

Regional-Scale Variation in Litter Production and Seasonality in Tropical Dry Forests of Southern Mexico¹

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ABSTRACT

Highly seasonal rainfall creates a pulse of litterfall in the southern Yucatan peninsula region, with cascading effects on the timing of essential nutrient fluxes, microbial dynamics, and vegetation growth. I investigated whether forest age or a regional environmental gradient related to rainfall has a greater effect on patterns of litterfall in this increasingly human-dominated landscape. Litterfall was sampled in 10–13 stands in each of three locations spanning a rainfall gradient of ca 900–1400 mm/yr. Litter was collected monthly from November 1998 through January 2000 in mature forests and in secondary forests aged 2–25 yr. Despite a substantial precipitation gradient, age was the only significant predictor of annual litter mass. Two- to five-yr-old forests produced significantly less litter than 12–25-yr-old secondary forests (4.6 vs. 6.2 Mg/ha/yr), but the difference between older secondary forests and mature forests (9 percent) was not significant. Litter production increased with rainfall, but not significantly so. The pattern of litterfall was similar across locations and age classes, with a peak during late March or early April. However, litterfall seasonality was most pronounced in the old secondary and mature forests. Litterfall was more evenly distributed throughout the year in forests under 10 yr old. Seasonality of litterfall was also less pronounced at the wettest site, with less disparity between peak litterfall and off-peak months. Seasonality was not related to soil texture. Forest age and rainfall are important drivers of litterfall dynamics; however, both litter mass and degree of seasonality depended more strongly on forest age. Thus, the impact of land-use change on litter nutrient cycling is as great, if not greater, than the constraint imposed by the major natural environmental factor affecting tropical dry forests.

RESUMEN

Alta precipitación estacional en la Península de Yucatán causa un importante pulso de hojarasca el cual tiene efectos en el flujo de nutrientes, la dinámica microbiana y en el crecimiento de la vegetación. En este estudio se investiga cual de los dos aspectos tiene un mayor efecto en la producción de hojarasca: la edad del bosque o un gradiente ambiental regional relacionado con la precipitación. La hojarasca fue muestreada en 10 a 13 parcelas en tres localidades diferentes. Estas localidades poseen una precipitación que varía entre 900 y 1400 mm/año. La hojarasca fue recogida mensualmente entre noviembre de 1988 y enero del 2000 en parcelas de bosque maduro y de bosque secundario con edades que oscilan entre los 2 y los 25 años. A pesar de la existencia de un gradiente de precipitación importante, la edad de la parcela fue el único predictor de la masa anual de hojarasca. Bosques con edades entre dos y cinco años produjeron menos hojarascas que los bosques de 12 a 24 años, pero la diferencia entre el bosque secundario tardío y el bosque maduro no fue significativa. El patrón de caída de hojas fue similar en cada localidad y entre edades, con un pico entre el final de marzo o principios de abril. Sin embargo, la caída de hojas fue más pronunciada en el bosque secundario tardío y los bosques maduros. La caída de hojas fue además uniformemente distribuida a lo largo del año en bosques de menos de 10 años. La estacionalidad no se relaciono con la textura del suelo. Finalmente, el impacto del cambio en el uso de la tierra en la producción de hojarasca es quizás más importante que las limitaciones impuestas por la mayor limitación ambiental que afecta a los bosques secos tropicales.

Key words: land-use change; litterfall; Mexico; precipitation gradient; seasonality; secondary forest; tropical dry forest.

LITTER INPUTS ARE A MAJOR SOURCE OF NUTRIENTS IN TROPICAL DRY FORESTS, as in many terrestrial systems (*e.g.*, Vitousek 1984, Jaramillo & Sanford 1995, Campo *et al.* 2001). The amount and pattern of litterfall are thus important determinants of nutrient availability (Lodge 1994). Both local and regional factors, including anthropogenic effects, can influence the spatial and temporal pattern of litterfall and ultimately constrain nutrient cycling in dry tropical forests. In this study, I investigate the relative influence of stand age and regional-scale environmental gradients on the timing and magnitude of litterfall in the southern Yucatan peninsula.

The vegetation of dry tropical forest responds to periods of drought stress by shedding leaves (Holbrook *et al.* 1995). This response is most likely cued by a shift in soil moisture and atmospheric

evaporative demand (Reich & Borchert 1982, 1984; but see Wright & Cornejo 1990). Thus, the timing of litterfall is regulated by three major factors: precipitation inputs, the water-holding capacity of the soil, and plant demand related to biomass (after Borchert 1980). Land-use and land cover change have the potential to create anthropogenic gradients in the latter two factors, whereas the former varies naturally at regional scales.

In forests recovering from shifting cultivation, the predominant agent of land cover change in the Yucatan, aboveground live biomass increases with age, but even 25 yr after cultivation, secondary forest biomass is approximately 60 percent of mature forest biomass (Eaton & Lawrence, pers. comm.). Increasing annual litter mass is likely to reflect biomass and canopy development during succession (Ewel 1976). At the stand level, plant demand for water should be lower in young secondary forests because of lower biomass and leaf area. This could result in lower drought stress and reduced seasonality in litter production. Thus, due to patterns of

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TABLE 1. Site characteristics of stands sampled in the southern Yucatan peninsula, Mexico.

Location	Land owner	Forest age (yr)	Number of cycles ^a	Total crop yr ^b	Clay (percent) ^c	Silt (percent)	Sand (percent)	Soil organic matter (percent)	pH	Soil depth (cm) ^c	Above-ground biomass (Mg/ha)	Annual litter mass (Mg/ha)
ER (ca 890 mm/yr)	Hermelindo	2	1	5	55	27	18	11.09	7.7	83	22.4	3.1
	Juventino	3	2	3	21	37	42	9.71	7.7	>100	10.6	4.1
	Juan	4	2	5	35	27	38	9.67	7.7	>100	16.3	4.4
	Hermelindo	5	1	2	41	39	20	11.21	7.4	65	17.5	4.8
	Rufino	8	1	2	41	27	32	12.1	7.5	65	29.1	5.5
	Juan	8	1	4	41	37	22	8.55	7.5	>100	20.5	4.1
	Juventino	10	1	2	21	49	30	8.22	7.8	>100	39.7	6.6
	Hermelindo	12	1	2	21	37	42	13.81	7.6	>100	54.7	7.6
	Juventino	12	1	2	33	45	22	9.21	7.3	>100	61.0	7.0
	Juan	12	1	1	na ^d	NA	NA	13.45	7.2	>100	45.6	6.9
	Cam. Princ.	Mature	0	0	27	19	54	11.69	7.7	>100	138.5	6.1
	Victor	Mature	0	0	27	25	48	13.21	7.7	>100	120.3	4.9
	Roberto	Mature	0	0	15	33	52	9.35	7.8	>100	123.7	8.1
NB (ca 1144 mm/yr)	Agustin	3	3	4	21	33	46	10.51	7.8	>100	18.2	4.1
	Pedro	5	2	4	21	35	44	12.83	7.6	>100	34.4	4.4
	Enrique	6	2	2	67	15	18	5.56	7.0	>100	64.1	5.2
	Agustin	6	2	4	21	47	32	10.56	7.2	>100	20.7	6.2
	Benito	8	2	4	21	39	40	11.01	7.8	>100	24.9	5.2
	Pedro	16	2	4	31	29	40	10.08	7.4	85	50.0	6.3
	Benito	18	1	2	21	51	28	14.11	7.5	63	50.4	6.8
	Pedro	24	1	1	31	31	38	13.03	7.2	75	97.6	8.8
	Agustin	25	1	1	31	29	40	14.16	7.5	>100	94.2	5.5
	Enrique	25	1	1	31	43	26	14.51	7.3	>100	60.5	5.2
AN (ca 1420 mm/yr)	NB-1	Mature	0	0	13	37	50	13.94	7.2	>100	163.3	5.5
	NB-4	Mature	0	0	13	39	48	15.77	7.4	>100	157.9	8.6
	NB-2	Mature	0	0	31	25	44	13.84	7.6	>100	133.1	5.6
	Antonio	4	4	7	21	37	42	11.74	7.7	>100	12.3	3.5
	Gilberto	5	1	1	21	37	42	11.2	7.8	>100	25.2	6.0
	Fermin	5	2	4	15	33	52	10.62	8.0	>100	31.6	5.8
	Gilberto	7	2	2	31	21	48	11.3	7.8	>100	11.9	4.6
	Antonio	8	2	3	31	33	36	10.89	7.7	>100	62.6	7.3
	Fermin	9	3	3	31	1	68	12.27	7.6	>100	20.4	5.1
Fermin	15	2	2	21	33	46	11.94	7.8	>100	36.2	4.9	
Antonio	18	2	2	31	45	24	8.94	7.6	>100	27.6	4.7	
Antonio	Mature	0	0	15	25	60	27.45	7.7	73	136.3	10.1	
Jose	Mature	0	0	13	30	57	16.17	7.6	85	118.2	5.5	

^aNumber of prior cycles of shifting cultivation (including slash, burn, crop, and fallow).

^bCumulative number of yrs under crops over all cycles.

^cSoil characteristics for the top 15 cm of soil (see Lawrence & Foster 2002).

^dNot applicable; data not available.

^eSoils were sampled only to 100 cm. Sites where weathered material was observed to at least 100 cm are indicated by ">100." An impenetrable layer was reached at a shallower depth for eight sites. The depth of this layer is noted.

forest development, both litter production and degree of seasonality are expected to increase with forest age.

However, water-holding capacity could be depressed in secondary forests if soil organic matter is lost during land-use change (as observed in Brown & Lugo 1990, but not in Hughes *et al.* 1999).

In the wetter southern part of the Yucatan, organic matter (SOM) in soils 0–15 cm deep is twice as high in mature as in secondary forest (Table 1). In the drier north, SOM is only modestly higher, if at all, in mature forests, conveying little added water-holding capacity. Sand content is significantly higher in mature than in secondary

forest (52% vs. 36% sand). Clay content is significantly higher in secondary than in mature forests (28% vs. 20%), but there are no significant differences with age among secondary forests. Because differences in texture run counter to differences in SOM, the predicted net effect on water-holding capacity is unclear. Consequently, age-based differences in litter dynamics would not be attributable to systematic change in water-holding capacity of the soil.

Land-use effects on critical factors controlling litter production are underlain by regional environmental gradients. Annual rainfall increases from north to south, and the length of the dry season declines from 5 or 6 to 3 or 4 mo (Read & Lawrence 2003a). The region has relatively uniform soils on a moderately undulating, karst landscape (*ca* 100–300 m a.s.l.). Soils are mostly >100 cm deep, and occasionally as shallow as 63–85 cm, with no significant or systematic differences from north to south (Table 1). Soils are coarser in the south than in the north (mean of 48% vs. 35–38% sand), but SOM increases significantly from north to south (10.9–13.3%). Clay content is significantly greater in the north (32% vs. 23–24%) if one high value is excluded from the middle of the precipitation gradient. Thus, depending on the countervailing influence of organic matter, the water-holding capacity of the soil may be greater at the low end of the precipitation gradient.

Read and Lawrence (2003a) found that aboveground biomass did not increase significantly from north to south, but confounding effects of regional land-use history and small sample size suggest that further research is warranted. All else being equal, higher precipitation should increase annual litter production and reduce seasonality in the south. Because soil texture and SOM could affect seasonality independent of forest age and precipitation, they are also examined here.

Both anthropogenic and natural environmental gradients can potentially impact the temporal and spatial dynamics of litterfall. Examining fine litter collected in 36 forest stands at three locations spanning a precipitation gradient, I asked the following questions: Does annual litter production increase with forest age and annual precipitation? Do seasonal patterns in litter production vary with forest age, soil texture, SOM, and annual precipitation? In resolving these questions, the relative influence of land-use legacies and natural environmental gradients on litter dynamics in tropical dry forests will be addressed.

METHODS

STUDY SITES.—Among a stratified-random sample of communities studied as part of a broader investigation of land-use change, I chose three areas for study. They are 60–120 km apart in a region of the southern Yucatan extending north from the Guatemalan border (see Turner *et al.* 2001). Thirteen plots were established in El Refugio (ER), the northernmost and the driest site, and in Nicolas Bravo (NB), an area of intermediate rainfall to the south and east. In the wettest part of the region further south, I established ten plots in the village of Arroyo Negro (AN). In all three sites, I sampled two to three mature forest stands (never cleared for agriculture in recent history) and eight to ten secondary forest stands regenerating after

shifting cultivation of maize with no inputs of fertilizer, pesticide, or herbicide. The secondary forest stands ranged in age from 2–25 yr since the last harvest and had experienced one to four cycles of shifting cultivation (Lawrence & Foster 2002; Table 1). The exact age of mature forests was impossible to determine. Care was taken to avoid sampling gaps from current logging. Nevertheless, these mature forests probably experienced some timber extraction in the last 40–100 yr (Klepeis & Turner 2001), which produced variation in basal area (Read & Lawrence 2003a). Stand-level data on soil texture and organic matter in the top 15 cm of soil were taken from Lawrence and Foster (2002). Clay content varied from 13–67 percent, sand content varied from 18–68 percent, and SOM varied from 5–16 percent (with one extremely high value of 27.5%; Table 1).

REGIONAL PRECIPITATION GRADIENT.—Precipitation records were acquired from INEGI (Instituto Nacional de Geografía Estadística e Informática, Mexico) for three villages, which were nearest to the study sites: Zoh Laguna, 20 km south of ER, NB, and Agua Blanca, 70 km east-northeast of AN. Although monthly and annual precipitation differed substantially, the seasonal rainfall pattern was consistent across sites, with a peak occurring in September (Fig. 1). Median annual precipitation varied from *ca* 892 mm/yr in the northernmost location to *ca* 1418 mm/yr in the southernmost. In addition, sites in the northern part of the region tend to experience one to two additional extremely dry months (rainfall <50 mm) in addition to February, March, and April. In Zoh Laguna (a proxy for ER), the severe dry season typically begins in December or January. Both NB and ER are still relatively dry in May. AN (through proxy data from Agua Blanca) is likely to receive more rain early and late in the dry season. The year of study (1999) was very wet, with monthly totals in the middle of the gradient (NB) surpassing the long-term average for the wettest area.

LITTERFALL.—In October and November of 1998, I established a circular 500 m² plot at least 20 m from the forest edge in each stand to correspond with on-going vegetation studies (Perez-Salicrup 2004). Four 1 m² litter traps were established along each of the ordinal axes, 8 m from the center of the plot (0.8 percent of plot area was sampled). The traps were made of 1 mm fiberglass mesh attached to a polyvinyl chloride (PVC) frame and mounted on PVC stakes *ca* 10–15 cm off the ground. In some of the most dense young stands, larger traps were replaced by two 0.5 m² traps as needed. Fine litter (leaves, flowers, fruits, bark, and wood <1.8 cm in diameter) was collected monthly from December 1998 through January 2000. Litter from each trap was collected separately, placed in a drying oven at <70° C until dry, and weighed, yielding four values per plot. I analyzed the mean of these four values (monthly) for this study.

STATISTICAL APPROACH.—To assess the influence of the regional precipitation gradient on litter production, I performed a two-factor analysis of variance (ANOVA) on annual litter mass (January to December 1999) by age class and location (a surrogate for precipitation regime). Secondary forests were categorized into young (2–5 yr

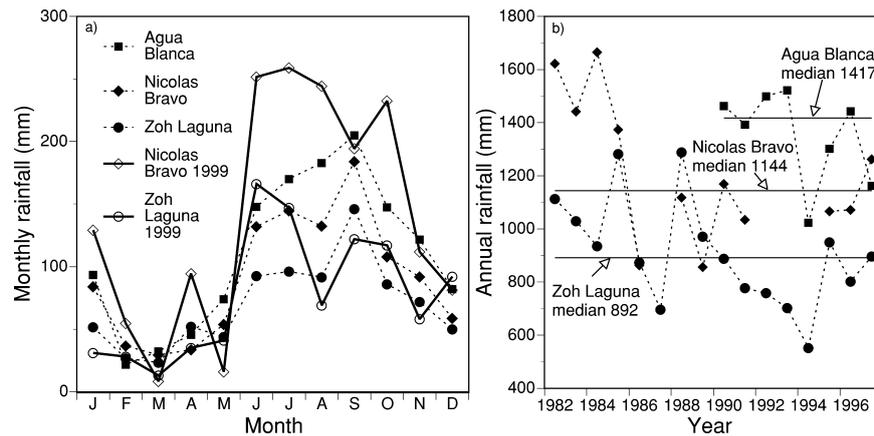


FIGURE 1. Mean monthly precipitation from 1986 to 1998 (dashed lines) and for the year of study (1999, solid lines) at three locations along a northwest-southeast precipitation gradient in the southern Yucatan. No data were available for Agua Blanca, the proxy for AN, in 1999. (a). Annual precipitation is highly variable at the same sites (b).

since the last harvest), middle (6–10 yr since the last harvest), and old secondary forests (12–25 yr since the last harvest). The fourth category was mature forests. The effect of forest age was analyzed by regression, excluding mature forests because their age was unknown. Mature forests were compared to secondary forests using Tukey's *post hoc* tests in the above ANOVA. The relationship between biomass (from Read & Lawrence 2003a) and litter production was also examined by regression. Biomass was considered a proxy for the development of leaf area during the course of succession.

To investigate seasonal pattern without the confounding influence of differences in the amount of litterfall, I normalized monthly litterfall data. The data for a given plot were normalized with respect to the maximum amount of litter in any month (most often March) for that plot. This process yielded a fraction with a maximum value of 1.0. I performed repeated measures analysis of variance (RMANOVA) on normalized monthly litter categorized by age class or location. These analyses were followed by separate ANOVAs on data from each month to determine when significant differences among age classes or locations occurred.

The degree of seasonality in litterfall was examined in two ways. First, the difference between normalized peak and off-peak litterfall was analyzed, with higher relative off-peak measures indicating less seasonality. Second, the coefficient of variation (CV) was determined for the raw data in the 13-mo series, with higher CV indicating more seasonality. The effect of forest age, aboveground live biomass, clay, silt, sand, and SOM content on CV of monthly litterfall was determined by regression.

In ER and AN, the data sets were complete. Due to theft of traps, however, 14 out of 468 litterfall values (3 percent) were lost. The missing values were filled with estimates derived from the relationship between litterfall in the desired month and that of the previous month and the subsequent month in plots of similar age at the same study area.

RESULTS

ANNUAL LITTER PRODUCTION.—Annual litter production increased significantly with forest age, from an estimated 3.8 Mg/ha/yr in 2-yr-old forest to 6.6 Mg/ha/yr in 20-yr-old forest ($P = 0.006$, $R^2 = 0.37$; Fig. 2a). Among secondary forests, age explained only 37 percent of variation in litterfall. Annual litter production did not differ significantly between mature forests (6.8 ± 0.5 Mg/ha/yr) and 12–25-yr-old forests (6.2 ± 0.4 Mg/ha/yr, $P > 0.05$ in Tukey's following 2-factor ANOVA). Litter production increased logarithmically with aboveground biomass (Fig. 3), showing substantial variation at higher biomass.

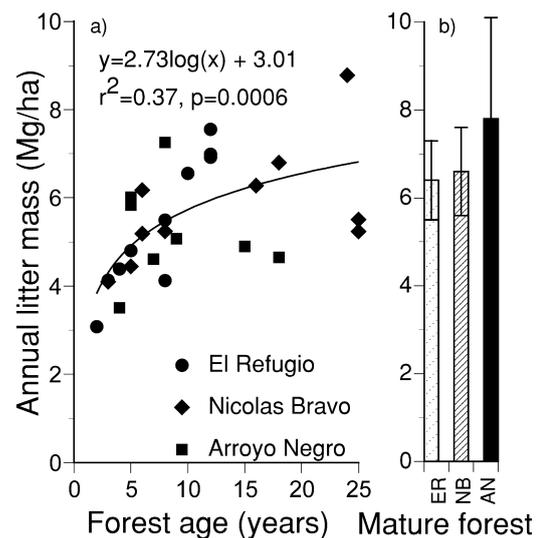


FIGURE 2. Annual litter production as a function of forest age among secondary forests (a) and mature forests at three sites in the southern Yucatan (b).

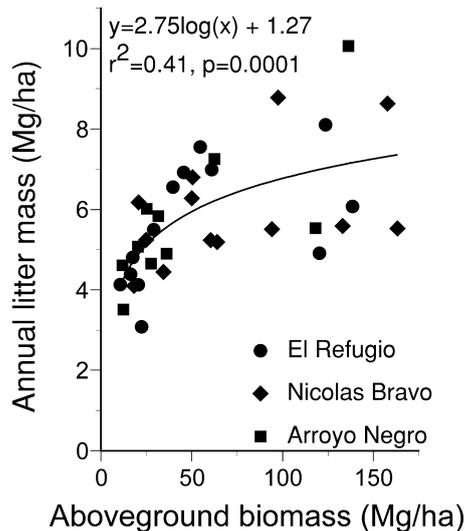


FIGURE 3. Annual litter production as a function of aboveground biomass (>1 cm DBH, from Read & Lawrence 2003a).

Regional differences were not significant ($P = 0.98$ in 2-factor ANOVA), despite a 23 percent increase in mature forest litterfall from north to south (Fig. 2b). Secondary forests were highly variable, more heavily sampled, and less responsive to the precipitation gradient (trend of 9% increase from north to south over all age classes).

PATTERN AND DEGREE OF SEASONALITY IN LITTERFALL: REGIONAL EFFECTS.—Regardless of location or age, all stands showed a similar pattern of litterfall through the year, with a peak occurring during the month of March (Fig. 4). Historically the fourth consecutive month with <100 mm of rain, March is also the driest month of the dry season. Analysis of normalized litterfall data, however, revealed that the temporal patterns were significantly different across the region (RMANOVA by location, $P = 0.032$). Seasonality of litterfall at AN was less pronounced as indicated by higher inputs at nonpeak times (ca 30–40 percent of the peak value vs. ca 20 percent for ER and NB; Fig. 4). The two non-dry season months with elevated litterfall in AN coincided with an 18-day drought in August and an 11-day drought in November (2.4 and 10 mm of rain, respectively, as measured in NB). The mean CV of monthly litterfall was lower at AN (62%) than at ER (79%) and NB (82%). Despite a lower degree of seasonality, the onset of peak litterfall was significantly earlier at AN than at ER or NB (January vs. February, Fig. 4). ER and NB had similar, high coefficients of variation, indicating a high degree of seasonality. However, NB showed a bimodal peak in litterfall, especially at the older sites (Fig. 4). Despite regional and age-based differences in soil texture, litterfall seasonality was not significantly related to clay, silt, sand, or organic matter content.

PATTERN AND DEGREE OF SEASONALITY IN LITTERFALL: AGE EFFECTS.—Litterfall seasonality was most pronounced in the old

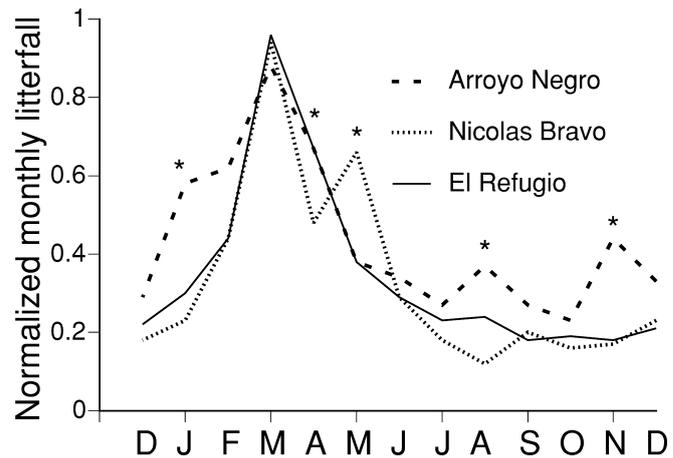


FIGURE 4. Mean normalized monthly pattern of litterfall by region. Litter production was normalized with respect to peak litterfall at each site within each study area such that the month with peak litterfall was set at 1.0 and values for all other months were proportional to this maximum. Patterns of litterfall varied significantly among regions (repeated measures ANOVA, $P < 0.05$). Asterisks indicate significant monthly differences in normalized litter production.

secondary and mature forests (RMANOVA by age class, $P = 0.0009$) and did not differ significantly between them. Although the monthly pattern was similar across age classes, the distribution of litterfall was significantly more even in the two youngest age classes. Off-peak litterfall was often >30 percent of the peak value in forests <10 yr old vs. <20 percent in older secondary and mature forests (Fig. 5). The CV for monthly litterfall increased from 55 percent in 2–5-yr-old forest to 88 percent in mature forest,

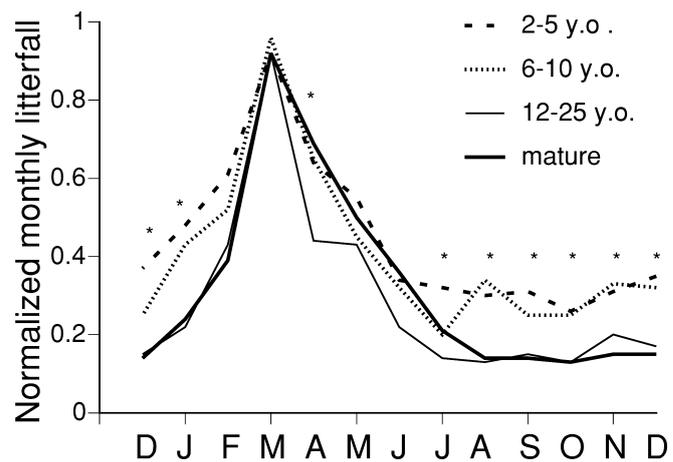


FIGURE 5. Mean normalized monthly pattern of litterfall by age class. Litter production was normalized with respect to peak litterfall at each site within each age class such that the month with peak litterfall was set at 1.0 and values for all other months were proportional to this maximum. Patterns of litterfall varied significantly among age classes (repeated measures ANOVA, $P < 0.05$). Asterisks indicate significant monthly differences in normalized litter production.

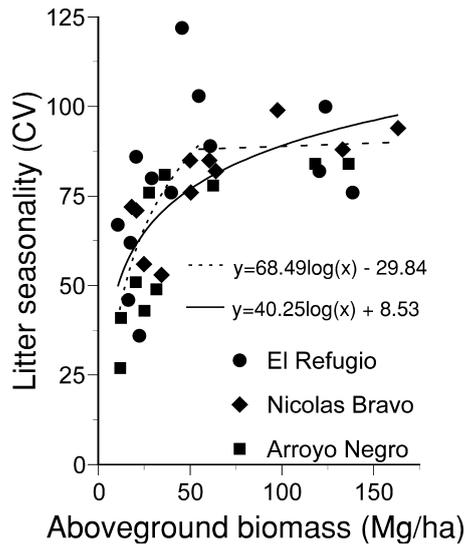


FIGURE 6. Seasonality of litterfall, indicated by the coefficient of variation (CV) of monthly litterfall, as a function of aboveground biomass (> 1 cm DBH, from Read & Lawrence 2003a). A logarithmic relationship was fit to the entire range of biomass (solid line, $R^2 = 0.44$, $P = 0.0001$). The alternative model features a logarithmic rise in CV to an asymptote at *ca* 60 Mg/ha (dashed line, logarithmic increase, $R^2 = 0.41$, $P = 0.0018$).

increasing logarithmically with age among secondary forests ($R^2 = 0.40$, not shown). Clay, silt, sand, and SOM failed to explain the residuals from the relationship between age and litterfall seasonality. Litterfall seasonality increased with aboveground biomass (Fig. 6). A logarithmic relationship for the full range ($R^2 = 0.44$) fit only modestly better than a logarithmic rise to an asymptote at an aboveground live biomass of *ca* 60 Mg/ha ($R^2 = 0.41$). Rather than a continuous increase in the degree of seasonality, a (soft) threshold occurs.

DISCUSSION

REGIONAL DRIVERS OF ANNUAL LITTER PRODUCTION: RAINFALL VS. LAND-USE CHANGE.—Across the region, litterfall varied primarily with forest age. Aboveground, live biomass increases over six-fold during the transition from young secondary forest to mature forest (<20 Mg/ha to >130 Mg/ha, Read & Lawrence 2003a). Thus, it is not surprising that litter production should increase almost 80 percent from a 2-yr-old forest to mature forest (Fig. 2). Data on litter production from other tropical dry secondary forests are rare, but Lugo and Murphy (1986) found that a 1–2-yr-old forest in Puerto Rico produced a third as much litter as observed here, with rainfall comparable to ER (1.2 Mg/ha vs. 3 Mg/ha). Swift *et al.* (1981) found higher litterfall (8.6 Mg/ha/yr vs. 5.6 in this study) in a 5–8-yr-old forest in Ibadan (Nigeria), with annual rainfall at the upper end of the gradient studied here. In the wetter forests of Guatemala (*ca* 2000 mm/yr) just to the south, Ewel (1976) found the greater magnitude of litterfall expected due to higher rainfall.

As in this study, litter production increased rapidly, from 4.5 to 8.0 Mg/ha/yr in 2–10-yr-old forests, and 14-yr-old forest had levels similar to mature forest (9.0–9.5 Mg/ha/yr; Ewel 1976). Litter production of secondary forest was comparable to that of mature forest after only 8 yr in Yangambi, Zaire, with a wetter climate than this study (1716 mm/yr seasonal forest, Laudelot & Meyer 1955, in Klinge & Rodriguez 1968).

In contrast to the profound change in biomass during succession, median annual precipitation increased by an estimated 60 percent from north to south in the southern Yucatan. Nevertheless, it was surprising that the gradient did not significantly affect litter mass. I expected litter mass to follow aboveground biomass, which was expected to increase with precipitation. However, biomass was not systematically higher in the forests sampled at the southern site because of logging history in the mature forests (Read & Lawrence 2003a) and cultivation history in the secondary forests (Lawrence *et al.* 2004). Thus, despite a significant relationship between biomass and litterfall (Fig. 3), the forests sampled in AN did not produce significantly more litter mass than those in ER. The effect of disturbance history on litter production, through effects on biomass or species composition, is an important area for future research. Given high variability, small sample size within each age class limited my ability to detect an effect of precipitation on annual litter production within the study area.

Comparing mature forests in the southern Yucatan with those on similar soils in the greater Mesoamerican region shows that litter production is expected to increase with precipitation (solid symbols; Fig. 7). An almost four-fold increase in precipitation (more comparable to the increase in biomass during the course of succession) results in a doubling of litter production. The relationship between annual precipitation and litter production in seasonal forests around the globe also suggests a positive relationship (all symbols, Fig. 7). At a smaller regional scale, however, this study shows that the legacy of land use has a stronger effect on litter production than a

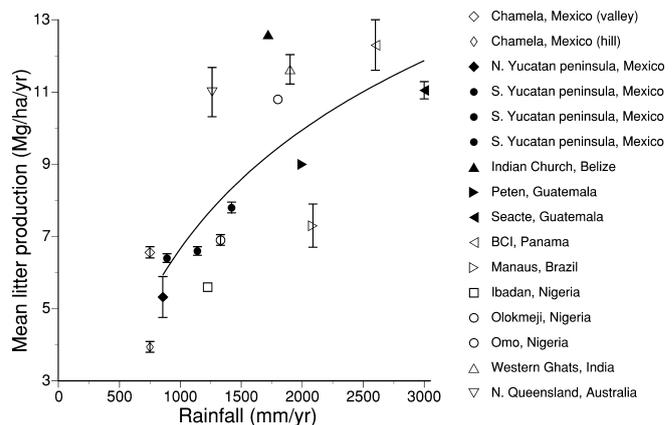


FIGURE 7. Mean annual litter production in seasonally dry, mature tropical forests around the globe. Logarithmic relationship is fit for all forests on similar, karstic soils in the Yucatan, Belize, and Guatemala (solid symbols, $R^2 = 0.66$). See Appendix for references.

precipitation gradient does. These results may be specific to the southern Yucatan region; however, the gradient examined here (890–1420 mm) covers 30 percent of the precipitation range in which dry forests are found (250–2000 mm/yr, Murphy & Lugo 1986) and a greater proportion of the range in which closed-canopy dry forests are found.

REGIONAL EFFECTS ON SEASONALITY.—As expected, litterfall was least seasonal in the wettest area, AN. However, the onset of peak litterfall also occurred earliest in AN, rather than in the drier areas to the north (Fig. 4). Early onset of peak litterfall is not incompatible with lower seasonality in the wettest study area. Frankie *et al.* (1974) observed the same phenomenon when comparing wet and dry forests in Costa Rica. Trees in AN routinely experience higher monthly precipitation. Therefore, they may be more sensitive to periodic drought than trees in the drier areas to the north. Early response to the beginning of the dry season is compatible with sensitivity to shorter drought periods (Fig. 4). Given the failure of soil texture to explain variation in the degree of seasonality at the stand level, regional variation in litterfall patterns cannot be attributed to differences in water-holding capacity of the soil. Furthermore, rainfall is often substantially greater in the south than in the north at the onset of peak litterfall (Fig. 1a). Thus, differences in vegetation or the response of vegetation, rather than in soil moisture *per se*, are likely to cause litterfall early and often in AN. Soil moisture can be sufficient to explain the timing of leaf fall (Reich & Borchert 1984, Martinez-Yrizar & Sarukhan 1990). However, atmospheric conditions also affect plant water status (Reich & Borchert 1984), especially in wetter seasonal forests (Wright & Cornejo 1990, Wieder & Wright 1995), such as those in AN.

Regional differences in vegetation involve both shifts in species composition and shifts in species function. Many species dominant in mature and secondary forests occur throughout the precipitation gradient (Read & Lawrence 2003b); however, some species are found exclusively in the drier zone (D. Perez-Salicrup, pers. comm.). Even in this limited sample, five of the top ten mature forest species in ER were also found in NB or AN (Table 2). Eight of ten at NB and AN overlapped with the top ten of another region. Similar patterns held among secondary forest species. Despite substantial overlap among the dominant trees, systematic differences in species composition, rather than lower drought-resistance within species, could help explain a lower degree of seasonality and early onset of peak litterfall in the south. Tropical tree species differ markedly in leaf fall patterns (Frankie *et al.* 1974, Kunkel-Westphal & Kunkel 1979, Reich & Borchert 1984, Wieder & Wright 1995, Enquist & Leffler 2001). Regional differences in leaf phenology, within and across species, may also explain the timing of leaf fall. Some species in the wetter forests of AN may drop leaves early while flushing new leaves, as a higher proportion of trees in the south remain evergreen throughout the dry season (H. Vester *et al.*, pers. comm.).

DEVELOPMENT OF SEASONALITY WITH FOREST AGE.—An increase in seasonality with age has also been observed in Costa Rican dry forest (1500 mm/yr). The CV of leaf area loss increased from 57 percent in one early successional stand to 76 percent in one

late successional stand (during the 7 mo of highest litterfall, calculated from Kalacska *et al.* 2005). This shift is of the same degree and magnitude as that found between ten young and eight mature stands in the southern Yucatan (increase in mean CV from 55 to 88%). In the wet forest of Brazil (2600 mm/yr), seasonality was much less pronounced, but still lower in a 3-yr-old secondary forest than in a mature forest (CV of 26 vs. 30 percent, calculated from Dantas & Phillipson 1989).

The development of litterfall seasonality with age also supports the importance of vegetation characteristics in driving stand-level response to seasonal drought. Species differences associated with leaf lifespan, phenology, and physiology could explain the disparity between young secondary and mature forests (see Table 2). For example, diel variation in leaf water potential correlates with wood density (James *et al.* 2003), which generally increases with forest age. If diel variation is a good proxy for water relations on a seasonal timescale, then physiological mechanisms at the leaf scale could mediate differences between young and mature forests.

However, species turnover would have to occur very rapidly for species composition to account for significant differences in seasonality between 6–10-yr-old and 12–25-yr-old forests (Fig. 5). Seasonality increased with forest age despite similarity in soil clay content. Given similar species composition, a profound decline in leaf turnover rate after 10 yr could result in lower off-peak litterfall and higher apparent seasonality; however, data are not available to test this hypothesis. Increasing biomass, leaf area, and associated transpirational demand is currently the most parsimonious explanation for a higher degree of seasonality in older secondary forests (Fig. 6). In closed-canopy seasonal tropical forests, soil water leaves predominantly through transpiration (Moreira *et al.* 1997). Thus, greater biomass should exacerbate water stress in larger, older forests, holding precipitation constant. In this study, seasonality increased with biomass only to a point. The threshold may coincide with the development of a critical canopy leaf area, leaf mass, or ratio between leaf area and sapwood (see McDowell *et al.* 2002).

The seasonality of individual stands in this study was quite variable (Fig. 6), although regional and age effects on seasonality were significant (Figs. 4 and 5). The stand history inducing this variation is a very real part of most tropical landscapes and should be analyzed explicitly (*e.g.*, Hughes *et al.* 1999, Moran *et al.* 2000, Turner *et al.* 2001, Lawrence 2005). When it is not possible to obtain land-use history data, sample sizes can be adjusted to compensate for unexplained variation. Sample size was certainly a limitation in this study; however, the variation induced by historical contingencies can never be eliminated completely from studies in human-dominated landscapes.

CONCLUSIONS AND IMPLICATIONS.—Of the major influences on soil moisture, precipitation is beyond the scope of direct human influence at a local scale. In contrast, soil physical properties, soil organic matter, and the stature and composition of vegetation are all subject to change in a human-dominated landscape. As shown in this study, human alteration of vegetation factors profoundly affected the magnitude and pattern of litterfall, eclipsing the effects of natural environmental gradients at the regional scale.

TABLE 2. The ten most frequent species > 5 cm DBH observed in 28 secondary forest plots and 8 mature forest plots in the southern Yucatan, classified by region (increasing annual precipitation from top to bottom)^a.

Region	Secondary forest species	Abundance (percent stems ^c)	Mature forest species	Abundance (percent stems)
ER ^b	<i>Dendropanax arboreum</i> L. Dence. & Planch.	26	<i>Sideroxylon meyeri</i> Standl.	23
	<i>Lonchocarpus castilloi</i> Standl.	23	<i>Ampelocera hottlei</i> (Standl.) Standl.	17
	<i>Piscidia piscipula</i> (L.) Sarg.	8	<i>Myrciaria floribunda</i> Berg.	8
	<i>Bursera simarouba</i> (L.) Sarg.	6	<i>Protium copal</i> Schltdl. & Cham.	6
	Unknown species	6	<i>Krugiodendron ferreum</i> (Vahl.) Urb.	4
	<i>Lysiloma latisiliqua</i> A. Gray ex Sauvalle	4	<i>Manilkara zapote</i> L. P. Royen	4
	<i>Cecropia peltata</i> (L.)	4	<i>Guettarda gaumeri</i> Standl.	3
	<i>Myrciaria floribunda</i> Berg.	4	<i>Malmea depressa</i> (Baill.) R. E. Fr.	3
	<i>Nectandra salicifolia</i> (Kunth.) Nees	3	<i>Neea choriophylla</i> Standl.	3
	<i>Pouteria reticulata</i> (Engl.) Eyma	3	<i>Trichilia</i> spp. P. Browne	3
<i>Zuelaria guidonia</i> (Sw.) Britton & Millsp.	3			
NB ^b	<i>Lysiloma latisiliqua</i> A. Gray ex Sauvalle	22	<i>Pouteria reticulata</i> (Engl.) Eyma	19
	<i>Exothea diphylla</i> (Standl.) Lundell	16	<i>Bursera simarouba</i> (L.) Sarg.	12
	<i>Croton icche</i> Lundell	12	<i>Psidium sartorianum</i> (O. Berg) Nied.	10
	<i>Guettarda combsii</i> Urb.	8	<i>Brosimum alicastrum</i> (Sw.)	7
	<i>Nectandra salicifolia</i> (Kunth.) Nees	7	<i>Manilkara zapote</i> L. P. Royen	6
	<i>Simarouba</i> spp. (Aubl.)	5	<i>Ampelocera hottlei</i> (Standl.) Standl.	5
	<i>Dendropanax arboreum</i> L. Dence. & Planch.	4	<i>Pouteria amygdalia</i> (Standl.) Baehni	5
	<i>Hampea trilobata</i> Standl.	4	<i>Pouteria campechiana</i> (Kunth.) Baehni	4
	<i>Vitex gaumeri</i> Greenm.	3	<i>Gymnanthes lucida</i> (Sw.)	3
	<i>Cocoloba belizensis</i> Standl.	3	<i>Malmea depressa</i> (Baill.) R. E. Fr.	3
		<i>Rochefortia lundellii</i> Camp	3	
		<i>Nectandra salicifolia</i> (Kunth.) Nees	3	
AN ^b	<i>Bursera simarouba</i> (L.) Sarg.	29	<i>Myrciaria floribunda</i> Berg.	24
	<i>Brosimum alicastrum</i> (Sw.)	18	<i>Talisia olivaeformis</i> (Kunth.) Radlk.	16
	Unknown species	8	<i>Pouteria reticulata</i> (Engl.) Eyma	14
	<i>Cecropia peltata</i> (L.)	6	<i>Brosimum alicastrum</i> (Sw.)	12
	<i>Lonchocarpus rugosa</i> Benth.	6	<i>Pouteria amygdalia</i> (Standl.) Baehni	7
	<i>Myrciaria floribunda</i> Berg.	6	<i>Neea choriophylla</i> Standl.	5
	<i>Ampelocera hottlei</i> (Standl.) Standl.	5	<i>Laetia thamnia</i> L.	4
	<i>Cocoloba</i> spp. P. Browne	4	<i>Malmea depressa</i> (Baill.) R. E. Fr.	4
	<i>Pouteria reticulata</i> (Engl.) Eyma	2	<i>Nectandra salicifolia</i> (Kunth.) Nees	4
	<i>Pouteria amygdalia</i> (Standl.) Baehni	2	<i>Ampelocera hottlei</i> (Standl.) Standl.	3
<i>Dendropanax arboreum</i> L. Dence. & Planch.	2			

^aSecondary forest plots were sampled 2–25 yr after shifting cultivation; mature forest had not been cleared in recent history. Adapted from Read and Lawrence 2003b.

^bTen secondary and three mature forests were sampled in ER and NB; eight secondary and two mature forests were sampled in AN. At each forest stand, stems > 10 cm DBH were sampled in one 500-m² plot and stems > 5 cm DBH were sampled in a concentric 100-m² plot. Forest age, soils, and structure of the plots are detailed in Table 1.

^cStem numbers for each plot size were scaled to 1 ha and then combined across all plots. Abundances were tallied separately for mature and secondary forests of each region.

ER, El Refugio; NB, Nicolas Bravo; AN, Arroyo Negro; DBH, diameter at breast height.

Seasonality in litterfall strongly influences the pattern of soil nutrient availability through effects on decomposition and the activity and turnover of soil microbes (Singh *et al.* 1989, Davidson *et al.* 1993, Roy & Singh 1995, Campo *et al.* 1998). Nutrient retention following rainfall depends on uptake by plants or microbes.

The karstic soils of the southern Yucatan drain rapidly, especially in the younger secondary forests, where both canopy interception and plant uptake are reduced. Thus, the risk of nutrient leaching is greater in secondary than in mature forest, *moreso*, since the litter is higher in nutrients (Ewel 1976, Dantas & Phillipson 1989, Read

& Lawrence 2003b). The lower proportional input of litter during the dry season peak may reduce nutrient loss in young secondary forests and enhance forest recovery.

Understanding the drivers of litterfall seasonality will facilitate the ability to scale up ecological phenomena using remote sensing. One of the major limitations to constraining carbon and nutrient cycles in human-disturbed landscapes is the difficulty of reliably distinguishing different stages of successional forest with remote sensing. This study shows that litterfall responds to seasonal drought in predictable, significantly different ways in younger vs. older secondary forest. If indices derived from remote sensing (*e.g.*, Normalized Difference Vegetation Index or NDVI) could be used to track litterfall, inverse modeling techniques would allow better classification and biomass estimation of young secondary forest based on spectral signatures (*e.g.*, Gamon *et al.* 2005, Kalacska *et al.* 2005, Arroyo-Mora *et al.* 2005). Because of similarity in patterns of litterfall, temporal signatures based on leaf fall alone are not likely to differ between older secondary and mature forest, the two classes most problematic to distinguish. Further refinements using hyperspectral sensors will be necessary and promising research is already underway (Sánchez-Azofeifa *et al.* pers. comm.).

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APPENDIX

Reference studies for sites in Fig. 7.

Chamela, Mexico. Martinez-Yrizar and Sarukhan 1990; North Yucatan, Mexico. Whigham *et al.*, 1991; Southern Yucatan, this study; Indian Church, Belize. Lambert *et al.*, 1980; Peten, Guatemala. Ewel 1976; Seacte, Guatemala. Kunkel-Westphal and Kunkel, 1979; BCI, Panama. Wieder and Wright 1995; Manaus, Brazil. Klinge and Rodriguez 1968; Ibadan, Nigeria. Madge 1965 (cited in Klinge & Rodriguez 1968); Olokemeji and Omo, Nigeria. Hopkins 1966; Western Ghats, India. Swamy and Proctor 1994; North Queensland, Australia. Stocker *et al.* 1995.