al., 1995). These values are intermediate compared to other forests. Delaney et al. (1998) found woody debris was 2.0–3.4% of total aboveground biomass in dry to very dry mature forest in Venezuela. Coarse woody debris was 25% of total aboveground biomass (not including forest floor litter and fine woody debris) in a Costa Rican rainforest (Clark et al., 2002). Krankina and Harmon (1995) reported that woody debris accounted for 20% of the total wood mass in southern taiga old-growth forests of north-western Russia.

4.2. Inputs of woody debris

Although Gholz et al. (1979) and Harmon and Sexton (1996) have developed methods for measuring or estimating the inputs of coarse and/or fine woody debris, few studies to date have utilized their methods. Clark et al. (2002) measured 4.9 Mg ha^{-1} year^{-1} of coarse woody debris input in Costa Rica, over five times the inputs measured in this study (0.91 Mg ha^{-1} year^{-1}). Live aboveground biomass of stems >10 cm dbh was less than twice as great in Costa Rica (161 Mg/ha, Clark and Clark, 2000) as in montañas of El Refugio (90 Mg/ha, after Read and Lawrence, 2003b). Harmon et al. (1986) postulated that coarse woody debris inputs vary as a function of both ecosystem productivity and the massiveness of the trees. The removal of large trees through selective logging helps to explain this difference, as coarse woody debris by definition derives from larger trees (Klepeis, 2000). Using an analysis of sample variance, Clark et al. (2002) suggested that inputs of coarse woody debris were measured with low precision in their 18 0.5 ha plots. This study, based on 0.16 ha per site, may suffer from low precision as well, despite the lower stature of dry forests. Even if our inputs were doubled, they would be low relative to inputs in the Costa Rican rainforest, reflecting differences in productivity and disturbance history.

The significant difference in coarse woody debris inputs between montaña and secondary forest fallows was expected because trees >10 cm dbh do not occur until age 8 (Read and Lawrence, 2003b). Although secondary forests are productive ecosystems, the small stature of trees in young forests limits natural coarse woody debris inputs. Almost all coarse woody debris inputs resulted from large branch fall rather than tree mortality, except in areas that were accidentally burned. Higher input rates from January to June are more likely due to escaped agricultural fires in April and May rather than water stress during this dry period. The similarity between coarse and fine woody debris input rates in montaña was surprising but is most likely particular to mature forests recovering from selective timber harvest.

4.3. Decomposition of woody debris

In a mixed hardwood forest in North Carolina, Mattson et al. (1987) found 10-fold variation in decomposition rates among species. They also found that fine woody debris decomposed twice as fast as coarse woody debris. The findings of this study broadly agree. The average decomposition rates here, 0.278 year^{-1} for coarse woody debris and 0.501 year^{-1} for fine woody debris, are 30–40% higher than values for similar size classes in the northern Yucatán (0.197 year^{-1} for coarse woody debris and 0.384 year^{-1} for fine woody debris, Harmon et al., 1995), despite higher precipitation in the north. Differences in decomposition rates are likely due to species differences and the effect of fire on decomposition. In this study, we assessed the decomposition of woody debris derived from a burned secondary forest (<25-years old), whereas Harmon et al. (1995) studied decomposition in undisturbed and disturbed mature forest. In El Refugio, the dominant species differ between montaña and secondary forest (Read and Lawrence, 2003a). Secondary forest species are likely to have a lower woody density and higher nutrient concentration than mature forest species. Fire could increase the rate of decomposition by removing bark and facilitating colonization by decomposers.

Our decay constant for coarse woody debris is higher than all 20 decomposition rates compiled by Chambers et al. (2000). Most of the studies focused on decomposition of CWD from older trees of late-successional species. As found here, Harmon et al. (1995) did not observe a slowing of mass loss with time in northern Yucatán, although this assumption underpins the concept of a decay constant in models such as the negative exponential decomposition model (Olson, 1963). Decomposition has been shown to follow a pattern of colonization by decomposers, a period of exponential mass loss, and finally a period of slow decomposition (Harmon et al., 1986, 2000). Neither coarse nor fine woody debris showed exponential mass loss, nor did they conform to the pattern of decomposition found in Harmon's studies. The discrepancy may be caused by the shorter duration of this study.

5. Conclusion

Following forest conversion to shifting cultivation, stocks of woody debris are initially large. They decrease with age until woody debris inputs balance decomposition. Then, upon re-clearing, the cycle begins again, but with lower initial socks, because the newly cleared secondary forest had smaller trees. Thus, the number of prior cultivation cycles significantly alters the relationships between woody debris and forest age. The amount of coarse woody debris in milpas and young secondary forest fallows of southern Mexico is a considerable percentage (88 and 50%, respectively) of the total aboveground biomass stock. Our hypothesis that the number of prior shifting cultivation cycles, and therefore fire frequency, was the main factor affecting the size of aboveground woody debris stocks was only partially substantiated by this study. Forest age also affects the stocks of woody debris, and significantly controls inputs. Although we did not compare decomposition rates in young and old forest, we did find that coarse woody debris decomposed half as rapidly as fine woody debris. Thus as the proportions of fine and coarse woody debris change with repeated disturbance, and through succession, we would expect systematic variation in loss rates as well.

Coarse woody debris stocks account for approximately 75% of total woody debris over all age classes in this human-disturbed forest ecosystem. As a consequence, studies that overlook fine woody debris will ignore 25% of the pool. Ignoring the changing role of woody debris in secondary forest has lead to mischaracterization of forest carbon stocks and the timing of carbon fluxes. Decreased inputs of woody debris, and dead biomass in general, to the forest floor following forest conversion for agriculture will likely result in decreased soil carbon storage.

If carbon cycling models are used to estimate and predict the impact of land-use change on atmospheric carbon dioxide, the fluxes and pools of woody debris must not be over looked.

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References

Arthur, M.A., Fahey, T.J., 1990. Mass and nutrient content of decaying boles in an Engelmann spruce-subalpine fir forest, Rocky Mountain National Park, Colorado. Can. J. Forest Res. 20, 730–737.

Boddy, L., Watkinson, S.C., 1995. Woody decomposition, higher fungi, and their role in nutrient redistribution. Can. J. Bot. 73, S1377–S1383.

Brown, S., Lugo, A.E., 1990. Tropical secondary forests. J. Trop. Ecol. 6, 1–32.

Brown, S., Mo, J., McPherson, J.K., Bell, D.T., 1996. Decomposition of woody debris in western Australian forests. Can. J. Forest Res. 26, 954–966.

Cairns, M.A., Haggerty, P.K., Alvarez, R., De Jong, B.H.J., Olmsted, I., 2000. Tropical Mexico's recent land-use change: a region's contribution to the global carbon cycle. Ecol. Appl. 10, 1426–1441.

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L.V., Melack, J.M., 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122, 380–388.

Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecol. Manage. 137, 185–198.

Clark, D.B., Clark, D.A., Brown, S., Oberbauer, S.F., Veldkamp, E., 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. Forest Ecol. Manage. 5646, 1–112.

Currie, W.S., Nadelhoffer, K.J., 2002. The imprint of land-use history: patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. Ecosystems 5, 446–460.

Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Bello Quintero, N., 1998. The quality and turnover of dead wood in permanent forest plots in six life zones of Venezuela. Biotropica 30, 2–11.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process. BioScience 37, 550–556.

Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Oregon State University Forest Research Laboratory. Research Paper No. 41.

Graham, R.L., Cromack Jr., K., 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Can. J. Forest Res. 12, 511–521.

Grove, S.J., 2001. Extent and composition of dead wood in Australian lowland tropical rainforest with different management histories. Forest Ecol. Manage. 154, 35–53.

Harmon, M.E., Sexton, J., 1996. Guidelines for measurements of woody detritus in forest ecosystems. US LTER Publication no. 20.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Lattin, J.D., Anderson, N.H., Gregory, S.V., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–301.

Harmon, M.E., Whigham, D.F., Sexton, J., Olmsted, I., 1995. Decomposition and mass of woody detritus in the dry tropical forests on the north-eastern Yucatán peninsula, Mexico. Biotropica 27, 305–316.

Harmon, M.E., Krankina, O.N., Sexton, J., 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. Forest Res. 30, 76–84.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T., Tosi, J.A., 1971. Forest Environments in Tropical Life Zones. A Pilot Study. Pergamon Press Inc., Elmsford, New York.

Houghton, R.A., Skole, D.L., 1990. Carbon. In: Turner, II, B.L., Clark, W.C., Kates, R.W., Richards, J.F., Mathews, J.T., Meyer, W.B. (Eds.), The Earth as Transformed by Human Action: Global and Regional Changes in the Biosphere over the Past 300 Years. Cambridge University Press, Cambridge, pp. 393–408.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80, 1892–1907.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 2000. Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. Ecol. Appl. 10, 515–527.

International Tropical Timber Organization, 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. ITTO Policy Development Series No. 13.

Klepeis, P., 2000. Deforesting the once deforested: land transformation in south-eastern Mexico. Ph.D. Dissertation, Clark University, Worcester, MA.

Krankina, O.N., Harmon, M.E., 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. Water Air Soil Pollut. 82, 227–238.

Larsen, M.J., Jurgensen, M.F., Harvey, A.F., 1978. N_2 fixation associated with wood decayed by some common fungi in western Montana. Can. J. Forest Res. 8, 341–345.

Lawrence, D., Foster, D.R., 2002. Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: an overview. Interciencia 27, 400–408.

Mattson, K.G., Swank, W.T., Waide, J.B., 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Can. J. Forest Res. 17, 712–721.

McFee, W.W., Stone, E.L., 1966. The persistence of decaying wood in humus layers of northern forests. Soil Sci. Soc. Am. Proc. 30, 513–516.

Means, J.E., MacMillan, P.C., Cromack Jr., K., 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, USA. Can. J. Forest Res. 22, 1536–1546.

Miranda, F., 1958. Vegetacion de la peninsula Yucateca. In: Beltran, E. (Ed.), Los recursos naturales del sureste y su aprovechamiento, Tomo 2. Instituto Mexicana Recursos Naturales Renovable, Mexico, D.F., pp. 215–227.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Pyle, C., Brown, M.M., 1998. A rapid system of decay classification for hardwood logs of eastern deciduous forest floor. J. Torrey Bot. Soc. 125, 237–245.

Read, L., Lawrence, D., 2003a. Litter nutrient dynamics during succession in dry tropical forests of the Yucatan: regional and seasonal effects. Ecosystems 6, 747–761.

Read, L., Lawrence, D., 2003b. Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatán. Ecol. Appl. 13, 85–97.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman & Co., New York, pp. 887.

SPSSv.11.5, 2002. SPSS Inc., Chicago.

Triska, F.J., Cromack, K., 1980. The role of wood debris in forests and streams. In: Waring, R.H. (Ed.), Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings of the 40th Biology Colloquium. Oregon State University Press, Corvallis, pp. 171–190.

Vester, H.F.M., Lawrence, D., Eastman, J.R., Turner, B.L. II, Calme, S., Dickson, R., Pozo, C., Sangermano, F., in preparation. Land Change in the Southern Yucatán and Calakmul Biosphere Reserve: Implications for Habitat and Biodiversity.

Whigham, D.F., Towle, P.Z., Cano, E.C., O'Neill, J., Ley, E., 1990. The effect of annual variation in precipitation on growth and litter production in a tropical dry forest in the Yucatán of Mexico. Trop. Ecol. 31, 23–34.

White, D.A., Darwin, S.P., 1995. Woody vegetation of tropical lowland deciduous forests and Mayan ruins in the north-central Yucatán peninsula, Mexico. Tulane Studies Zool. Bot. 30, 1–25.