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Multiple Factors Influence Seasonal and Interannual Litterfall Production in a Tropical Dry Forest in Mexico

Hernán Morffi-Mestre ¹, Gregorio Ángeles-Pérez ², Jennifer S. Powers ³,
José Luis Andrade ¹, Astrid Helena Huechacona Ruiz ¹, Filogonio May-Pat ¹,
Francisco Chi-May ¹ and Juan Manuel Dupuy ^{1,*}

¹ Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, Calle 43 # 130 x 32 y 34. Colonia Chuburná de Hidalgo, Mérida, Yucatán 97205, Mexico; morffihernan76@gmail.com (H.M.-M.); andrade@cicy.mx (J.L.A.); helena.huechacona@gmail.com (A.H.H.R.); filosmaypat@gmail.com (F.M.-P.); frankcm@cicy.mx (F.C.-M.)

² Colegio de Postgraduados, Campus Montecillo, Carretera México-Texcoco Km. 36.5, Montecillo, Texcoco, Estado de México 56230, Mexico; gangeles@colpos.mx

³ Department of Ecology, Evolution and Behavior, University of Minnesota, 140 Gortner Lab, 1479 Gortner Avenue, Saint Paul, MN 55108, USA; powers@umn.edu

* Correspondence: jmdupuy@cicy.mx

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Abstract: Litterfall production plays a fundamental role in the dynamics and function of tropical forest ecosystems, as it supplies 70–80% of nutrients entering the soil. This process varies annually and seasonally, depending on multiple environmental factors. However, few studies spanning several years have addressed the combined effect of climate variables, successional age, topography, and vegetation structure in tropical dry forests. In this study, we evaluated monthly, seasonal, and annual litterfall production over a five-year period in semideciduous dry forests of different successional ages growing on contrasting topographic conditions (sloping or flat terrain) in Yucatan, Mexico. Its relationship with climate and vegetation structural variables were also analyzed using multiple linear regression and generalized linear models. Litterfall was measured monthly in 12 litterfall traps of 0.5 m² in three sampling clusters (sets of four 400 m² sampling plots) established in forests of five successional age classes, 3–5, 10–17, 18–25, 60–79, and >80 years (in the latter two classes either on sloping or on flat terrain), for a total of 15 sampling clusters and 180 litterfall traps. Litterfall production varied between years (negatively correlated with precipitation), seasons (positively correlated with wind speed and maximum temperature), and months (negatively correlated with relative humidity) and was higher in flat than in sloping sites. Litterfall production also increased with successional age until 18–25 years after abandonment, when it attained values similar to those of mature forests. It was positively correlated with the aboveground biomass of deciduous species but negatively correlated with the basal area of evergreen species. Our results show a rapid recovery of litterfall production with successional age of these forests, which may increase with climate changes such as less precipitation, higher temperatures, and higher incidence of hurricanes.

Keywords: leaf litter; seasonality; interannual variation; successional age; topographic position; vegetation structure; precipitation; temperature; wind speed

1. Introduction

Litterfall production (amount of plant material that falls to the ground per unit area and time) is a key process of the carbon cycle in terrestrial ecosystems [1–5]. It is the main source of reincorporation

of organic nutrients to the soil, where they can be mineralized for plant uptake [6–8], as well as an important component of net primary production [9]. Quantifying litterfall production is a necessary step to estimate productivity and evaluate phenology, carbon dynamics, biogeochemical cycles, and the capacity of forests to recover from natural and human disturbances [10]. Moreover, identifying the factors that govern litterfall production can help us to better understand the response of forest ecosystems to climate change [11,12]. Most studies on litterfall production in tropical forests have been conducted in humid forests, while fewer have addressed tropical dry forests (TDF) [13], although the latter cover a greater extent and are more threatened by human activities [13,14].

Litterfall production in TDF occurs mostly in the dry season, as a strategy to avoid water loss by transpiration and cope with water stress—low soil water availability and high vapor-pressure deficit [15–18]. Therefore, litterfall production in TDF is negatively correlated with annual, seasonal, and monthly precipitation [16,19–23]. However, most studies conducted to date on litterfall production in TDF have been short-term [24,25], but see [26–28], which limit the possibility of evaluating, modeling, and predicting the effects of climate change. The few multi-year studies of litterfall production in TDF and its relationship with precipitation [29] have documented several patterns of monthly litterfall production with one, two, or irregular peaks at different times of the year [16,19], mostly associated with scarce or nil precipitation [16,19,30].

Other climatic factors shown to be (positively) correlated with litterfall production in tropical forests include temperature [24,31], wind speed [15,32], and solar radiation [33], which, together with drought, are closely related to the abscission of leaves—the main component of plant litter. Therefore, the temporal patterns of leaf abscission govern the variations in litterfall production both between and within ecosystems [19,34].

Litterfall production is also related to species composition and vegetation structure [35–37], which change over the course of forest succession [38–41]. Litterfall production increases during succession as tree size, aboveground biomass, and leaf area index increase as a result of changes in microenvironmental conditions [15,40,42] and the life history strategies of species [43–47]. Environmental conditions such as high solar radiation, high temperature, and low water availability in the uppermost layers of the soil prevail during the early successional stages in TDFs. Species with strategies that allow for conserving acquired and allocated resources (e.g., evergreen, long-lived leaves) tend to predominate under such conditions, while species with strategies that maximize resource acquisition when they are in high availability (e.g., deciduous, short-lived leaves) tend to predominate in later successional stages, when environmental conditions become less restrictive [40,42,48,49]. However, some authors have reported an inverse successional pattern in TDF: predominance of plants with acquisitive strategies in early successional stages, which are then replaced by species with conservative strategies in later stages [50–52]. Such conflicting behaviors suggest that plant species in TDF possess a wide range of strategies to cope with drought.

Litterfall production is also influenced by landscape topography, as the latter affects incident solar radiation and soil water availability and, thus, plant phenology [35,53–57]. For instance, sites located on hilltops or hill slopes have shallower soils with lower water retention capacity, compared with sites located on flat areas [54,58,59]. Accordingly, species with conservative strategies (evergreen, slow-growing, with long-lived leaves) have been reported to predominate in sites located on hill slopes [50], where litterfall production is lower than on flat sites [27]. However, other studies [53,60] have reported the opposite pattern: a higher abundance of evergreen species on flat vs. sloping sites, which would lead to an opposite pattern of litterfall.

To the best of our knowledge, this is the first study that evaluates the influence of multiple factors (successional age, vegetation structure, topography, and climatic variables) on monthly, seasonal, and interannual litterfall production patterns in a TDF. We had three objectives: (a) to analyze the temporal (interannual, seasonal, and monthly) dynamics of litterfall production; (b) to evaluate the effects of successional age and topography on annual and seasonal litterfall production; and (c) to examine the relationships of seasonal and annual litterfall production with vegetation structure

and climatic variables. We posit three hypotheses: (1) given that aboveground biomass and, likely, the proportion of deciduous species in TDF increase with successional age, we expect litterfall production to also increase with successional age and to be positively correlated with aboveground biomass or basal area (particularly of deciduous species); (2) since lower water availability in sloping sites leads to a predominance of drought-tolerant species (evergreen species with long-lived leaves and long roots), we expect litterfall production to be lower on sloping versus flat sites; (3) since litterfall production in TDF is correlated with periods of water stress, we expect a negative correlation with monthly, seasonal, and annual precipitation and a positive correlation with maximum temperature and vapor-pressure deficit.

2. Materials and Methods

2.1. Study Area

The study area is located in Kaxil Kiuc Biocultural Reserve and its surroundings ($20^{\circ}5' 20^{\circ}7' N$; $89^{\circ}32' 89^{\circ}34' W$), at the central part of the Yucatán Peninsula (Figure 1a). The reserve stretches across 1800 ha, mostly covered by semi-deciduous tropical dry forest.

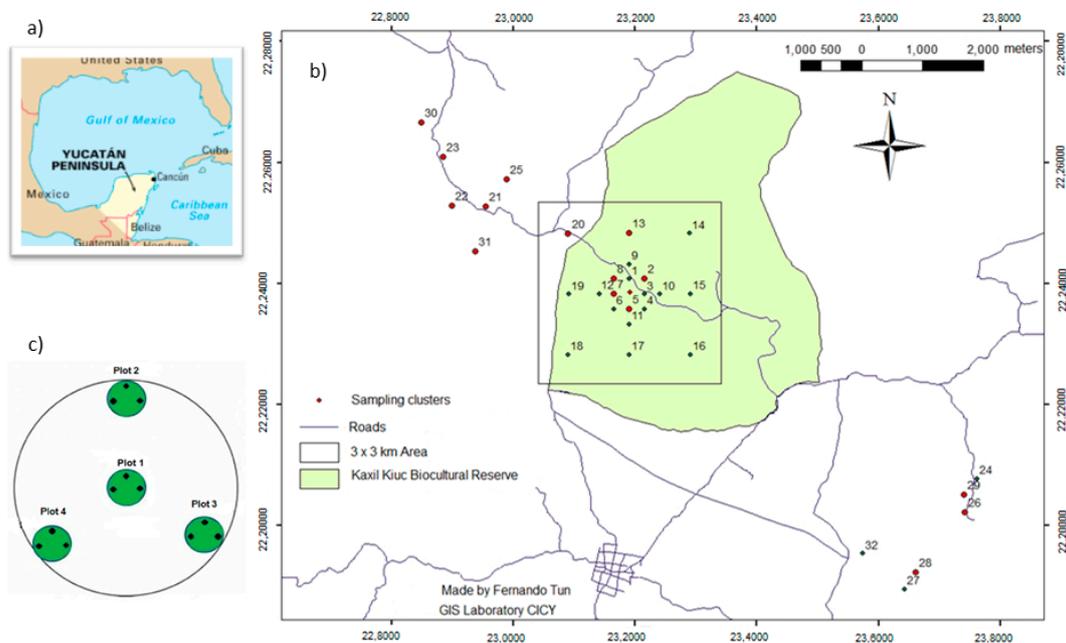


Figure 1. (a) Map showing the location of the study area, (b) distribution of the sampling clusters following the design of the National Forest and Soil Inventory of Mexico, (c) arrangement of the four 400 m² plots (green circles) within each sampling cluster and of the three litterfall traps (black dots) within each plot. Red dots denote the sampling clusters that were used in this study. The inset square is a 3 × 3 km area where the late successional sampling clusters were established following a stratified systematic design; early successional sampling clusters were established outside the reserve following a chronosequence design (see Appendix A).

The local climate is warm subhumid (Aw), with mean annual temperature of 26 °C and mean annual precipitation of 1000–1200 mm [61]. The rainy season lasts from May to October and accounts for over three quarters of the total annual precipitation (763–916 mm), whereas the dry season lasts from November to April and contributes only 237–284 mm. The geomorphology of the region consists of karstic limestone, with flat areas alternating with gently sloping hills (10–25%). Cambisol and luvisol soils predominate in flat areas, and leptosol soils on hills and sites with rocky outcrops [62]. Secondary vegetation of different ages since abandonment predominates in the region as a result of

the long-standing use of slash-and-burn subsistence agriculture [63,64]. The dominant vegetation is a medium-stature semideciduous tropical forest, in which 50–75% of the trees shed their leaves during the dry season and canopy height is 13–18 m in late successional forests. The most abundant tree species include *Neomillspaughia emarginata* (H. Gross) S.F. Blake and *Gymnopodium floribundum* Rolfe. (Polygonaceae), *Lonchocarpus xuul* Lundell, *Mimosa bahamensis* Benth. and *Caesalpinia gaumeri* Greenm. (Fabaceae), and *Bursera simaruba* (L.) Sarg. (Burseraceae), among others.

2.2. Selection of Sampling Sites

The sampling design was based on the one used by the National Forest and Soil Inventory of Mexico [65], which consists of 1-ha sampling clusters of four 0.04-ha (400 m²) plots arranged in an inverted Y shape (Figure 1b,c). Three sampling clusters were established in forests of five successional age classes (years since abandonment from cultivation at the beginning of this study), I: 3–5, II: 10–17, III: 18–25, IV: 60–79, and V: ≥80 years, for a total of 15 sampling clusters and 60 plots (Appendix A). Sampling clusters in age classes I–III were selected to form a chronosequence of stands of different successional age on predominantly flat terrain (the prime land for farming activities). Sampling clusters in age classes IV and V were established following a stratified systematic design irrespective of topographic position, which varied among plots in each cluster. Thus, the effect of topography was assessed only in clusters in age classes IV and V. From these clusters, we used only those plots located on the predominant topographic position (flat (0–9% slope) or sloping (10–20% slope) terrain), including three plots from each of the three clusters for each topographic position (Appendix A).

2.3. Estimation of Litterfall Production

Litterfall production was measured over five years in a total of 180 litterfall traps (12 per sampling cluster). Three litterfall traps were established in each sampling plot, 6 m from the center, along three compass directions (north, east, and west) (Figure 1c). We used 80-cm-diameter (0.503 m²) circular traps made of fine, 1-mm mesh plastic net to allow rainwater to escape while retaining fine plant material; the traps were placed 80 cm above the ground. Litterfall (leaves, twigs, bark, flowers, fruits, seeds, and frass) was collected monthly, as recommended by Aceñolaza et al. [66], from October 2013 to September 2018. The litter samples were dried at 70 °C to constant weight and weighed using an analytical balance. The monthly litterfall production rate (P; Mg/ha/month) was estimated using the following equation (modified from Honorio and Baker, [67]):

$$P = \frac{\text{Total dry weight in each litterfall trap (g)} \times 10^8 \text{ cm}^2 \times 30 \text{ days} \times 1 \text{ Mg}}{\text{Area of the litterfall trap (503.56 cm}^2) \times \text{collection duration (days)} \times 1 \text{ ha} \times 1 \text{ month} \times 10^6 \text{ g}}$$

2.4. Climatic Variables

Climatic data were obtained from the weather station of the nearest town, Oxkutzcab, located 27.4 km from the study site and operated by the Comisión Nacional del Agua (National Water Commission). Data on monthly precipitation (mm), mean, maximum, and minimum air temperature (°C), relative air humidity (%), wind speed (km/h), and wind gusts (km/h) were recorded every 10 min over the entire study period by the automatic weather station. Cumulative temperature values were calculated from daily maximum and minimum temperature values recorded by a conventional weather station at the same site; the daily values were added up to obtain monthly cumulative maximum and minimum temperatures (ACTmax and ACTmin, respectively). Vapor-pressure deficit (δe) was estimated after the equations proposed by Jones [68].

2.5. Measurement and Estimation of Vegetation Variables

All woody plants (trees, shrubs, lianas, and palms) with DBH (diameter at breast height, measured at 1.3 m above the ground) ≥ 7.5 cm present in all the plots where litterfall production was monitored were censused from 2013 to 2016 and in 2018 (2465 plants in total). Plants with DBH ≥ 2.5 cm were

sampled in 80 m² subplots nested in the center of each 400 m² plot (2660 plants in total). Each plant was identified to species (see the complete species list in Appendix B), and the diameter and height of each stem were measured. Sample specimens of those plants that could not be identified in the field were collected and taken to the herbarium of the Centro de Investigación Científica de Yucatán for identification.

Aboveground biomass was estimated using allometric equations either developed or used in previous studies on forests of the Yucatán Peninsula. We used the equation of Ramírez-Ramírez et al. [69] for trees with DBH < 10 cm, and the equation of Chave et al. [70] for larger trees. All plant species recorded in each plot were classified according to their leaf phenology (deciduous vs. evergreen) based on specialized literature [71,72] as well as on the knowledge of local inhabitants and one of the co-authors (F May-Pat). Basal area, aboveground biomass, and stem density in each plot were calculated for all species as well as for evergreen and deciduous species separately.

2.6. Data Analysis

Each cluster was regarded as a sampling unit; the litterfall production values of the 12 litterfall traps in each sampling cluster (three traps × four 400 m² plots) were averaged. As indicated above, the effect of topographic position was evaluated based on the mean value of the three plots located on the predominant topographic position in the cluster. All sampling clusters were separated by at least 250 m; the spatial independence of the data was tested separately for each study year using Moran's Index (I) [73] implemented in the spatial autocorrelation tool of ArcMap 10.2 or Qgis 3.0 [74,75]. No spatial autocorrelation was found in any year ($I \geq -0.216$, $Z \geq -0.725$, $p \geq 0.468$).

Generalized linear mixed models (GLMM) were used, followed by Bonferroni post-hoc multiple comparison tests, to test for significant differences in the temporal (annual, seasonal, and monthly) litterfall production patterns between successional age classes or topographic positions. These analyses were carried out using the software SPSS v.17.0 [76].

The relationships between litterfall production and climatic or vegetation variables were examined by fitting multiple linear regression models using the regsubsets procedure in the “leaps” package in R (3.5.0) [77]. Annual and monthly averages of the climatic variables (over the entire study period) were used for these analyses, except for precipitation, for which the cumulative value was used. As vegetation variables were recorded only annually (except for 2017), climatic and vegetation variables (including successional age) were analyzed separately.

For each multiple regression analysis, the three best models identified by the regsubset procedure were considered and the best model was selected based on the Akaike information criterion (AIC). Akaike delta scores (Δ AIC, relative difference between the AIC of the best model and that of each other model) and Akaike weights (ω_i) [78] were calculated for the three selected models. We checked for multicollinearity among the explanatory variables based on the variance inflation factor (VIF). The best model for each case was the one yielding the lowest Δ AIC and the highest ω_i [79,80], provided it included neither non-significant explanatory variables nor high multicollinearity ($VIF \geq 2$).

3. Results

3.1. Total Annual Litterfall Production

Average annual litterfall production \pm 95% confidence interval was 5.651 ± 0.266 Mg/ha/year; annual production varied among the study years ($F = 43.047$; $p < 0.001$), with the highest value recorded in 2016 (6.173 ± 0.654 Mg/ha/year) and the lowest in 2017 (4.941 ± 0.502 Mg/ha/year) (Table 1). The highest annual production (2016) coincided with the lowest annual precipitation of the study period; however, the lowest annual production (observed in 2017) coincided with a similarly low annual precipitation (the second lowest of the study period).

Table 1. Annual litterfall production ($\pm 95\%$ confidence interval) and annual precipitation during the 5-yr study period. Different superscript letters denote significant differences among study years.

Year	Annual Litterfall Production (Mg/ha/yr)	Annual Precipitation (mm)
2014	5.963 \pm 0.955 "ab"	1148.0
2015	5.071 \pm 0.603 "ab"	1098.8
2016	6.173 \pm 0.654 "a"	885.2
2017	4.941 \pm 0.502 "b"	906.5
2018	6.109 \pm 0.508 "a"	945.2

3.2. Influence of Successional Age and Topography on Inter-Annual Litterfall Production

Litterfall production varied significantly among successional age classes over the entire study period ($F = 49.863, p < 0.001$) (Table 2), as well as within years ($F \geq 12.595, p < 0.001$ in all study years) (Figure 2). Although litterfall production varied widely among years, the lowest values were consistently recorded in forest age class I (3–5 years), whereas the highest values were observed in forest age class III (18–25 years) and/or V (≥ 80 years) (Figure 2).

Table 2. Total litterfall production ($\pm 95\%$ confidence interval) over the entire study period in forests of different successional age classes. Different superscript letters denote significant differences among successional age classes.

Successional Age Class	Total Litterfall Production (Mg/ha/yr)
I (3–5 years)	4.070 \pm 0.502 "a"
II (10–17 years)	5.674 \pm 0.274 "b"
III (18–25 years)	6.460 \pm 0.173 "c"
IV (60–79 years)	5.604 \pm 0.502 "b"
V (≥ 80 years)	6.440 \pm 0.281 "c"

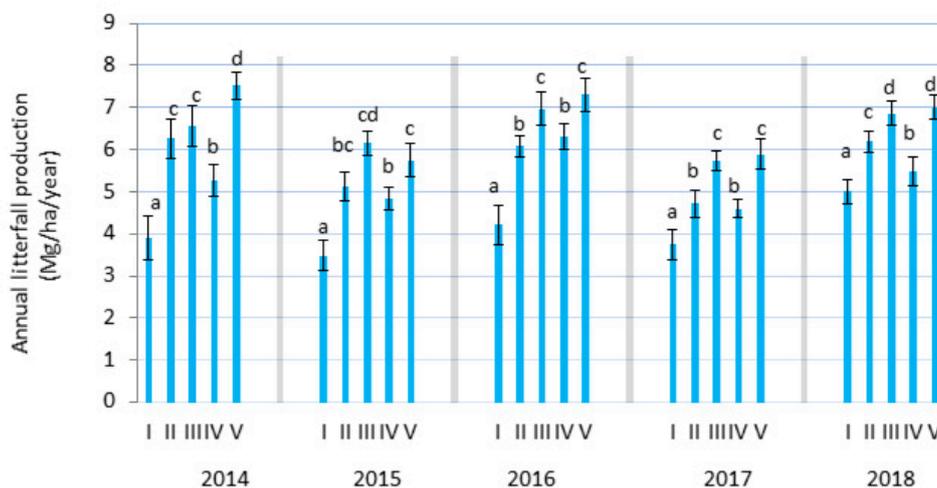


Figure 2. Annual litterfall production in forests of different successional age classes over the study period. The X-axis numbers indicate the successional age classes (see Table 2); vertical lines are $\pm 95\%$ confidence intervals. Different letters denote significant differences among successional age classes in each year.

Litterfall production also differed between topographic positions over the entire study period ($F = 4.660, p = 0.042$), as well as in 2015 ($F = 22.39, p < 0.001$), but not in other years ($F \geq 0.277; p \geq 0.067$). Over the study period (and in 2015), litterfall production was higher (mean $\pm 95\%$ CI) in flat (2.634 ± 0.321 Mg/ha/year) than in sloping sites (2.196 ± 0.244 Mg/ha/year).

3.3. Relationships between Litterfall Production and Vegetation Variables

The best multiple linear regression model over the study period explained 60.8% of the variation in total litterfall production. Litterfall production over the study period was positively correlated with aboveground biomass of deciduous species and negatively correlated with basal area of evergreen species ($F = 11.87, p = 0.0014$) (Table 3). The vegetation variables most closely related to annual litterfall production varied among years and included average tree height (positive correlation), biomass of evergreen species (negative correlation), basal area of deciduous species (positive), successional age (positive), and mean tree diameter (positive) (Table 3).

Table 3. Multiple linear regression models relating litterfall production to vegetation variables, either for each year or over the entire study period.

Year	Models	R^2_{aj}	AIC	Δ AIC	ω_i
2014	(1) $Y = 0.885 \times Ht$	0.379	13.77	2.69	0.004
	(2) $Y = 1.371 \times Ht - 0.044 \times Be$	0.491	11.54	0.46	0.666
	(3) $Y = 0.02 \times E - 0.054 \times Be + 1.16Ht$	0.529	11.08	0.00	0.003
2015	(1) $Y = 1.604 + 0.532 \times Ht$	0.424	-1.156	0.642	0.079
	(2) $Y = 0.141 \times BAd$	0.464	-1.424	0.374	0.255
	(3) $Y^* = -0.037 + 0.966 \times Ht + 0.019 \times Bd$	0.500	-1.798	0.000	0.666
2016	(1) $Y = 1.812 + 0.684 \times Ht$	0.624	-5.179	0.000	0.079
	(2) $Y^* = 1.437 - 0.04 \times BAe + 0.793 \times Ht$	0.608	-3.734	1.445	0.255
	(3) $Y = 1.74 + 0.009 \times Age$	0.607	-3.007	2.172	0.666
2018	(1) $Y = 3.819 + 0.718 \times Ht$	0.243	-2.260	4.270	0.079
	(2) $Y = 2.09 + 0.224 \times DBH$	0.320	-3.054	1.913	0.255
	(3) $Y'' = 1.053 + 0.292 \times DBH + 0.01 \times BAd$	0.322	-2.408	0.000	0.000
Total	(1) $Y = 3.772 + 0.115 \times BAd$	0.516	-2.670	4.270	0.124
	(2) $Y = 4.204 + 0.034 \times Bd - 0.158 \times BAe$	0.608	-5.027	1.920	0.452
	(3) $Y^* = 3.761 + 0.061 \times Abd + 0.024 \times Bd - 0.141 \times BAe$	0.607	-6.940	0.000	0.424

Y: litterfall production; Y^* indicates multicollinearity between explanatory variables ($VIF \geq 2$); Y'' : model including non-significant parameters. The best model for each case is shown in boldface. BAd: basal area of deciduous species; Bd: aboveground biomass of deciduous species; BAe: basal area of evergreen species; Be: aboveground biomass of evergreen species; Ht: average tree height; DBH: average stem diameter; Age: successional age; R^2_{aj} : adjusted coefficient of determination; AIC: Akaike's information criterion, Δ AIC: Akaike delta score, ω_i : Akaike weight. Vegetation was not censused in 2017.

3.4. Seasonal Dynamics of Litterfall Production

Litterfall production was significantly higher (mean \pm 95% CI) in the dry (3.036 ± 0.387 Mg/ha/year) than in the rainy season (1.794 ± 0.209 Mg/ha/year) over the entire study period ($F = 28.55, p < 0.001$), as well as in most years ($F \geq 10.209, p \leq 0.004$), except for 2014 ($F = 3.769, p = 0.06$). Litterfall production in the dry season accounted for between a low of 57.5% (in 2014) and a high of 77.5% (in 2018) of total annual litterfall production.

Litterfall production was consistently higher in the dry than in the rainy season in the five years across the different successional age classes (Figure 3a) and in the two topographic positions considered, except for sloping sites in 2015 (Figure 3b). There were significant interaction effects between seasons and age classes ($F \geq 5.906; p < 0.001$ in all study years) as successional patterns differed between seasons (Figure 3a) but not between seasons and topographic positions ($F = 0.336; p \geq 0.173$ in all years), except for 2015 ($F = 30.975; p < 0.001$) (Figure 3b).

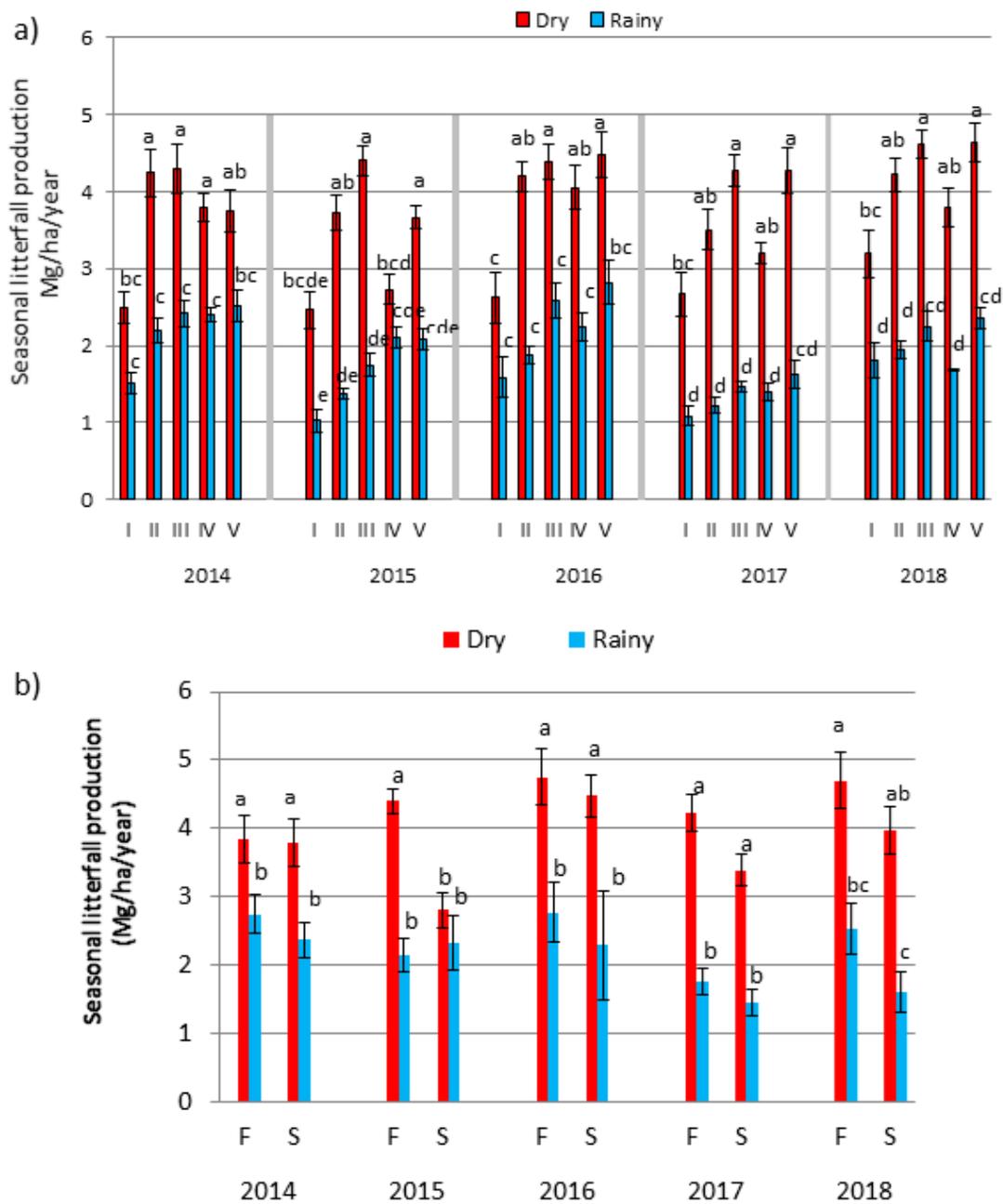


Figure 3. Seasonal (dry vs. rainy season) dynamics of litterfall production in forests of different successional age classes (a), and in contrasting topographic positions (b), over the study period. Numbers along the X-axis in (a) indicate successional age classes; vertical lines are \pm 95% confidence intervals. F: flat sites, S: sloping sites. Different letters denote significant differences between seasons and age classes or between seasons and topographic positions in each year.

3.5. Temporal Variation in Litterfall Production and Its Relationship with Climatic Variables

Average monthly litterfall production varied significantly among years ($F = 13.64$; $p < 0.001$ in all cases) (Figure 4). The highest average monthly production (mean \pm 95% CI) was recorded in 2018 (0.509 ± 0.174 Mg/ha/month) and the lowest in 2017 (0.410 ± 0.172 Mg/ha/month). The overall pattern of monthly litterfall production varied among years, being unimodal in 2014 and 2017 and bimodal in 2015, 2016, and 2018. Peak values were recorded in April 2014, January and March 2015, February and April 2016, January 2017, and March 2018 (Figure 4).

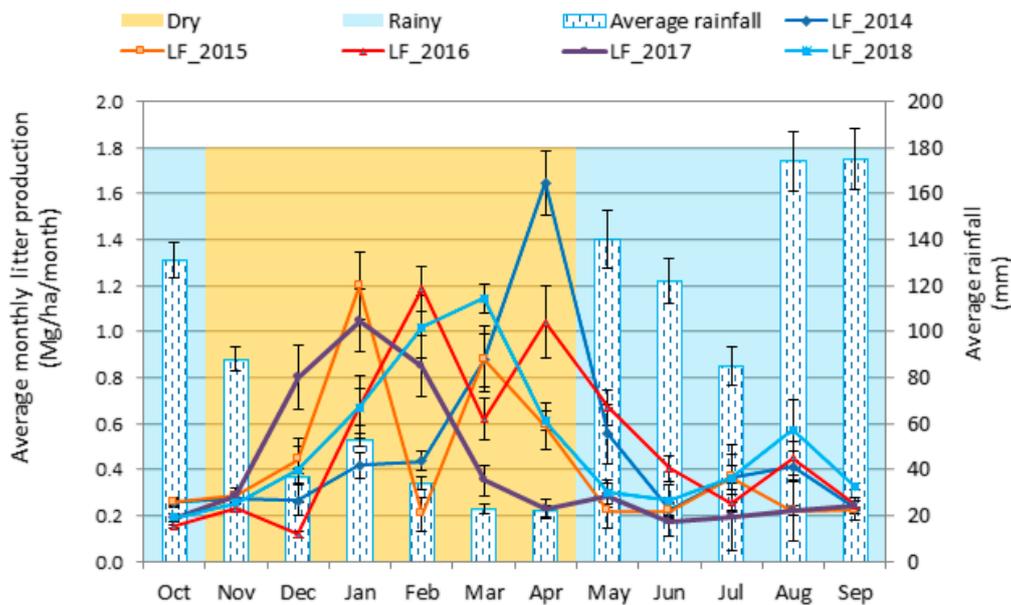


Figure 4. Average monthly litterfall production in each study year and average monthly precipitation over the study period. The blue shading corresponds to the rainy season and the peach shading to the dry season. Vertical bars lines denote \pm 95% confidence intervals.

Over the whole study period, annual litterfall production was negatively related to annual precipitation (which accounted for 94.4% of the total variation), whereas seasonal litterfall production was positively related to wind speed and the cumulative maximum temperature, which jointly accounted for 87.4% of the total variation (Table 4).

Table 4. Models relating annual or seasonal litterfall production to climatic variables over the entire study period.

Model	R ² _{aj}	AIC	Δ AIC	ω _i
<i>annual</i>				
(1) Y = 9.328 − 0.003 × P	0.944	−18.17	33.41	0.124
(2) Y* = 5.18 + 0.067 × RH − 0.04 × P	0.981	−24.81	26.77	0.452
(3) Y* = −0.0015 × P + 0.001 × W + 0.00009 × ACTmin	0.990	−51.58	0.000	0.424
<i>seasonal</i>				
(1) Y = −7.345 + 2.071 × W	0.629	5.758	9.744	0.009
(2) Y'' = 1.88 + 1.87 × V − 0.32 × Tmean	0.692	4.549	8.535	0.452
(3) Y = 2.16 × W + 0.0019 × ACTmax	0.874	−3.986	0.000	0.105

Y: litterfall production; Y* indicates multicollinearity between explanatory variables (VIF \geq 2); Y'': model including non-significant parameters. The best model for each case is shown in boldface. P: precipitation, RH: relative humidity, W: wind speed, Tmean: mean temperature, ACTmax: cumulative maximum temperature, ACTmin: cumulative minimum temperature, R²_{aj}: adjusted coefficient of determination; AIC: Akaike information criterion, Δ AIC: Akaike delta score, ω_i: Akaike weight.

The model that best described monthly litterfall production over the entire study period included relative humidity as the only explanatory variable, which was negatively related to the response variable (Table 5). The climatic variables most closely related to monthly litterfall production varied between years but often included maximum, minimum, or mean temperature. No significant relationships were found between monthly litterfall production in 2015 and any of the climatic variables analyzed.

Table 5. Multiple linear regression models relating average monthly litterfall production to climatic variables either for each year or over the entire study period.

Year	Model	R ² _{aj}	AIC	Δ AIC	ω _i
2014	(1) $Y = 4.215 - 0.045 \times RH$	0.77	−37.96	0.37	0.332
	(2) $Y = 1.625 - 0.06 \times Tmax + 1.63 \times DPV$	0.79	−38.33	0.00	0.399
	(3) $Y^* = 0.17 \times RH - 0.21 \times T + 6.81 \times DPV$	0.79	−37.54	0.79	0.269
2015	(1) $Y'' = 0.81 - 0.032 \times WG$	0.11	−30.54	0.34	0.303
	(2) $Y'' = 0.24 - 0.054 \times Tmin + 0.0009 \times ACTmax$	0.18	−30.75	0.13	0.337
	(3) $Y'' = -0.02 \times WG - 0.05 \times Tmin + 0.001 \times ACTmax$	0.23	−30.88	0.00	0.360
2016	(1) $Y = 1.31 - 0.059 \times Tmin$	0.45	−30.83	10.83	0.003
	(2) $Y = -0.023 \times RH - 0.003 \times ACTmin$	0.75	−39.87	1.79	0.289
	(3) $Y = 0.076 \times Tmax - 0.003 \times ACTmin$	0.80	−41.66	0.00	0.720
2017	(1) $Y = 3.95 - 0.131 \times Tmean$	0.43	−38.56	4.63	0.133
	(2) $Y = 3.391 - 0.094 \times Tmean - 0.035 \times Tmin$	0.76	−43.05	0.14	0.433
	(3) $Y^* = -0.37 + 0.13 \times RH - 0.37 \times Tmean + 4.08 \times DPV$	0.77	−43.19	0.00	0.433
2018	(1) $Y = 1.606 - 0.014 \times RH$	0.45	−33.60	3.12	0.049
	(2) $Y = 1.533 - 0.011 \times RH - 0.001 \times P$	0.55	−35.36	1.36	0.459
	(3) $Y^* = 0.07 \times RH + 0.05 \times Tmin - 1.79 \times DPV$	0.61	−36.72	0.00	0.492
Total	(1) $Y = 4.087 - 0.037 \times RH$	0.24	−150.00	8.13	0.079
	(2) $Y^* = 5.195 - 0.051 \times RH - 0.995 \times DPV$	0.34	−158.13	0.00	0.256
	(3) $Y^* = 4.087 - 0.037 \times RH - 0.01 \times Tmin - 0.67 \times DPV$	0.35	−158.09	0.04	0.666

Y: litterfall production; Y* indicates multicollinearity between explanatory variables ($VIF \geq 2$); Y'': model including non-significant parameters. The best model for each case is shown in boldface. P: precipitation, RH: relative humidity, Tmean: mean temperature, Tmin: minimum temperature, ACTmax: cumulative maximum temperature, ACTmin: cumulative minimum temperature, WG: wind gusts, DPV: vapor-pressure deficit, R²_{aj}: adjusted coefficient of determination; AIC: Akaike's information criterion, Δ AIC: Akaike delta score, ω_i: Akaike weight.

4. Discussion

The goal of this study was to assess how forest successional age, topography, vegetation structure, and climatic variables influence seasonal and interannual variations in litterfall production over a five-year period in a tropical dry forest (TDF). We expected litterfall production (1) to increase with successional age associated with basal area or aboveground biomass of deciduous species; (2) to be higher on flat than on sloping sites; and (3) to be negatively associated with precipitation and positively with maximum temperature and vapor-pressure deficit across months, seasons, and years. Our results showed large annual, seasonal, and monthly variations in litterfall production, which were related to various environmental factors including precipitation (negative correlation), wind speed (positive correlation), and maximum temperature (mostly positive correlation). As expected, litter production was higher in the dry versus rainy season and on flat versus sloping sites (overall, but not in most years); also, litter production increased with successional age and was positively correlated with aboveground biomass of deciduous species but negatively correlated with basal area of evergreen species. Below, we discuss our results in detail in light of the proposed hypotheses and relate them to previous findings as well as to predicted trends of climate change.

4.1. Annual Litterfall Production

Annual litterfall production ranged between 4.94 and 6.17 Mg/ha/year, with an average value of 5.65 Mg/ha/year. These values are well within the range (3.8–7.70 Mg/ha/year) reported by previous studies in TDF [16,21,25,27,28,81] (Appendix C). Souza et al. [81] studied TDFs of different successional ages in Brazil and reported litterfall production values lower (4.0–4.5 Mg/ha/year) than those found in our study. In contrast, Martínez-Yrizar and Sarukhan [27] reported higher values (6.5 Mg/ha/year) for a mature dry forest in Jalisco, Mexico.

4.2. Influence of Successional Age and Vegetation Structure on Litterfall Production

Our results partially supported hypothesis 1. As expected, litterfall production increased with successional age, being lower in the youngest age class, where vegetation structure is still poorly developed. However, and contrary to our expectations, litterfall production in age class IV (60–79 years) was lower than in age classes III (18–25 years) and V (≥ 80 years), which generally did not differ from each other. Average values of total aboveground biomass (14.5 Mg/ha), tree height (4.59 m), stem diameter (5.85 cm), and total basal area (6.21 m²/ha) were also lower in age class I (3–5 years) than in the older classes ($F \geq 6.816$; $p \leq 0.006$ in all cases), and most of these variables did not differ between age classes III to V (≥ 18 years)—see also [82]. Lawrence [21] found no significant differences in litterfall production between 12 to 25-year-old and mature tropical forests in the Yucatan Peninsula.

These results evidence a rapid increase in structural variables and litterfall production during the first 25 years of succession. This is consistent with findings from previous studies [46,83,84] and suggests that the structure of TDF can recover rapidly, likely due to the low structural complexity of these forests [46]. These results also indicate that successional age has a marked effect on litterfall production, as reported in other studies on tropical forests [16,21,81,85]. Other factors that might also explain the rapid recovery of litterfall production in our study site include its high soil fertility [47,63] and low intensity of land use associated with traditional slash-and-burn agriculture.

Annual litterfall production was positively related to the aboveground biomass of deciduous species (which account for 57.3–83.8% of the total basal area) and negatively related to the basal area of evergreen species. This indicates that the phenological strategy of plants in this seasonally dry tropical forest had a major and differential effect on litterfall production. Deciduous species characteristically exhibit a water-stress avoidance strategy consisting of shedding their leaves during the dry season (and, in some cases, storing water in stems and roots) to reduce water loss by transpiration and to avoid cavitation [86–89]. The leaves of these species generally show photosynthetic rates and nitrogen contents higher than those of evergreen species [51,87–89]. Thus, our results suggest that the rapid recovery of litterfall production during secondary succession in these forests might have a synergistic effect on the recovery of soil fertility through the supply of litter from deciduous species (especially legume species), which have high foliar nitrogen contents and low C/N ratios that favor rapid litter decomposition [26,90,91].

On the other hand, the low litterfall production values recorded in successional age class IV (60–79 years) compared to those in age classes III (18–25 years) and V (≥ 80 years) were unexpected, especially since vegetation structure did not differ substantially among age classes III–V, as mentioned above. This unexpected result suggests a lower net primary productivity in age class IV compared to that in classes III and V, likely related to a negative net balance in the demographic processes underlying the gain (recruitment and growth) and loss (mortality) of biomass. Estimating demographic rates is beyond the scope of our study; however, we obtained preliminary estimates of the net balance between the number of plants that recruited and those that died over the entire study period in age classes III, IV, and V. Although the net balance was negative (deaths > recruits) in the three age classes, there were significant differences between them ($F = 3.572$; $p = 0.037$), being more negative in age class IV (−236 plants) than in age classes III and V (−178 and −112 plants, respectively). Future studies should address the demographic processes as well as the plant life-history strategies and functional traits underpinning these patterns.

4.3. Influence of Topography and Vegetation Structure on Litterfall Production

Our results partially supported hypothesis 2. As expected, litterfall production was significantly higher on flat than on sloping sites over the entire study period. However, significant differences between topographic positions were found only in one of the five years of the study. These results demonstrate the importance of conducting multi-year studies to identify overall patterns beyond the interannual variations that are common in seasonally dry tropical forests. In another multi-year study of a TDF on the Pacific coast of Mexico, Martínez-Yrizar and Sarukhán [27] also found litterfall production to be higher on flat than on sloping sites.

Previous studies on TDFs in the Yucatán Peninsula [63,82,92,93] reported higher tree height, aboveground biomass, and basal area, but lower tree density, on flat versus sloping sites. Exploratory analyses carried out as part of our study showed that biomass, basal area, and stem density of deciduous species were higher on flat than on sloping sites ($F \geq 9.509$, $p \leq 0.037$). Flat sites provide more favorable conditions for vegetation development since they have deeper soils than sloping sites [62]. Besides the above, runoff and erosion take away water, mineral nutrients, and soil particles from sloping sites and deposit them on flat sites at the bottom. More favorable microenvironmental conditions on flat sites would favor the establishment of deciduous species, which often show acquisitive strategies that require a high availability of soil resources. Sanaphre et al. [50] found a higher proportion of deciduous species on flat areas and of evergreen species on sloping sites, within the same study area. A higher proportion of evergreen species may entail a lower litterfall production on sloping sites. However, Nafarrate-Hecht et al. [94] and Huechacona-Ruíz [15] found no significant effects of topography on leaf area index or litterfall production, respectively, in the same study area. More detailed studies would be necessary to elucidate the causes underlying these contrasting litterfall production patterns in flat vs. sloping sites. Such studies should examine the factors that co-vary with slope, such as water availability and soil properties, as well as other key factors such as slope aspect and the proportion of deciduous/evergreen species.

4.4. Temporal Variation in Litterfall Production and Its Relationship with Climatic Variables

Our results partially supported hypothesis 3, namely that temporal variations in litterfall production would be negatively correlated with precipitation and positively with maximum temperature and vapor-pressure deficit (VPD). Annual litterfall production was indeed negatively correlated with precipitation, while seasonal production was positively related to maximum temperature (Table 4). However, seasonal and monthly litterfall production were also related to other climatic variables. For instance, seasonal litterfall production was positively correlated with wind speed (Table 4), while monthly litterfall production was related overall to relative humidity (negative correlation) and, in some years, to minimum or mean temperature—negative correlations (Table 5).

As expected, litterfall production was higher in the dry season and was related to low values of precipitation and high values of VPD and maximum temperature, i.e., to limiting conditions for photosynthesis and other metabolic processes. Under these circumstances, most plants in this type of forest respond by shedding their leaves to avoid water loss by transpiration and cope with water stress [18,53,95,96]. Moreover, wind causes additional shedding of leaves and branches, reduces relative humidity, and causes the soil to dry out (especially at high temperatures), leading to a high VPD [97,98]. Previous studies have documented that litterfall production during the dry season may account for 25 to 100% of total annual production [20,85,99–101]. In our study, litterfall production during the dry season accounted for 67.5% of the total production (over the entire study period), with annual values ranging between 57.5 and 77.5%. These values are similar to those reported by Aryal et al. [16], who documented that dry season production accounted for 70% of the total annual litterfall production in Calakmul, south of the Yucatán Peninsula, Mexico.

Average monthly litterfall production over the study period was 0.460 Mg/ha/month and was negatively related to relative humidity. However, the influence of climatic factors varied among years, with maximum (positive or negative correlation) and minimum temperature (negative correlation)

being the variables most closely related to average monthly litterfall production. These results show that monthly litterfall production is influenced by small variations in temperature, precipitation, and other climatic variables including VPD (and possibly solar radiation), as reported in previous studies [16,19,25,27,29,30].

Climate change models for the period 2010 to 2039 project a >2 °C increase in mean annual temperature, more intense and longer droughts, a slight decrease in annual precipitation, and more frequent and intense tropical storms and hurricanes for Mexico under the A2 emissions scenario, which assumes large regional differences in economic and population growth [102]. Based on the relationships between litterfall production and climatic variables considered in our study, under this climate change scenario, an increase in both the proportion of deciduous species and litterfall production would be expected in the TDF that we examined, but not necessarily in the rate of litter decomposition, due to the likely adverse effects of the altered environmental conditions on decomposers.

On the other hand, increased rates of forest disturbance due to logging, land use change, extractive activities, and forest fires are also projected [103–106]. This would lead to forest cover loss, especially of older successional forests (which are commonly targeted by human activities), and an increase in the proportion of young secondary or disturbed forests, all of which would lead to lower litterfall production and decomposition—likely overriding potential climate-change-driven increases in litterfall production. Given these scenarios, there is an urgent need to document the temporal changes in the various components of primary productivity and in the biogeochemical cycles related to litterfall production and decomposition, as well as their relationships with climatic variables and environmental conditions.

5. Conclusions

As we expected, successional age, seasonality, and topography (slope) are drivers of litterfall production. This production was higher in the dry season, increased with successional age (recovering in just 18–25 years), and was positively correlated with the aboveground biomass of deciduous species and negatively with the basal area of evergreen species. This suggests that the nutrients contained in litter are recycled rapidly in this landscape, which consists of a matrix of TDF interspersed with low-intensity land uses.

Litterfall production over the entire study period was higher on flat versus sloping sites, as environmental conditions in the latter are less favorable for vegetation development. Protecting and conserving forests on sloping areas should be prioritized in order to reduce erosion and soil degradation.

The temporal patterns of litterfall production were related to several climatic variables including precipitation (negative correlation), maximum temperature, wind speed, and VPD (positive correlations). This suggests that litterfall production (but not necessarily its decomposition rate) might increase with climate change. However, land use changes would reduce litterfall production and decomposition, impairing the capability of TDF to sequester and store carbon and compromising the biogeochemical cycles that regulate the long-term sustainability of these ecosystems and the services they provide to human societies. Further multi-year studies such as the one reported here are necessary to broaden our understanding of the dynamics and functioning of tropical dry forests and to inform the design of more effective strategies for their conservation, restoration, and sustainable management.

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Appendix A

Table A1. Characteristics of the sampling clusters in which litterfall production was monitored. The effect of slope was evaluated only in age classes IV and V, using the average slope of the three plots of each cluster that fell in the predominant topographic position in the cluster (*).

Cluster	Age as of 2013 (Years)	Age Class (Years)	Predominant Topographic Position	Average Slope (%)
21	3	I (3–5)	Flat	2.01
22	4	I (3–5)	Flat	1.22
23	3.5	I (3–5)	Flat	1.52
25	10	II (10–17)	Flat	0
26	17	II (10–17)	Flat	0
28	16	II (10–17)	Flat	5.01
29	18	III (18–25)	Flat	6.63
30	20	III (18–25)	Flat	0
31	24	III (18–25)	Flat	5.89
5	60	IV (60–79)	Slope *	13.41
7	65	IV (60–79)	Slope *	14.55
13	70	IV (60–79)	Flat *	3.42
2	100	V (≥80)	Slope *	15.1
8	80	V (≥80)	Flat *	5.49
20	100	V (≥80)	Flat *	3.00

Appendix B

Table A2. List of woody plant species sampled in fifteen 1-ha sampling clusters of four 0.04-ha (400 m²) plots.

No.	Species Name and Authority	Family
1	<i>Acacia dolichostachya</i> S.F. Blake	Fabaceae
2	<i>Acacia gaumeri</i> S.F. Blake	Fabaceae
3	<i>Acacia pennatula</i> (Schltdl. & Cham.) Benth.	Fabaceae
4	<i>Albizia tomentosa</i> (Micheli) Standl.	Fabaceae
5	<i>Alvaradoa amorphoides</i> Liebm.	Picramniaceae
6	<i>Amphilophium paniculatum var molle</i> (Schltdl. & Cham.) Standl.	Bignoniaceae
7	<i>Apoplanesia paniculata</i> C. Presl	Fabaceae
8	<i>Ardisia escallonioides</i> Schltdl. & Cham.	Primulaceae
9	<i>Arrabidaea floribunda</i> (Kunth) Loes.	Bignoniaceae
10	<i>Asemnantha pubescens</i> Hook. f.	Rubiaceae

Table A2. Cont.

No.	Species Name and Authority	Family
11	<i>Attilaea abalak</i> E. Martínez & Ramos	Anacardiaceae
12	<i>Bauhinia divaricata</i> L.	Fabaceae
13	<i>Bauhinia unguolata</i> L.	Fabaceae
14	<i>Bonelia macrocarpa</i> Cav.	Primulaceae
15	<i>Bourreria pulchra</i> (Millsp.) Millsp.	Ehretiaceae
16	<i>Bourreria oxyphylla</i> Standl.	Ehretiaceae
17	<i>Bunchosia glandulosa</i> (Cav.) DC.	Malpighiaceae
18	<i>Bunchosia swartziana</i> Griseb.	Malpighiaceae
19	<i>Bursera simaruba</i> (L.) Sarg.	Burseraceae
20	<i>Caesalpinia gaumeri</i> Greenm.	Fabaceae
21	<i>Caesalpinia mollis</i> (Kunth) Spreng.	Fabaceae
22	<i>Caesalpinia yucatanensis</i> Greenm.	Fabaceae
23	<i>Callicarpa acuminata</i> Kunth.	Lamiaceae
24	<i>Calyptanthes pallens</i> Griseb.	Myrtaceae
25	<i>Cardispermum halicacabum</i> L.	Sapindaceae
26	<i>Casearia emarginata</i> C. Wright ex Griseb.	Salicaceae
27	<i>Ceiba aesculifolia</i> (Kunth) Britten & Baker f.	Malvaceae
28	<i>Ceiba pentandra</i> (L.) Gaertn.	Malvaceae
29	<i>Ceiba schotti</i> Britten & Baker f.	Malvaceae
30	<i>Celtis iguanaea</i> (Jacq.) Sarg.	Cannabaceae
31	<i>Ceratophytum tetragonolobum</i> (Jacq.) Sprague & Sandwith	Bignoniaceae
32	<i>Chiococca alba</i> (L.) Hitchc.	Rubiaceae
33	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	Fabaceae
34	<i>Chlorophora tinctoria</i> (L.) Gaudich.	Moraceae
35	<i>Cissus gossypifolia</i> Standl.	Vitaceae
36	<i>Cnidocolus aconitifolius</i> (Mill.) I.M. Johnst.	Euphorbiaceae
37	<i>Coccoloba acapulcensis</i> Standl.	Polygonaceae
38	<i>Coccoloba diversifolia</i> Jacq.	Polygonaceae
39	<i>Coccoloba spicata</i> Lundell	Polygonaceae
40	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	Bixaceae
41	<i>Colubrina elliptica</i> (Sw.) Brizicky & W.L. Stern	Rhamnaceae
42	<i>Colubrina greggii</i> S. Watson	Rhamnaceae
43	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae
44	<i>Cordia gerascanthus</i> L.	Boraginaceae
45	<i>Cosmocalyx spectabilis</i> Standl.	Rubiaceae
46	<i>Croton glabellus</i> L.	Euphorbiaceae
47	<i>Croton reflexifolius</i> Kunth	Euphorbiaceae
48	<i>Cydista diversifolia</i> (Kunth) Miers	Bignoniaceae
49	<i>Cydista heterophylla</i> Seibert	Bignoniaceae
50	<i>Cydista potosina</i> (K. Schum. & Loes.) Loes.	Bignoniaceae

Table A2. Cont.

No.	Species Name and Authority	Family
51	<i>Cynanchum schlechtendalii</i> (Decne.) Standl. & Steyerm.	Apocynaceae
52	<i>Diospyros anisandra</i> S.F. Blake	Ebenaceae
53	<i>Diospyros cuneata</i> Standl.	Ebenaceae
54	<i>Diospyros salicifolia</i> Humb. & Bonpl. ex Willd.	Ebenaceae
55	<i>Diospyros verae-crucis</i> (Standl.) Standl.	Ebenaceae
56	<i>Diospyros yatesiana</i> Standl. ex Lundell	Ebenaceae
57	<i>Diphysa carthagenensis</i> Jacq.	Fabaceae
58	<i>Ehretia tinifolia</i> L.	Ehretiaceae
59	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Fabaceae
60	<i>Erythrina standleyana</i> Krukoff	Fabaceae
61	<i>Erythroxyllum rotundifolium</i> Lunan	Erythroxyllaceae
62	<i>Eugenia axillaris</i> (Sw.) Willd.	Myrtaceae
63	<i>Eugenia buxifolia</i> (Sw.) Willd.	Myrtaceae
64	<i>Exostema caribaeum</i> (Jacq.) Roem. & Schult.	Rubiaceae
65	<i>Exostema mexicanum</i> A. Gray	Rubiaceae
66	<i>Forchhammeria trifoliata</i> Radlk.	Resedaceae
67	<i>Gliricidia sepium</i> Kunth ex Steud.	Fabaceae
68	<i>Guettarda combsii</i> Urb.	Rubiaceae
69	<i>Guettarda elliptica</i> Sw.	Rubiaceae
70	<i>Guettarda gaumeri</i> Standl.	Rubiaceae
71	<i>Gymnopodium floribundum</i> Rolfe	Polygonaceae
72	<i>Hampea trilobata</i> Standl.	Malvaceae
73	<i>Helicteres baruensis</i> Jacq.	Malvaceae
74	<i>Heliocarpus donnellsmithii</i> Rose	Malvaceae
75	<i>Heteropterys brachiata</i> (L.) DC.	Malpighiaceae
76	<i>Heteropterys laurifolia</i> (L.) A. Juss.	Malpighiaceae
77	<i>Hippocratea celastroides</i> Kunth	Celastraceae
78	<i>Hippocratea excelsa</i> Kunth	Celastraceae
79	<i>Hiraea reclinata</i> Jacq.	Malpighiaceae
80	<i>Jacquinia macrocarpa</i> Cav.	Primulaceae
81	<i>Karwinskia humboldtiana</i> (Schult.) Zucc.	Rhamnaceae
82	<i>Krugiodendron ferreum</i> (Vahl) Urb.	Rhamnaceae
83	<i>Laetia thamnia</i> L.	Salicaceae
84	<i>Leucaena leucocephala</i> (Lam.) de Wit	Fabaceae
85	<i>Lonchocarpus</i> sp Kunth	Fabaceae
86	<i>Lonchocarpus hondurensis</i> Benth.	Fabaceae
87	<i>Lonchocarpus longistylus</i> Pittier	Fabaceae
88	<i>Lonchocarpus rugosus</i> Benth.	Fabaceae
89	<i>Lonchocarpus xuul</i> Lundell	Fabaceae
90	<i>Lonchocarpus yucatanensis</i> Pittier	Fabaceae

Table A2. Cont.

No.	Species Name and Authority	Family
91	<i>Luehea candida</i> (DC.) Mart.	Malvaceae
92	<i>Luehea speciosa</i> Willd.	Malvaceae
93	<i>Lysiloma latisiliquum</i> (L.) Benth.	Fabaceae
94	<i>Macfadyena unguis-cati</i> (L.) A.H. Gentry	Bignoniaceae
95	<i>Machaonia lindeniana</i> Baill.	Rubiaceae
96	<i>Malpighia glabra</i> L.	Malpighiaceae
97	<i>Manihot aesculifolia</i> (Kunth) Pohl	Euphorbiaceae
98	<i>Mansoa verrucifera</i> (Schltdl.) A.H. Gentry	Bignoniaceae
99	<i>Melicoccus oliviformis</i> Kunth	Sapindaceae
100	<i>Mimosa bahamensis</i> Benth.	Fabaceae
101	<i>Montanoa atriplicifolia</i> (Pers.) Sch. Bip.	Asteraceae
102	<i>Neea psychotrioides</i> Donn. Sm.	Nyctaginaceae
103	<i>Neea</i> sp. Ruiz & Pav.	Nyctaginaceae
104	<i>Neomillspaughia emarginata</i> (H. Gross) S.F. Blake	Polygonaceae
105	<i>Parathesis cubana</i> (A. DC.) Molinet & M. Gómez	Primulaceae
106	<i>Parmentiera millspaughiana</i> L.O. Williams	Bignoniaceae
107	<i>Phyllanthus acuminatus</i> Vahl	Phyllanthaceae
108	<i>Piscidia piscipula</i> (L.) Sarg.	Fabaceae
109	<i>Pisonia aculeata</i> L.	Nyctaginaceae
110	<i>Pithecoctenium crucigerum</i> (L.) A.H. Gentry	Bignoniaceae
111	<i>Platymiscium yucatanum</i> Standl.	Fabaceae
112	<i>Plumeria obtusa</i> L.	Apocynaceae
113	<i>Psidium sartorianum</i> (O. Berg) Nied.	Myrtaceae
114	<i>Psychotria microdon</i> (DC.) Urb.	Rubiaceae
115	<i>Randia longiloba</i> Hemsl.	Rubiaceae
116	<i>Randia obcordata</i> S. Watson	Rubiaceae
117	<i>Randia truncata</i> Greenm. & C.H. Thomps.	Rubiaceae
118	<i>Sabal japa</i> C. Wright ex Becc.	Arecaceae
119	<i>Sabal yapa</i> C. Wright ex Becc.	Arecaceae
120	<i>Samyda yucatanensis</i> Standl.	Salicaceae
121	<i>Schoepfia schreberi</i> J.F. Gmel.	Schoepfiaceae
122	<i>Senna atomaria</i> (L.) H.S. Irwin & Barneby	Fabaceae
123	<i>Senna racemosa</i> (Mill.) H.S. Irwin & Barneby	Fabaceae
124	<i>Senna villosa</i> (Mill.) H.S. Irwin & Barneby	Fabaceae
125	<i>Sideroxylon obtusifolium</i> (Humb. ex Roem. & Schult.) T.D. Penn.	Sapotaceae
126	<i>Solanum erianthum</i> D. Don	Solanaceae
127	<i>Spondias mombin</i> L.	Anacardiaceae
128	<i>Tabebuia chrysantha</i> (Jacq.) G. Nicholson	Bignoniaceae
129	<i>Talisia olivaeformis</i> (Kunth) Radlk.	Sapindaceae
130	<i>Thevetia gaumeri</i> Hemsl.	Apocynaceae

Table A2. Cont.

No.	Species Name and Authority	Family
131	<i>Thouinia paucidentata</i> Radlk.	Sapindaceae
132	<i>Trichilia glabra</i> L.	Meliaceae
133	<i>Vitex gaumeri</i> Greenm.	Lamiaceae
134	<i>Ximenia americana</i> L.	Ximeniaceae
135	<i>Zanthoxylum caribaeum</i> Lam.	Rutaceae
136	<i>Zapoteca Formosa</i> (Kunth) H.M. Hern.	Fabaceae

Appendix C

Table A3. Litterfall production values reported in the literature for different tropical dry forests.

Location	Forest Type	Production (Mg/ha/yr)	Source
Mexico	Subdeciduous	4.94–6.17	This study
Mexico	Semi-evergreen	5.20–7.10	Aryal et al. [16]
Mexico	Semi-evergreen and subdeciduous	3.80–6.80	Lawrence [21]
India	Evergreen and deciduous	5.76–8.65	Sundarapandian and Swamy [25]
Mexico	Deciduous	3.98–6.58	Martínez-Yrizar and Sarukhán [27]
Mexico	Semi-evergreen	5.00–7.70	Whigham et al. [28]
Brazil	Deciduous	4.00–4.50	Souza et al. [81]

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