CHANGES IN FOREST BIOMASS, LITTER DYNAMICS AND SOILS FOLLOWING SHIFTING CULTIVATION IN SOUTHERN MEXICO: AN OVERVIEW

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Over the past four decades the southern Yucatan peninsular region has undergone increasing amounts and intensity of land use change, ranging from selective logging to widespread shifting cultivation agriculture to land clearing for intensive agriculture and village establishment. These land uses alter the structure and function of forested lands and often generate new feedbacks in terms of subsequent human use. Consequently, a major goal in assessing regional environmental change is to understand how biogeochemical processes respond to land use change, emphasizing the potential of a human-dominated landscape to sustain continued human use. One of the greatest challenges in these studies is to distinguish the effects of environmental gradients in climate, geology or natural disturbance from the effects of human activity. In the Southern Yucatan Peninsula Region project (SYPR), our approach to this challenge has been to investigate ecosystem processes in several study sites arrayed across the dominant environmental gradients while focusing on the influence of local, human-controlled factors within a given area.

In the southern Yucatan, annual precipitation increases by more than 50% over 120km from the northeastern border of the Calakmul Biosphere Reserve to the Guatemalan Border. Median annual precipitation varies from ca. 900mm in the north of our study area to ca. 1400mm in the south. This range encompasses approximately 50% of the variation in precipitation of dry tropical forests worldwide (Murphy and Lugo, 1986). Thus, the gradient represents a broad sampling of the environment of the southern Yucatan peninsula and provides data relevant to many other dry forests. Rainfall is highly variable on an annual and a monthly basis, but all sites share a distinct seasonal pattern regardless of total annual precipitation. A pronounced dry period (<50 mm/mo) may begin as early as November or December, but often begins in January. It may last from three to seven months, depending on the year and the latitude (Figure 1).

The major stand-level factors determining the rate and dynamics of ecosystem processes are forest age, cultivation history, and management (land use type and landowner practices). Because shifting cultivation of maize (milpa) is the dominant cause of deforestation in the region (Turner *et al.*, 2001), forest recovery following this kind of disturbance was the central focus of investigations. The main objective of this study was to assess how nutrient cycling, productivity and biomass change throughout the course of secondary forest development following (temporary) abandonment of agricultural land. Plot-based studies of forest recovery within stands at a given site were placed into a broader context by comparing data across sites. This allowed us to test for the influence of regional environmental drivers.

The two-tiered conceptual approach, investigating local sites within a regional framework, facilitates an understanding of the multiple constraints on the trajectory of individual patches on the landscape. The landscape under shifting cultivation consists of many such patches at various stages of recovery. The approach employed also makes it possible to characterize the structure and function of the entire landscape at any one point in time, and to project it into the future, through integration with predictive models (Geoghegan *et al.*, 2001). Before making projections, it is necessary to understand current constraints on forest recovery in the SYPR. With that goal in mind, three questions are addressed in this paper:

1) What are the regional environmental influences on forest processes at the scale of 10s to 100s of kilometers? Do precipitation and soil fertility vary significantly at this scale?

2) How do natural environmental gradients in soil and precipitation affect ecosystem processes and characteristics?

3) Within a given region, how do ecosystem processes vary as a function of forest age?

KEYWORDS / Nutrient Cycling / Land Use Change / Forest Recovery / Phosphorus / Nitrogen /

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Methods

Study sites

Field work was concentrated in three study sites positioned 60-120km apart in order to sample across the regional precipitation gradient (Figure 2). Thirteen stands were studied in El Refugio (ER), the driest site (ca. 890mm/yr) near the northeastern border of Calakmul Biosphere Reserve in the State of Campeche. At Nicolás Bravo (NB), an area of intermediate rainfall (ca. 1150mm/yr) 60km to the southeast in the State of Quintana Roo, an additional 13 stands were studied. Approximately 120km south of ER on the border of Quintana Roo, Campeche, and Guatemala, 10 stands were studied in the village of Arroyo Negro (AN), the wettest part of the study area (ca. 1400mm/yr). Stands were sampled in both mature forest (2-3 per site) and secondary forest fallows regenerating after shifting cultivation of maize (8-10 per site). The mature forest stands were at least 50 years old (Read and Lawrence, in press) and had not been cleared for agriculture in recent history. None of the fallow stands had received inputs of fertilizer, pesticide, or herbicide. The secondary forest stands ranged in age from 2-25 years since the last harvest (Table I). Despite the absence of stumps or other evidence of past disturbance in the immediate vicinity of our stands, all of the forests may have experienced selective timber extraction in the last 40-100 years (Klepeis and Turner, 2001).

Secondary forest stands were selected from the database compiled by the socio-economic members of our research team (see Geoghegan *et al.*, 2001, Klepeis and Turner, 2001). We used information on the historical details of individual parcels, units of ownership and management by a single household. A parcel may encompass open, cultivated lands and forest stands of different age depending on when they were last used for cultivation. Information on parcel history made it possible to account for confounding factors such as differences in prior land use type, intensity of cultivation, and use of chemical inputs. These factors can modify the trajectory of recovery and should be sampled explicitly rather than inadvertently (e.g. Bushbacher *et al.*, 1988, Fernandes and Sanford, 1995, Hughes *et al.*, 1999). The effect of cultivation history was investigated in a separate paper, we deal primarily with forest age and regional environmental gradients in this study.

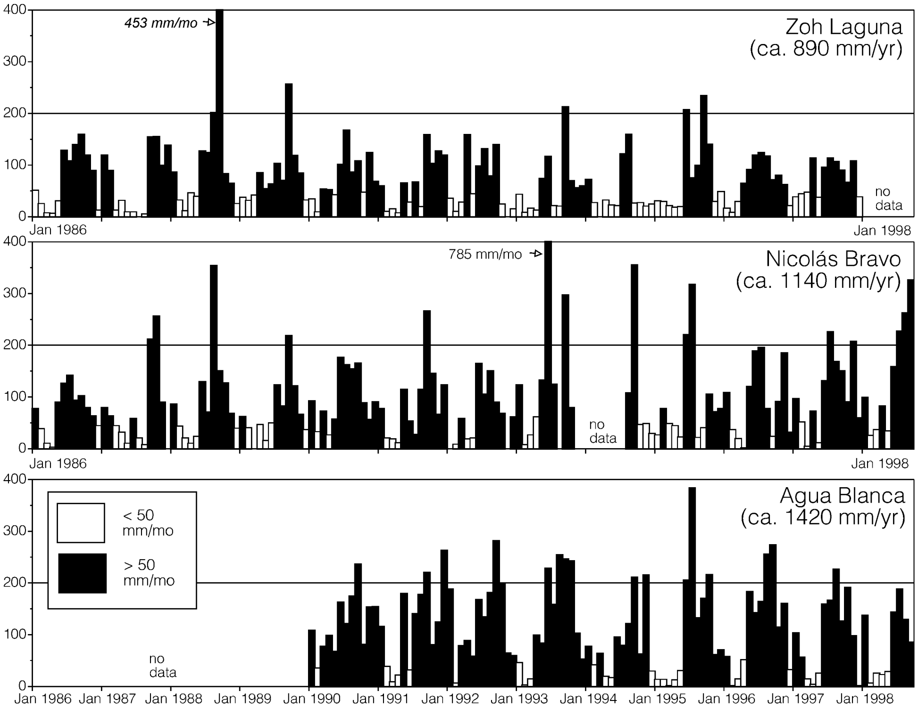

Figure 1. Monthly precipitation in the area of the principal study sites for the period 1986-1998 (courtesy of Instituto Nacional de Geografía Estadística e Informática, INEGI, Mexico). Records from the three villages nearest to the study sites: Zoh Laguna, 20km south of El Refugio, Nicolás Bravo, and Agua Blanca, 70km east-northeast of Arroyo. Zero precipitation values indicate missing data. Data from extreme storm events in 1988 and 1993 were clipped.

In each of the three study sites, several parcels were located containing young, middle-aged, and old fallow stands. Although clearing and cultivation practices may differ by landowner, within a given farmer's parcel it is possible to minimize management differences while also minimizing local differences in soil texture, inherent soil fertility, and topography. Thus, in establishing chronosequences within a given parcel, we expect to sample the effects of forest age, rather than the effects of contrasting management approaches or subtle edaphic variation. The true sampling unit was, in a sense, the farmer. The various forest stands owned by each farmer represents one trajectory of forest recovery. This approach, using the uniformity of practice within farm ownership is unusual and was facilitated by the cross-disciplinary nature of our project.

Litter production and nutrient cycling

One 500m^2 circular plot was established in each stand within a given parcel (Figure 3). Litter was collected once a month (Nov. 1998 - Jan. 2000) in four 1m^2 litter traps per plot. The plots were located permanently, about 20cm off the ground and 8m from the center along orthogonal axes. Fine litter (leaves, reproductive material, bark and wood <2cm diam.) was separated

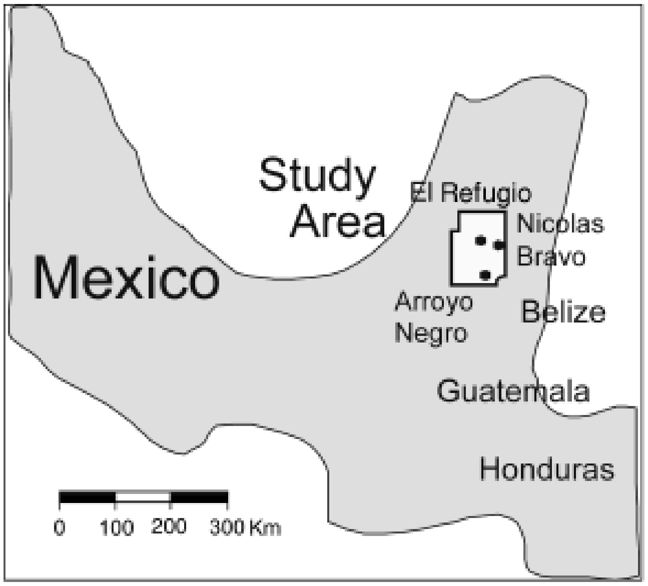

Figure 2. Map of study sites in the Southern Yucatan Peninsula Region (SYPR), Mexico.

TABLE I
LOCATION AND ELEVATION OF THE THREE STUDY SITES, PLUS OWNERSHIP, LAND-USE HISTORY, AND AGE IN 1998 OF STANDS INCLUDED IN ECOSYSTEM STUDIES

Location	Land-owner	Years in Maize Production	Number of Swidden Cycles	Forest Age (years)
El Refugio (ER)	Hermelindo	5	1	2
18° 49' N	Hermelindo	2	1	5
89° 23' W	Hermelindo	2	1	12
Mean Elevation	Juan	5	2	4
250m	Juan	4	1	8
	Juan	1	1	12
	Juventino	3	2	3
	Juventino	2	1	10
	Juventino	2	1	12
	Rufino	2	1	8
	Roberto	0	0	mature
	Víctor	0	0	mature
	Reserva ER	0	0	mature
Nicolás Bravo (NB)	Agustin	4?	3	3
18° 27' N	Agustin	4?	2	6
88° 56' W	Agustin	1	1	25
Mean Elevation	Benito	4	2	8
120m	Benito	2	1	18
	Enrique	2+	2	5
	Enrique	1	1	25
	Pedro	4	2	5
	Pedro	4	2	16
	Pedro	1	1	24
	ReservaNB1	0	0	mature
	ReservaNB2	0	0	mature
	ReservaNB4	0	0	mature
Arroyo Negro (AN)	Antonio	7	4	4
17° 53' N	Antonio	3+	2	8
89° 17' W	Antonio	2	2	18
Mean Elevation	Fermín	4	2	5
180m	Fermín	3+	3	9
	Fermín	2+	2	15
	Gilberto	1	1	5
	Gilberto	1	2	7
	Antonio2	0	0	mature
	José	0	0	mature

from coarse litter (bark and wood >2cm in diam.), dried at <70°C and weighed. The nutrient content (C, N, and P) of the fine litter was used to gauge the effects of land use change and forest recovery on nutrient cycling (c.f. Odum, 1969, Vitousek, 1984, Proctor *et al.*, 1983). The dry mass of fine litter was used as an index of productivity. Although biomass accumulation in stems and branches represent a substantial portion of productivity in secondary forests, our analysis suggests that the rate is constant throughout the first 25 years of growth at approximately 3-4 Mg/ha/yr (Read and Lawrence, in press). Furthermore, the rate of litter production was found to be 50-100% higher than total biomass production across the study area.

Aboveground biomass

In each plot, aboveground biomass was sampled, including live vegetation and detritus. To estimate the biomass of detritus on the forest floor, all fine litter was sampled in four 1m^2 areas, each 1-2m from an existing litter trap, during Nov. and Dec. 1998. This data yields a low estimate of forest floor biomass as peak litterfall had occurred in all regions and all forest ages eight to nine months prior. All stems >10cm in diameter at breast height (dbh) were recorded for the entire 500m^2 plot. A nested design was used to sample smaller stems, with stems 5-10cm dbh measured in a central 100m^2 plot, and stems 1-5cm dbh measured in three 10m^2 plots (see Figure 3; Read and Lawrence, in press). At 13 systematically arrayed points within the large plot, measurements of height and diameter were taken on the nearest individual in each dbh class. These data (1395 trees from all plots) were used to create regressions to estimate heights for all trees sampled. Then, standing live biomass was estimated from dbh, height and wood density, using established regressions based on studies of dry tropical forest of similar structure (cf. Martínez-Yrizar *et al.*, 1992; see Read and Lawrence, in press for further details).

Soil properties

In each stand, composite samples (32 cores per plot) were collected of the top 15cm of mineral soil (Figure 3). Sieved, air-dried samples (one composite per stand) were analyzed for physical and chemical properties by

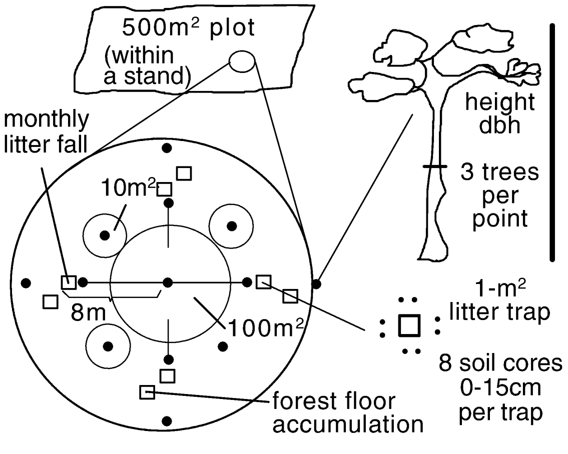

Figure 3. Methods for sampling soil, litter and vegetation. All trees >10cm dbh were measured for dbh in one circular 500m^2 plot within the stand. Stems 5-10cm dbh were measured in a central 100m^2 plot and stems 1-5cm dbh were measured in three 10m^2 plots. Tree heights were measured at 13 points systematically arrayed throughout the plot. Permanent litter traps (1m^2) were established 8m from the plot center along orthogonal axes. Forest floor mass was measured in 1m^2 plots adjacent to litter traps. Eight soil cores were taken around each litter trap to a depth of 15cm.

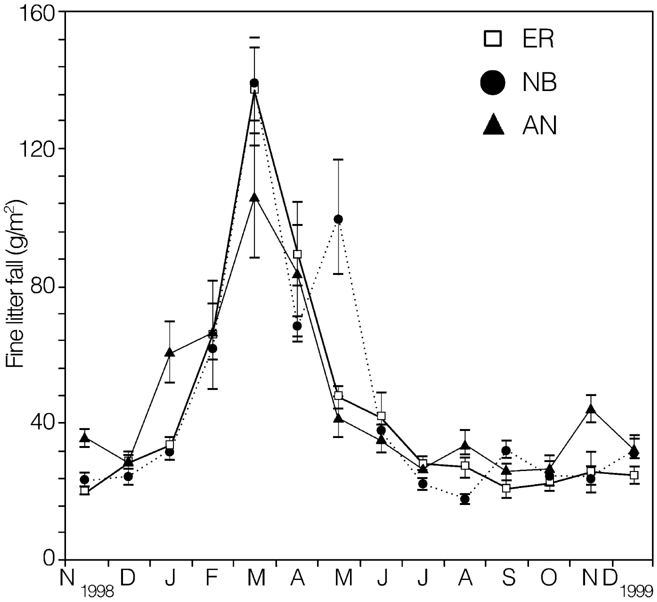

Figure 4. Seasonal pattern of fine litter production (leaves, twigs, and wood <2cm in diameter). Mean ±SE across all plots within a given region. Variation indicative of the range in productivity as a function of forest age. Region is indicated by symbol as shown in legend.

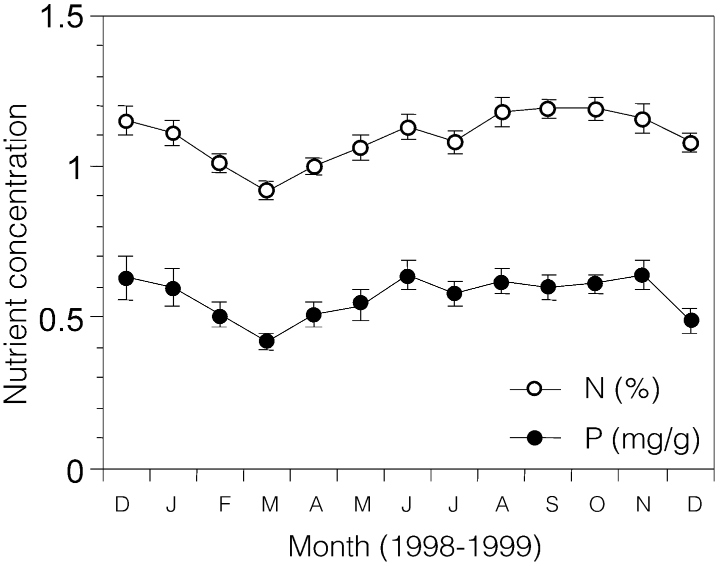

Figure 5. Seasonal pattern in litter nitrogen and phosphorus concentrations. Mean ±SE for all 36 plots.

Brookside Laboratories (New Knoxville, OH). To assess regional soil differences while avoiding the confounding influences of shifting cultivation, mature forest soils were compared. To determine changes in soil properties as a function of forest age, stands were divided into three secondary forest age classes (2-5 y.o., 6-10 y.o., and 12-25 y.o.) plus mature forests, and analyzed without regard to region. Secondary forest age classes were based on apparent physical similarities and the degree of certainty with which actual age could be determined. As stated previously, mature forest stands had not been cleared for agriculture in the past 100 years.

Results and Discussion

Effects of seasonal variation in rainfall

As in the dry forests of Western Mexico and portions of the Northern Yucatan, and in the wetter forests of Guatemala further south, litter production in the southern Yucatan peninsula was strongly tied to the timing of precipitation (Kunkel Westphal and Kunkel, 1979, Martínez-Yrizar and Sarukhan, 1990, Whigham *et al*., 1990). Both the production and nutrient concentration of litter responded to seasonal drought from Dec. to May. Fine litter production was relatively constant throughout most of the year, at 25-30 g/m^2/mo. Several months into the dry season, however, litterfall increased five-fold, apparently due to water stress (Reich and Borchert, 1984, Holbrook *et al*., 1995; Figure 4). Thirty percent of total annual litter production fell during the peak, between Mar. and Apr., and roughly 60% fell from Jan. to May.

Litter nutrient concentrations reached their minima during peak litterfall (Figure 5; Read and Lawrence, submitted). This evidence suggests that the trees reabsorbed essential nutrients prior to massive leaf loss (Chapin, 1980, Killingbeck, 1996). Litter P concentrations were

TABLE II
CHARACTERISTICS OF MATURE FOREST SOILS (MEAN ± SE) ALONG A PRECIPITATION GRADIENT IN THE SOUTHERN YUCATAN

	El Refugio (n=3)	Nicolás Bravo (n=3)	Arroyo Negro (n=2)	P-value
Physical properties				
Clay (%)	23 ± 4	19 ± 6	14 ± 1	0.51
Silt (%)	25 ± 4	33 ± 4	27 ± 3	0.39
Sand (%)	51 ± 2^{a}	47 ± 2^{a}	59 ± 2^{b}	0.022
Organic matter (%)	11.4 ± 1.1^{a}	14.5 ± 0.6^{ab}	21.8 ± 5.6^{b}	0.077
pH	7.7 ± 0.0^{a}	7.4 ± 0.1^{b}	7.7 ± 0.1^{ab}	0.068
TEC[1] (meq/g)	134 ± 18^{a}	54 ± 10^{b}	139 ± 4^{a}	0.012
Chemical properties (ppm)				
Sulfur	58 ± 4^{a}	42 ± 3^{b}	70 ± 7^{a}	0.014
Calcium	25,700 ± 3,600^{a}	9,800 ± 2,000^{b}	26,900 ± 800^{a}	0.011
Magnesium	495 ± 21	469 ± 43	489 ± 54	0.87
Potassium	384 ± 67^{ab}	441 ± 45^{a}	197 ± 14^{b}	0.071
Sodium	25 ± 3	23 ± 2	29 ± 7	0.64
Manganese	30 ± 5^{a}	83 ± 29^{b}	18 ± 3^{a}	0.023
Boron	2.0 ± 0.2	2.0 ± -.3	2.6 ± 0.4	0.32
Iron	6.7 ± 1.3^{a}	23 ± 6.5^{b}	3.5 ± 0.5^{a}	0.053
Copper	1.7 ± 0.1^{a}	2.4 ± 0.1^{b}	1.5 ± 0.1^{a}	0.003
Zinc	1.2 ± 0.0	1.5 ± 0.4	1.6 ± 0.2	0.63
Aluminum	30 ± 7^{a}	164 ± 55^{b}	17 ± 2^{a}	0.066

One value analyzed per stand based on a composite of 32 soil cores 0-15cm deep, and 2-3 stands analyzed per site. Listed left to right from driest (ca. 900mm annual ppt) to wettest (ca. 1400mm annual ppt). P value indicates significance of separate ANOVAs by region. Significant differences among regions indicated by different letters.

[1] TEC= total exchangeable cations.

reduced 47% from the maximum observed in a given site. In contrast, litter N concentrations were reduced by only 33% (Read and Lawrence, submitted). Lower nutrient concentrations in the dry season have been reported elsewhere as well, in both wetter and drier forests (Swift *et al*., 1981, Wieder and Wright, 1995, McGrath *et al*., 2001). Despite a reduction in nutrient concentration, the increase in litterfall during the dry season is likely to result in a pulse of nutrients with the onset of the rains in June (Swift *et al*., 1981, Singh *et al*., 1989, Campo *et al*., 1998, McGrath *et al*., 2001). The entire SYPR is likely to exhibit a similar pattern of highly seasonal soil nutrient dynamics.

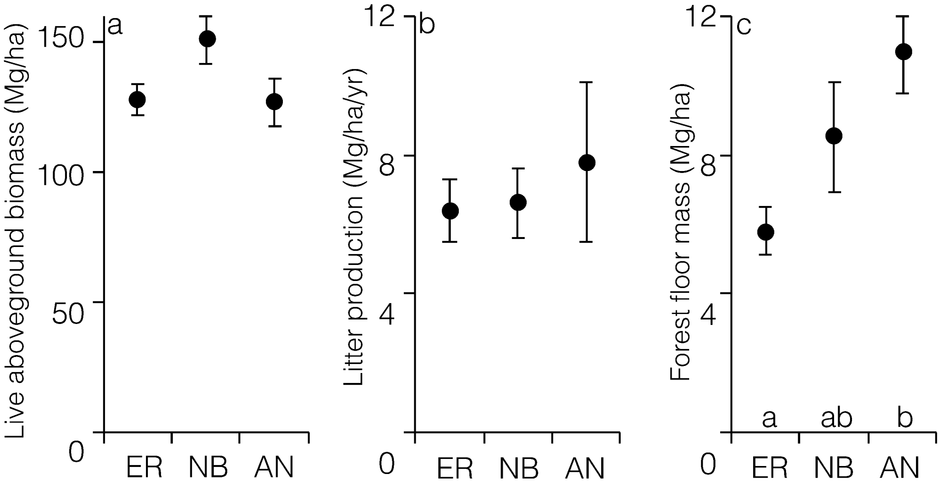

Figure 6. Aboveground live biomass (>1cm dbh) (a), annual fine litter production (b) and forest floor biomass (c) in mature forests, by study region. ER = El Refugio (n=3), NB = Nicolás Bravo (n=3), AN = Arroyo Negro (n=2). Mean ±SE for all plots within a region. Statistically significant differences between regions indicated by different letters.

Soil gradients: driver of inter-regional variability and consequence of land use history

Although the study area is relatively homogeneous in topography and parent material, the physical and chemical properties of mature forest soils did vary (Table II). Some of this variation results from interactions between vegetation and soils through geologic time. It may also be caused by differences in the intensity of historic land use during the past century. It could also result from ancient Mayan activity. An important part of the variation, especially in soil organic matter, is most likely a result of the regional precipitation gradient. In particular, the southern site tended to have a higher organic matter content, as expected if litter inputs were higher due to greater precipitation (c.f. Vitousek, 1984). Other aspects of soil variation, such as the higher percentage of sand-sized particles at AN may relate to the topographic position of the sampled stands. Over time, smaller particles tend to move downslope, leaving a coarser soil texture at the top of a catena (Brady, 1990). Mature sites in AN were somewhat higher and closer to the ridge top. Sites in ER and NB were lower on the slope.

Soil pH was generally quite high across the region (7.4-7.7) as a result of parent material rich in calcium carbonate. However, the Ca content of soils in NB was significantly lower than that of the other two sites. Consequently, soils in NB also had lower pH and lower concentrations of total exchangeable cations. Overall fertility may be lower in NB given lower levels of soluble sulfur and higher concentrations of detrimental and potentially toxic metals (Al, Cu, Fe, and Mn; Table II). This lower fertility could reflect the longer history of agriculture there. ER and AN were established 20-30 years ago, but NB has been settled since the 1950s. NB has large areas of Bracken fern, an invasive species whose dominance may be facilitated by nutrient-poor soils (Suazo, 1998) and/or by repeated fire such as that associated with shifting cultivation.

Unlike the other indices of fertility noted above, K levels were significantly higher in NB. This result is consistent with more rapid turnover of organic matter or greater amounts of material cycling through the forest floor litter layer. In either case, K could accumulate in the mineral soil due to greater leaching from litter on the forest floor. This is not incongruent with limitations on productivity due to soil fertility. Rapid nutrient cycling through the litter can be an important mechanism for conserving and efficiently using essential nutrients that have been depleted in the mineral soil (Chapin, 1980, Jordan and Herrera, 1981).

The simplest explanation for enrichment in metals and loss of Ca may be topography. NB is at a slightly lower elevation, on a flatter part of the study area, and thus it is relatively older geologically than the more hilly areas we sampled to the northwest and the southwest (Grant Goodell, personal communication). The timeframe for weathering is at least modestly longer in NB. The relative abundance of metals can increase during the weathering process through differential loss rates of the elemental constituents of minerals (Brady, 1990). Over time, more Ca could have been lost from the system through weathering followed by leaching. It is unclear whether the difference in geological age is adequate to explain the differences observed. An alternative explanation is that ancient Mayan land use may have disproportionately and negatively affected the soils around NB. Ruins are extremely abundant from NB west to Becan (Turner, 1974). ER is also within the potential realm of influence of major temple sites, and yet its soils were more fertile than those in NB. The intensity of recent historic land use seems to be the best explanation for the difference among sites, but further study is necessary to eliminate the alternative hypotheses.

Effects of regional environmental gradients on biomass and nutrient cycling

Differences in total annual precipitation and soil characteristics may contribute to variation in structure and function among the study sites (Figure 6). To isolate the regional influence on forest processes from the effects of forest age and cultivation history, mature forests were examined separately. Forest floor biomass increased with increasing precipitation (Figure 6c). Higher precipitation should enhance decomposition, leading to lower forest-floor biomass if litter production were to remain constant. Thus, the observed increase in forest floor biomass suggests a concomitant increase in litter production. Mean litter production was greater in the south (Figure 6b), but the result was not statistically significant due to small sample size and high variability in AN. One of the two sites demonstrated surprisingly low biomass and production. Martínez-Yrizar and Sarukhan (1990) found higher litter production in the moister of their two study sites in Chamela, Mexico. Their results support our contention that differences in annual precipitation may have led to differences in litter production between the driest and the wettest sites.

Despite significant differences in rainfall and certain soil properties, live aboveground biomass did not vary significantly among the regions (Figure 6a). The highest values came from NB, where soils were apparently less fertile. The lower than expected values in AN may be due to unquantified impacts of recent logging (see Klepeis and Turner, 2001). Mature forests in AN had fewer trees (>10cm dbh) and lower basal area than mature forests in the drier sites, suggesting that some trees may have been extracted in recent history (Read and Lawrence, in press). On the other hand, high biomass in NB may be the result of an over-abundance of lianas, perhaps another legacy of historic disturbance, human or natural (Boose *et al*, 1994, Gerwing and Lopes Farias, 2000). The mean contribution of lianas to total biomass was 10.2% in NB *vs*. 5.6% in ER and 4.8% in AN (Read and Lawrence, in press).

Phosphorus, but not nitrogen, dynamics followed trends in annual precipitation. Total annual inputs of P were greater in the wettest region, AN (Figure 7a), as a result of both greater productivity (Figure 6b) and higher P concentrations in the litter (Read and Lawrence, submitted). The exception to this trend was in NB, where intermediate P inputs would be expected. Instead, the low relative soil fertility discussed above seems to have mitigated the effect of added precipitation on P cycling. Nitrogen inputs increased slightly with increasing precipitation, but the trend was not significant (Figure 7b). This modest trend reflects only differences in total productivity, as litter nitrogen concentrations did not vary significantly among regions (Read and Lawrence, submitted). The response of forest P cycling to regional precipitation gradients and the lack of response in the N cycle suggest that forests in the SYPR are more limited by P than by N. When water stress was alleviated, additional P, but not additional N, was introduced into the system. Thus, the manifestation of nutrient limitation depends upon water availability. This may explain why Campo *et al*. (2001) reported that P did not appear to be limiting in the very dry forests of Chamela, although small amounts of P were retained in the system. The indication of P limitation in this study came out of a regional analysis, where more P, but not more N, was observed to cycle in the wettest region. N cycling appears less sensitive to increased precipitation than P cycling.

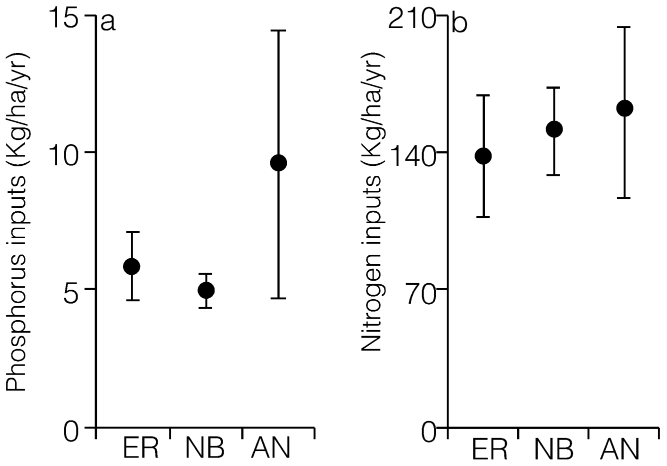

Figure 7. Total annual phosphorus (a) and nitrogen (b) inputs deposited via fine litter in mature forests of each region. Calculated from monthly dry mass and monthly litter nutrient concentrations (Read and Lawrence, submitted). Mean ±SE for all plots within a region.

Effects of forest age on biomass and nutrient cycling

As defined by the range of variation induced, forest age had a greater impact on ecosystem properties and function than did regional environmental gradients. Across all regions, live aboveground biomass increased significantly as a function of forest age (Figure 8a). There was a pronounced difference between mature forests and the oldest secondary forests sampled (12-25 y.o.). Although total woody basal area of stems >1cm dbh had recovered to 63% of mature forest levels by 25 years, live biomass reached only 40% of mature forest levels (58 *vs*. 136 Mg/ha; Read and Lawrence, in press). Earlier analysis, based on tree basal area only, suggested that basal area (>10cm dbh) increased to 80% of mature forest levels within 25 years (Turner *et al*., 2001). Subsequent analysis of biomass based on all stems (including lianas and small trees <5cm dbh) suggests a slower rate of recovery (Read and Lawrence, in press). Our prior analysis depended on the assumption of a linear increase in biomass beyond 25 years. If biomass growth is not linear, and the biomass increment declines, for example, by 50% after forests achieve a closed canopy, then recovery would be slowed further. If we assume that total canopy closure occurs 25 years following abandonment, instead of reaching mature forest levels in another 15-35 years, it may take 30-70 years. Thus, our most conservative estimate is 55-95 years for recovery to current mature forest levels.

As noted previously, the mature forests of study were logged for mahogany and Spanish cedar, removing the largest stems. Domination by these or other large trees might take an additional 10-25 years, assuming an ultimate density of 6 trees/ha with diameters of 100cm (see Rodríguez Caballero, 1944; Snook, 1998). Thus, we estimate that forests similar in total aboveground biomass to those observed in the 19th century (before logging) might be reached 65-120 years after agricultural abandonment. This estimate is more in line with estimates of recovery time in the wet tropical forests of Los Tuxtlas, Mexico, which

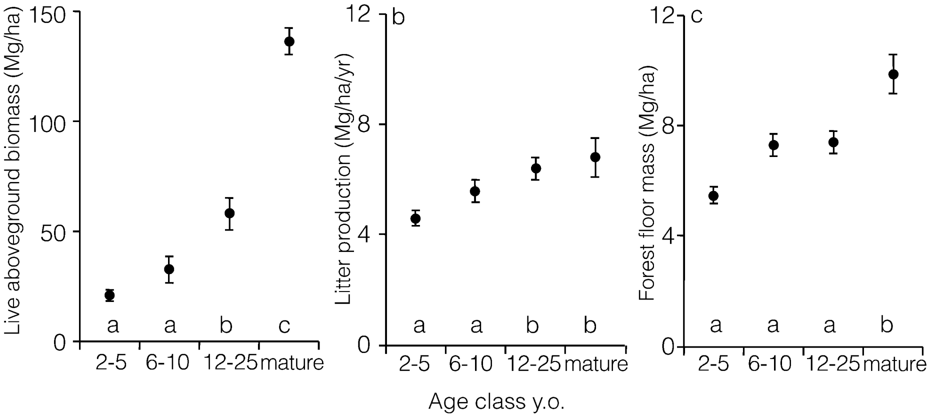

Figure 8. Aboveground live biomass (>1cm dbh) (a), annual fine litter production (b), and forest floor biomass (c), as a function of forest age across all sites. Mean ±SE for all plots within an age class. Statistically significant differences between age classes indicated by different letters.

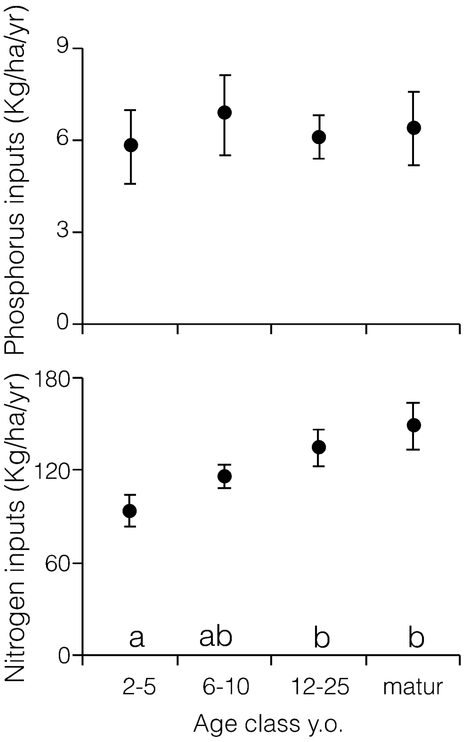

Figure 9. Total annual phosphorus (a) and nitrogen (b) inputs deposited in fine litter as a function of forest age. Calculated from monthly dry mass and monthly litter nutrient concentrations (Read and Lawrence, submitted). Mean ±SE for all plots within an age class. Statistically significant differences between age classes indicated by different letters.

may take 70 years or more to reach biomass equivalent to mature forests (Hughes *et al.*, 1999).

Both litter production and forest floor biomass increased consistently with age (Figures 8b,c). The difference between old secondary and mature forests was not as dramatic as it was for live biomass. With only 15% of the aboveground biomass, the youngest forests produced almost 70% as much fine litter as mature forests. Similar results were reported by Ewel (1976) in Guatemala. The pattern of high productivity in young forests matches that observed in successional forests of the temperate zone as well (Odum, 1969). The increase in forest floor biomass was more rapid than that expected due to the increase in litter production, suggesting that decomposition slows with forest age. Experimental studies confirmed that decomposition is slower in older forests. Lower decomposition rates seemed to occur in response to lower litter quality rather than to changes in microclimate (Xuluc-Tolosa *et al.*, in press). In fact, as an indicator of litter quality, litter P concentration declined as a function of forest age but no significant change in litter N concentration occurred (data not shown; Read and Lawrence, submitted).

Whereas P, but not N, responded to increased precipitation, mean P inputs across all regions did not increase as a function of forest age, whereas N inputs did so (Figure 9). Thus, P cycling changes markedly during the process of forest recovery, with P use efficiency increasing as a function of age as suggested by Brown and Lugo (1990). Older forests produced significantly greater amounts of litter (Figure 8b), while cycling the same amount of P as younger forests (Figure 9a), resulting in a decline in litter P concentration with age (Read and Lawrence, submitted). In contrast, the pool of N cycled through litter increased in step with increasing litter production in older forests. Litter N concentration did not increase significantly, although there was a tendency for slightly higher concentrations in older forests. Taken together, these data suggest that N-use efficiency declined, if it changed at all, as a function of forest age.

Understanding changes in nutrient cycling during forest recovery depends on the nutrient examined. Furthermore, evaluating nutrient constraints on ecosystem processes depends on understanding interactions between water -and nutrient- limitation. When water is broadly limiting (as in the above analysis of nutrient dynamics as a function of forest age, regardless of regional precipitation gradients), productivity seems to be limited by N availability. More N cycling through the system was correlated with higher litter production. All forests cycled similar amounts of P regardless of age. This level may represent the maximum P accessible given the soil-climate regime. P could still be limiting productivity, but we cannot determine the limitation by simply comparing P return with litter production, as a function of forest age. Time alone (as a forest ages) will not allow more P to enter the system, unless fixed biogeochemical constraints are lifted. Although the potential exists for N uptake through biological fixation, there are no additional pools to tap to alleviate P limitation. Increasing production depends, then, on increasing nitrogen availability as the forest and its soils recover from cultivation. When water limitation is alleviated and soil biological activity is enhanced (as it appears to be in AN), certain biogeochemical constraints on P cycling do seem to be lifted. Only then,

TABLE III
CHANGES IN SOIL PROPERTIES (MEAN ± SE) AS A FUNCTION OF FOREST AGE, ACROSS THE THREE FOCAL STUDY SITES IN THE SOUTHERN YUCATAN

	2-5 y.o. (n=10)	6-10 y.o. (n=8)	12-25 y.o. (n=10)	Mature (n=8)	P-value
Physical properties					
Clay (%)	28 ± 4	34 ± 5	28 ± 2	20 ± 3	0.074
Silt (%)	34 ± 1	30 ± 5	38 ± 3	29 ± 2	0.22
Sand (%)	38 ± 4^{a}	36 ± 5^{a}	34 ± 3^{a}	52 ± 2^{b}	0.011
Organic matter (%)	11.0± 0.3^{a}	10.1± 0.7^{a}	12.3± 0.7^{ab}	15.2± 1.9^{b}	0.009
pH	7.7± 0.1^{a}	7.5± 0.1^{ab}	7.4± 0.1^{b}	7.6± 0.1^{ab}	0.070
TEC[1] (meq/g)	94 ±15	98 ±14	68 ±11	105 ±16	0.27
Chemical properties (ppm)					
Sulfur	54 ± 5	55 ± 6	43 ± 5	55 ± 5	0.25
Calcium	17,600 ±3,000	18,400 ±2,800	12,400 ±2,300	20,000 ±3,300	0.26
Magnesium	523 ± 24	579 ± 47	539 ± 31	483 ± 19	0.26
Potassium	616 ± 70^{a}	483 ± 43^{ab}	508 ± 35^{a}	359 ± 45^{b}	0.013
Sodium	26 ± 1	31 ± 2	28 ± 2	25 ± 2	0.14
Manganese	83 ± 19	93 ± 34	108 ± 15	47 ± 12	0.28
Boron	1.9± 0.1	1.7± 0.2	1.8± 0.1	2.1± 0.2	0.20
Iron	17 ± 3	22 ± 6	26 ± 4	12 ± 4	0.19
Copper	2.1± 0.1	2.3± 0.3	2.3± 0.1	1.9± 0.1	0.39
Zinc	1.5± 0.1	1.4± 0.2	1.5± 0.2	1.4± 0.1	0.97
Aluminum	176 ± 54	203 ± 68	258 ± 68	77 ± 31	0.16

One value analyzed per stand based on a composite of 32 soil cores 0-15cm deep, and 8-10 stands analyzed per age class. P value indicates significance of separate ANOVAs by age. Significant differences among age classes indicated by different letters.

[1] TEC = total exchangeable cations.

can additional P enter the system (see Figures 6 and 7). This P apparently yielded gains in litter production in AN, suggesting that P becomes limiting to productivity when water is no longer the primary limiting factor.

Changes in soil properties with forest age suggest that N availability may increase during forest regeneration. Although data on the N and P content of soils are lacking, soil organic matter did increase significantly with age (Table III). In the top 15cm of soil, organic matter increased from 10-11% in young secondary forests to 15% in mature forests. An increase in N availability associated with an increase in organic matter would allow litter concentrations to remain stable while productivity increases. This increase in soil organic matter probably represents a slowing of mineralization rates in the soil along with a demonstrated increase in litter inputs. Likewise, we attributed the increase in forest floor mass with age to added inputs and slowed decomposition. Data on K concentrations support this interpretation: K concentration was lowest in mature forest soils, where turnover rates of organic matter are expected to be slowest due to a decline in litter quality.

Surprisingly, both decomposition experiments (Xuluc-Tolosa *et al.*, in press) and field observations suggest that P may limit changes in decomposition and mineralization with forest age, although N appears to limit plant productivity when water is broadly limiting. P may also limit N fixation. This effect has been suggested in other studies (e.g. Crews *et al.*, 2000, Uliassi *et al.*, 2000). With the potential to constrain decomposition, mineralization, and N fixation, P may play a critical role in limiting N availability to recovering vegetation (Ewel, 1986). It is important to emphasize the difficulty in identifying either P or N as the limiting nutrient in this system, especially if P mediates N limitation. Both nutrients appear to limit key ecosystem processes.

Implications

The study of nutrient dynamics in the region provided important clues about the regenerative capacity of the forests. Any assessment of land use and land cover change must take into account several critical points. Regional precipitation gradients strongly influenced nutrient cycling through soil organic matter and litter, but had a more limited effect on plant productivity and biomass. Increased precipitation allowed additional phosphorus to enter the system. Although forest age profoundly influenced many aspects of nutrient cycling, its greatest effect was to alter litter production and aboveground biomass. P use efficiency tended to increase and N use efficiency tended to decrease slightly with age. Water limitation seems to be the predominant environmental factor limiting ecosystem processes in these dry forests, and phosphorus may be the most significant limiting nutrient.

Sampling along natural and human-made gradients has allowed the evaluation of broad environmental and stand-level drivers of ecosystem processes. Environmental factors do constrain litter production, forest floor mass, and soil organic matter in mature forest. However, to understand differences in the biomass of mature forests, further information about the human history of the area is critical, including logging history and decisions about what areas have purposefully been left untouched (perhaps the upper slopes). Structure and function in secondary forests (biomass, litter production, forest floor mass and critical soil properties) are strongly influenced by the age of the stand. The presence of humans on the landscape results in changes that are greater than those induced by natural, environmental variation at the regional scale. For the best understanding of these landscapes, and for scaling up from case studies to regional and global assessments, integrating human impacts on ecosystem processes is vital.

Efforts to use remotely sensed data to scale up from point samples to regional values will depend critically on the ability to distinguish young and old secondary forest. Models that predict landscape-scale carbon stocks, for example, will be extremely sensitive to the mapping of field-derived age categories onto image-derived land cover classes (e.g. Cairns *et al*, 2000). On the other hand, distinguishing older secondary forest and mature forests will be less critical for determining regional productivity, given the similarity in litter production. The amount of classification error that can be safely tolerated thus depends on the goal of the model: carbon stocks or carbon fluxes. Our studies of nutrient cycling suggest that similar considerations must be made when trying to model other biogeochemical cycles at the regional scale.

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REFERENCES

Brady NC (1990) *The Nature and Properties of Soils*. Tenth Edition. MacMillan. New York. 621 pp.

Boose ER, Foster DR, Fluet M (1994) Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs 64*: 369-400.

Brown S, Lugo AE (1990) Tropical secondary forests. *J. Tropical Ecol. 6*: 1-32.

Buschbacher R, Uhl C, Serrão EAS (1988) Abandoned pastures in eastern Amazonia. II: Nutrient stocks in the soil and vegetation. *J. Ecol. 76*: 682-699.

Cairns MA, Haggerty PK, Álvarez R, DeJong BHJ, Olmsted I (2000) Tropical Mexico's recent land-use change: A region's contribution to the global carbon cycle. *Ecological Applications 10*: 1426-1441.

Campo J, Jaramillo VJ, Maass JM (1998) Pulses of soil phosphorus availability in a Mexican tropical dry forest: effects of seasonality and level of wetting. *Oecologia 115*: 167-172.

Campo J, Maass JM, Jaramillo VJ, Martínez-Yrizar A, Sarukhan J (2001) Phosphorus cycling in a Mexican tropical dry forest ecosystem. *Biogeochemistry 53*: 161-179.

Chapin FS (1980) The mineral nutrition of wild plants. *Annual Rev. Ecol. Systematics 11*: 233-260.

Crews TE, Farrington H, Vitousek PM (2000) Changes in asymbiotic, heterotrophic nitrogen fixation on leaf litter of Metrosideros polymorpha with long-term ecosystem development in Hawaii. *Ecosystems 3*: 386-395.

Ewel JJ (1976) Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *J. Ecol. 64*: 293-307.

Ewel JJ (1986) Designing agricultural systems for the humid tropics. *Annual Rev. Ecol. Systematics 17*: 245-271.

Fernandes DN, Sanford RL (1995) Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biol. 9*: 915-922.

Geoghegan J, Cortina Villar S, Klepeis P, Macario Mendoza P, Ogneva-Himmelberger Y, Roy Chowdhury R, Turner BL II, Vance C (2001) Modeling Tropical Deforestation in the Southern Yucatan Peninsular Region: Comparing Survey and Satellite Data. *Agriculture, Ecosystems, and Environment 84*: 25-46.

Gerwing JH, Lopes Farias D (2000) Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *J. Tropical Ecol. 16*: 237-335.

Holbrook NM, Whitbeck JL, Mooney HA (1995) Drought responses of neotropical dry forest trees. In Bullock SH, Mooney HA, and Medina E (Eds.) *Seasonally Dry Tropical Forests*. Cambridge University Press. Cambridge. pp. 243-276.

Hughes RF, Kauffman JB, Jaramillo VJ (1999) Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology 80*: 1892-1907.

Jordan CF, Herrera R (1981) Tropical rain forests: are nutrients really critical? *The American Naturalist 117*: 167-180.

Killingbeck KT (1996) Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology 77*: 1716-1729.

Klepeis P, Turner II BL (2001) Integrated Land History and Global Change Science: The Example of the Southern Yucatán Peninsular Region project. *Land Use Policy 18*: 27-39.

Kunkel Westphal I, Kunkel P (1979) Litter fall in a Guatemalan primary forest, with details of leaf-shedding by some common tree species. *J. Ecol. 67*: 665-686.

Martínez-Yrizar A, Sarukhan J (1990) Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. *J. Tropical Ecol. 6*: 433-444.

Martínez-Yrizar A, Sarukhan J, Pérez-Jiménez E, Rincón E, Maass JM, Solís-Magallanes A, Cervantes L (1992) Above-ground phytomass of a tropical deciduous forest on the coast of Jalisco, Mexico. *J. Tropical Ecol. 8*: 87-96.

McGrath DA, Comerford NB, Duryea ML (2001) Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. *Forest Ecol. Management 131*: 167-181.

Murphy PG, Lugo AE (1986) Ecology of tropical dry forest. *Annual Rev. Ecol. Systematics 17*: 67-88.

Odum EP (1969) The strategy of ecosystem development. *Science 164*: 262-270.

Proctor J, Anderson JM, Fogden SCL, Vallack HW (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. *J. Ecol. 71*: 261-283.

Read L, Lawrence D (in press) Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications.*

Read L, Lawrence D (Submitted) Litter nutrient dynamics in secondary dry tropical forests.

Reich PB, Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol. 72*: 61-74.

Rodríguez Caballero R (1944) *La Explotación de los Montes de Caoba en el Territorio de Quintana Roo*. Ingeniero Agrónomo. México, D.F. Chapingo. 120 pp.

Singh JS, Raghubanshi AS, Singh RS, Srivastava SC (1989) Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature 338*: 499-500.

Snook LK (1998) Sustaining harvests of mahogany (Swietenia macrophylla King) from Mexico's Yucatan forests: Past, present, and future. In Primack RB, Bray D, Galletti HA, Paciano I (Eds.) *Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico*. Island Press. Washington, D.C. pp. 61-80.

Suazo I (1998) *Aspectos ecológicos de la especie invasora Pteridium aquilinum (L.) Kuhn en una selva húmeda de la región de Chajul, Chiapas, México*. Universidad Michoacana de San Nicolás de Hidalgo. México. 114 pp.

Swift MJ, Russell-Smith A, Perfect TJ (1981) Decomposition and mineral nutrient dynamics of plant litter in a regenerating bush-fallow in the sub-humid tropics. *J. Ecol. 69*: 981-995.

Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation 94*: 133-142.

Turner BL II (1974) Prehistoric intensive agriculture in the Mayan lowlands. *Science 185*: 118-124.

Turner BL II, Cortina Villar S, Foster D, Geoghegan J, Keys E, Klepeis P, Lawrence D, Macario Mendoza P, Manson S, Ogneva-Himmelberger Y, Pérez Salicrup D, Roy Chowdhury R, Savitsky B, Schneider L, Schmook B, Vance C (2001) Deforestation and Agricultural Change in the Southern Yucatán Peninsular Region: Integrative Land Change for Global Change Studies. *Forest Ecol. Management 154*: 353-370.

Uliassi DD, Huss-Danell K, Ruess RW, Doran K (2000) Biomass allocation and nitrogenase activity in Alnus tenuifolia: responses to successional soil type and phosphorus availability. *Ecoscience 7*: 73-79.

Vitousek P (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology 65*: 285-298.

Wieder RK, Wright SJ (1995) Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. *Ecology 76*: 1971-1979.

Whigham DF, Zugasty Towle P, Cabrera Cano E, 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 Yucatan of Mexico. *J. Tropical Ecol. 31*: 23-34.

Xuluc-Tolosa FJ, Vester HFM, Ramírez-Marcial N, Castellanos-Albores J, Lawrence D (in press) Leaf litter decomposition of tree species in three successional phases of tropical dry secondary forest in Campeche, Mexico. *Forest Ecol. Management.*