Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico

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Accepted 6 September 1994

Abstract

Light canopy transmittance and the Beer-Lambert equation were utilized to assess monthly leaf area index (LAI) of a tropical deciduous forest ecosystem on the west coast of Mexico. The light transmittance coefficient \(k\) was obtained by analyzing vertical leaf and light distribution in the forest canopy. An independent LAI estimate was obtained using litterfall data. The calculated \(k\) value was 0.610±0.035 (standard error). Average maximum LAI obtained with litterfall data was 4.2 ± 0.4 m\(^2\) m\(^{-2}\). There was a significant correlation \((P<0.001, r=0.98)\) between litter-LAI estimations and those obtained with the Beer-Lambert equation. The regression explained 95% of the variation; however, light-LAI overestimated litter-LAI by a constant of 0.87±0.12 m\(^2\) m\(^{-2}\) (the slope was 1.03 and \(Y\) intercept was 0.87). The discrepancy is partially attributed to leaf retention of the few evergreen species, and perhaps leaf retention of a few deciduous species beyond the end of the litterfall collection. Maximum annual LAI was similar in both study years (4.5 ± 0.3 m\(^2\) m\(^{-2}\) in 1990 and 4.9 ± 0.4 in 1991). Minimum LAI showed considerable variation between years with similar values in the dry seasons of 1990 and 1991 (1.0 ± 0.1 m\(^2\) and 0.9 ± 0.1 m\(^2\) m\(^{-2}\), respectively), but much higher values in 1992 (2.7 ± 0.2 m\(^2\) m\(^{-2}\)). The difference is probably attributed to an atypical rainfall event in January 1992 (644 mm), which retarded leaf abscission.

Keywords: Canopy light transmittance; Light extinction coefficient; Litterfall; Seasonal tropical forest; Tropical dry forest

1. Introduction

Leaf area index (LAI) is an important structural characteristic of forests because the forest canopy is the site of significant ecosystem processes such as transpiration, rainfall interception, dry deposition, and photosynthesis. As a result, LAI has been identified as a key parameter in studying and modelling ecosystem function at local, regional and global scales (Swift et al., 1975; Parton et al., 1992). LAI varies greatly among ecosystems, ranging from less than 1 m\(^2\) m\(^{-2}\) in arid ecosystems, up to 20 in some conifer stands (Kozlowski et al., 1991). LAI also varies within ecosystems depending on site conditions, particularly water supply and soil fertility. Although LAI is well documented for temperate forests, only a few determinations have been made for tropical ecosystems (Medina and
Klinge, 1983). Data for tropical deciduous forests are particularly scarce (Murphy and Lugo, 1986a). In deciduous, and some evergreen ecosystems, LAI varies seasonally, having a maximum during the growing season and a minimum in the dormant season. Quantifying this temporal variation is important for understanding variation in the rates of many ecosystem processes (e.g. transpiration); however, data on temporal LAI variability are extremely rare (Lugo et al., 1978; Murphy and Lugo, 1986b).

A variety of methods have been used to assess LAI in forest ecosystems (Chason et al., 1991). Sampling canopy light transmittance with a portable integrating radiometer, and applying the Beer-Lambert Law has been used to estimate LAI in coniferous forests (Pierce and Running, 1988; Bolstad and Gower, 1990; Vose and Swank, 1990; Burton et al., 1991). This approach requires an estimate of canopy light extinction efficiency (k). A significant advantage of light transmittance is the ability to non-destructively quantify seasonal changes.

The objective of the present study was to quantify total LAI and to assess seasonal LAI variation in a tropical deciduous forest ecosystem using the light transmittance method.

2. Methods

2.1. Study area

The study was conducted at the Estación de Biología Chamela of the Universidad Nacional Autónoma de Mexico. Chamela is located at 19°30’N, 105°03’W in the state of Jalisco on the Pacific coast of Mexico.

The climate of the area is influenced by tropical cyclones producing a highly variable annual rainfall regime (García-Oliva et al., 1991). Mean precipitation is 707 mm (1977–1988) with more than a 500 mm difference between the wettest and the driest year (897 mm in 1989 and 374 mm in 1985). Rainfall is strongly seasonal with 80% of the annual precipitation falling between July and October, with September being the wettest month. Temperature fluctuates little during the year, averaging 25°C. Monthly mean minimum and maximum temperatures are 15.9°C (February) and 32.2°C (August), respectively (Bullock, 1988).

Soils are young, often shallow (0.5-1 m depth), and poorly structured. The parent material is mostly rhyolite. Soils are predominantly sandy loams and rocks are common in the superficial horizon. Soils have low organic matter content (mean 2.5%) and low mineral nutrient concentrations (mean exchangeable Ca²⁺, Mg²⁺, and K⁺ content is 8.7 meq per 100 g of dry soil), and pH values vary between 6.0 and 7.0 (Maass et al., 1988).

The predominant vegetation in the area is the tropical deciduous forest type of Rzedowski (1978). Lott (1985) reports 758 plant species from 107 families for the area, with Leguminosae being the most important family with 15% of the species. According to Martínez-Yrízar et al. (1992) above-ground phytomass is 85 Mg ha⁻¹. Mean canopy height is 7 m with some trees up to 15 m tall located along the river channel. The stand basal area ranges from 14.0 to 26.1 m² ha⁻¹ for trees with a diameter at breast height of over 3.0 cm.

2.2. Site description

Within the field station, five contiguous small watersheds (12–28 ha each) have been gauged for long-term ecosystem research (Sarukhán and Maass, 1990). On one of the watersheds (Watershed I), three permanent plots were previously established for detailed analyses of ecosystem processes, and they were used for the present study. The plots are distributed along the altitude gradient of the watershed, and will be referred to here as upper, middle and lower plots. Each plot is 2400 m² (80 m x 30 m) with the long axis perpendicular to the stream channel. The general characteristics of each plot are shown in Table 1. According to L.A. Pérez-Jiménez, unpublished data, 1993, the most important species on each plot are: in the upper plot, Guapira macrocarpa Miranda, Plumeria rubra L., Lonchocarpus constrictus Pitt., Bursera instabilis McVaugh and Colubrina heteroneura.
Table 1
Site characteristics of the permanent sampling plots of a tropical deciduous forest at Chamela, Jalisco, Mexico (Watershed I). LAI estimated using litterfall and specific leaf area (SLA) data. Tree density and basal area were obtained from all individuals with a diameter at breast height of over 3.0 cm

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Lower plots</th>
<th>Middle plots</th>
<th>Upper plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation*</td>
<td>m above sea level</td>
<td>60-80</td>
<td>120-140</td>
<td>140-160</td>
</tr>
<tr>
<td>Slope range*</td>
<td>degrees</td>
<td>16-30</td>
<td>8-16</td>
<td>8-16</td>
</tr>
<tr>
<td>Soil depth*</td>
<td>cm</td>
<td>25-30</td>
<td>15-25</td>
<td>40-45</td>
</tr>
<tr>
<td>Soil organic matter*</td>
<td>%</td>
<td>3.0-3.5</td>
<td>2.5-3.0</td>
<td>2.0-2.5</td>
</tr>
<tr>
<td>Tree density*</td>
<td>individuals ha$^{-1}$</td>
<td>2113</td>
<td>3225</td>
<td>2492</td>
</tr>
<tr>
<td>Basal area*</td>
<td>m$^2$ ha$^{-1}$</td>
<td>19.77</td>
<td>17.18</td>
<td>11.22</td>
</tr>
<tr>
<td>Litterfall*</td>
<td>Mg ha$^{-1}$ year$^{-1}$</td>
<td>4.5</td>
<td>3.6</td>
<td>3.5</td>
</tr>
<tr>
<td>Specific leaf area (SLA)*</td>
<td>cm$^2$ g$^{-1}$</td>
<td>203</td>
<td>188</td>
<td>154</td>
</tr>
<tr>
<td>LAI (litter-LAI)*</td>
<td>m$^2$ m$^{-2}$</td>
<td>5.4</td>
<td>3.8</td>
<td>3.3</td>
</tr>
</tbody>
</table>


Two meteorological towers were used to quantify vertical LAI distribution through the canopy profile and to develop an extinction coefficient (discussed below). One of the towers is within the sampled area, the middle plot of Watershed-I. The other two towers are located on nearby sites with forests comparable to Watershed-I. One is located on Watershed II and the other on the highest point of an access trail (Tejón) to the watersheds (about 300 m away from the sampling plots, on a small hill of 130 m above sea level).

2.3. LAI determinations

Seasonal LAI was determined from May 1990 to May 1992 using the light transmittance technique. The method is based on the relationship between leaf area and light transmittance, described by the Beer-Lambert model (Monsi and Saeki, 1953)

$$\frac{Q_t}{Q_o} = e^{-k(LAI)}$$

where $Q_t$ is the sub-canopy diffuse and beam radiation, $Q_o$ is the above-canopy radiation, and $k$ is the radiation extinction coefficient. The model assumes that the foliage is randomly distributed in the canopy, and that leaf inclination angles are spherically distributed in space. However, as discussed by Jarvis and Leverenz (1983) and Pierce and Running (1988), the Beer-Lambert equation is fairly insensitive to all but major violations of these assumptions. To validate the light transmittance approach, we compared light transmittance LAI estimates (light-LAI) with LAI estimates derived from litterfall data (litter-LAI).

2.4. Litterfall collections and specific leaf area determinations

Litterfall was collected using conical fiberglass mesh traps, 0.5 m in diameter (area 0.1963 m$^2$) and 50 cm deep (for details see Martinez-Yrizar and Sarukhán, 1990). Eight traps were located randomly on each plot, giving a total of 24 traps. Litter was collected during 1 year at monthly in-
tervals starting on June 1990. The material was stored in paper bags and oven-dried at 80°C to constant mass. One-way ANOVA was performed to test for differences between sample plots.

To determine specific leaf-area values, ten randomly selected leaves were obtained from each of the 24 litterfall traps \((N=240)\). Leaves were sampled from the November collection, which represents the peak litterfall during the year. The leaves were carefully rehydrated, unfolded, pressed, and their leaf area measured using a Licor leaf area meter. The leaves were dried at 80°C to constant mass. To validate this procedure, 250 senescent leaves (but still attached to branches) were randomly selected from trees located in the permanent plots. Leaves were pressed fresh and the leaf area measurements were made within one week of sampling, and then oven-dried for dry weight measurements. An analysis of variance was conducted to compare the two independent specific leaf-area estimates.

2.5. Light transmittance readings

Canopy transmittance of the photosynthetically active radiation was measured 1 m above the forest floor, at the same locations as the litter traps. At each of the 24 locations, ten measurements of canopy transmittance \((Q_c)\) were taken using a ‘sunfleck’ ceptometer (Decagon Devices, 1989). The ceptometer consists of a narrow (80 cm long) probe with 80 photosynthetically active radiation sensors located at 1 cm intervals (for more details on the ceptometer description and its theory of operation, see Pierce and Running, 1988). To obtain the ten measurements per trap, the ceptometer was rotated 360°, and photosynthetically active radiation readings were taken at approximately 36° intervals. Samples were obtained on cloudless days, usually between 11:00 and 13:00 h. Total incoming PAR \((Q_o)\) was measured either above the canopy or in an opening at the beginning and at the end of the sampling period. The arithmetic mean of these two readings was used as \(Q_o\) for \(Q_o/Q_c\) calculations. Measurements were made seasonally during May and September of 1990, and monthly from January 1991 to May 1992.

Within-canopy photosynthetically active radiation transmittance was measured from meteorological towers. On each tower, PAR transmittance readings were taken every meter, from the forest floor to the top of the canopy. At each level, ten readings were taken rotating the ceptometer at 36° intervals, following the same procedure as described above.

2.6. Light extinction coefficient \((k)\) determination

To obtain \(k\), vertical LAI and \(Q_o/Q_c\) profiles were obtained on each of the towers. In October 1991, when the canopy was fully developed, direct LAI determinations were obtained using the following procedure. A string and plumb-bob were placed 1 m out from the tower and lowered vertically through the vegetation profile from the top of the canopy to the forest floor. LAI was determined by counting the number of times the string touched a leaf, and summarized by 1 m height intervals. The procedure was repeated five times in a circular fashion on each tower and the arithmetic mean per interval was recorded. A regression analysis was performed on cumulative LAI vs. \(\ln(Q_o/Q_c)\), where the slope of the regression line defines \(k\). A total of 30 data points was used in the analysis and each tower provided 8–12 measurements, depending on canopy height.

An independent LAI estimate was obtained from litterfall data (litter-LAI). Only litterfall from mid-wet season to end of the dry season (September–May) was considered, since maximum canopy development is obtained in September. Leaves represent 61% and 73% of the wet and dry season total litterfall amounts, respectively (Martinez-Yrizar and Sarukhan, 1990). Therefore, to calculate the actual leaf-fall values (leaves only, not woody litter, fruits, flowers, etc.), the cumulative litterfall during the September-October period (wet season) was multiplied by a factor of 0.61, and the cumulative litterfall from the November-May period (dry season) was multiplied by 0.73. To obtain the litter-LAI value for each trap location, the total
cumulative leaf-fall was multiplied by the specific leaf area calculated for the trap.

Since most tree and shrub individuals in this forest type are deciduous, almost all of the leaves are dropped by the end of the dry season (May–June); therefore, it was possible to calculate monthly litter-LAI values. LAI for a particular month was calculated by considering the cumulative leaf fall from that particular month to the end of the dry season. Since leaves are continuously produced and dropped during the rainy season, only those months after the end of leaf production were considered. We assumed October as the end of the leaf production month since it is when litterfall abruptly increased. Correlation analysis was used to compare estimated LAI using the Beer-Lambert equation (light-LAI) with the monthly litterfall-LAI values.

3. Results and discussion

3.1. Rainfall pattern during the study period

Two very distinctive annual rainfall patterns occurred during the study period (Fig. 1). During 1990-1991, 557 mm of rain fell from June to November (553 mm), but it was followed by an extreme rainfall event of 644 mm in January 1992. Precipitation during winter months has a strong influence on the forest phenology by reducing leaf senescence and abscission, and, in some cases, stimulating new leaf production (Bullock and Solís-Magallanes, 1990; Martínez-Yrizar and Sarukhán, 1990).

3.2. Canopy photosynthetically active radiation transmittance

Photosynthetically active radiation measurements were highly sensitive to canopy phenology and vertical distribution of foliage. Fig. 2 shows $Q_o/Q_o$ profiles measured for wet and dry seasons on the tower located on watershed I (middle plot). Minimum photosynthetically active radiation transmittance was observed during the wet season in both years (October). Maximum transmittance was observed during the 1990-1991 dry season (April 1991); however, the rainfall event of January 92 delayed leaf senescence and abscission, thus reducing photosynthetically active radiation transmittance during the 1991-1992 dry season (April 1992).

The same seasonal pattern was observed on the other two permanent plots. Also, consistently higher PAR transmittance was observed in the
Fig. 2. Light transmittance along the canopy vertical profile of a tropical deciduous forest in Chamela, Jalisco, Mexico. $Q_l/Q_o$ is the sub-canopy/above-canopy PAR ratio. Sampling was conducted during the dry (April) and wet (October) seasons.

upper and middle plots, compared with the lower plot.

3.3. Canopy light extinction coefficient ($k$)

Vertical LAI distributions determined by the plumb method are shown in Fig. 3. Differences between towers may reflect variation in species composition and stand structure, resulting from differences in topography and water availability. For example, the Watershed-II tower site was located next to an ephemeral stream. As a result, the Watershed-II tower site contains taller trees and different species than those found at the other two towers sites.

The regression analysis between the cumula-
LAI vs. Light Transmittance

\[ \ln \left( \frac{Q_i}{Q_o} \right) = -0.61 \text{ Cum LAI} \]
\[ r^2 = 0.78 \, (p > 0.05) \]

Cumulative LAI (m^2/m^2)

Fig. 4. Fitted line from the regression analysis between cumulative LAI (obtained by the plumb method) and canopy transmittance \((Q_i/Q_o)\) to obtain the light extinction coefficient \((k)\) for a tropical deciduous forest at Chamela, Jalisco, Mexico.

3.4. Litterfall, specific leaf area, and litter-LAI estimations

Annual litterfall was significantly greater \((0.05 > P > 0.025)\) than on the lower plot (4.5 Mg ha\(^{-1}\)) compared with the middle and upper plots (3.6 Mg and 3.5 Mg ha\(^{-1}\), respectively). Maximum litterfall occurred between November and December (Fig. 5). During these 2 months, more than 50% of the leaves in the upper and middle plots fell, whereas in the lower plot the percentage was 38%. Thus, leaf production was both higher and persisted longer on the lower plot.

Annual litterfall for the watershed (averaging all three plots) was 3.9 ± 0.2 Mg ha\(^{-1}\). This value is within the 6 year (June 1992–May 1988) average range of annual litterfall values (3.4-4.7 Mg ha\(^{-1}\)) in all five watersheds at Chamela, obtained from 168 litter traps (A. Martínez-Yrizar et al., unpublished data, 1988).

Average specific leaf area from leaves collected from the litter-traps was 182 ± 51 cm\(^2\) g\(^{-1}\). This value did not significantly differ from the average specific leaf area from senescent leaves collected from the trees (184 ± 75 cm\(^2\) g\(^{-1}\)). A pattern of decreasing specific leaf area with increasing altitude was observed: 203 cm\(^2\), 188 cm\(^2\), and 154 cm\(^2\) g\(^{-1}\) for the lower, middle, and upper plots, respectively. However, the differences between plots were not statistically significant \((0.25 > P > 0.10)\). Our specific leaf area values are high, but close to the average specific leaf area value of 195 cm\(^2\) g\(^{-1}\) for tropical deciduous forest trees reported by Medina and Klinge (1983).

Average annual maximum LAI obtained using litterfall data (litter-LAI) was 4.2 ± 0.4 m\(^2\) m\(^{-2}\). It was slightly but significantly higher \((0.10 > P > 0.05)\) in the lower plot than in the middle and upper plots (5.4 ± 0.7 m\(^2\) m\(^{-2}\), 3.8 ± 0.5 m\(^2\) m\(^{-2}\), and 3.5 ± 0.5 m\(^2\) m\(^{-2}\), respectively). There was a significant correlation \((r=0.98, P<0.001)\) between litter-LAI estimations and those obtained with the Beer-Lambert equation (light-LAI, Fig. 6). The regression
Fig. 5. Litterfall dynamics of a tropical deciduous forest at Chamela, Jalisco, Mexico. Sampling was conducted from June 1990 to May 1991 on three permanent 80 m x 30 m plots on Watershed I. The vertical bars indicate ± 1 SE.

Fig. 6. Correlation and fitted line of regression between LAI from litterfall data (litter-LAI) and LAI from light transmittance measurements (light-LAI) in a tropical deciduous forest at Chamela, Jalisco, Mexico.

equation explained 95% of the variation; however, light-LAI was greater than litter-LAI by a constant of 0.87 ± 0.12 m² m⁻² (the slope was 1.03 ± 0.05). The greater LAI predicted by the light technique may reflect LAI of evergreen species, and perhaps leaf retention of a few deciduous species beyond the end of the litterfall collection. In both cases, the light-LAI technique should provide a better estimate of stand LAI because it is based on the actual amount of foliage in the canopy.

3.5. Seasonal variations of light-LAI

Seasonal LAI calculated using the Beer-Lambert equation and the monthly $Q_o/Q_i$ recording from the permanent plots are shown in Fig. 7.
Seasonal Pattern of Leaf Area Index

Fig. 7. Seasonal LAI (determined by the light transmittance method) of a tropical deciduous forest at Chamela, Jalisco, Mexico. Sampling was conducted from May 1990 to May 1991, on three permanent 80 m x 30 m plots at Watershed I. The line quantifies the mean of the three plots (solid line shows the monthly sampling period, dashed line shows the 4 month sampling period).

The lower plot had consistently higher light-LAI than middle and upper plots. This pattern is the result of differences in site characteristics since deeper soils at lower slope positions result in higher soil moisture conditions and therefore longer leaf retention.

Light-LAI increases at the beginning of the rainy season, reaches a brief plateau during the August-October period, and then slowly decreases toward the end of the dry season. The average yearly maximum light-LAI for Ws-I was 4.7 m² m⁻² which was observed in September. In the 1990 and 1991 dry seasons, average annual minimum light-LAI was 1.0±0.1 m² m⁻² which occurred toward the end of the dry season (April-May). However, in the 1992 dry season, winter storms promoted leaf maintenance for a longer period, raising LAIs to 2.67±0.2 m² m⁻² in all plots.

Murphy and Lugo (1986b) report seasonal LAIs for tropical deciduous forest at Guanica, Puerto Rico (average annual precipitation of 860 mm). At their site, maximum LAI was 4.3 m² m⁻² during a wet period (July 1981), and minimum was 2.1 during the dry period (March 1982). The yearly rainfall variability in the vicinity of Guanica, explains the highly variable year-to-year LAI values. They also mention that only 26% of the species in the Guanica site are completely deciduous, which explains why minimum LAI never became less than 2 m² m⁻².

Ogawa et al. (1961) reports a higher LAI for a dry monsoon forest at Ping Kong, Thailand (6.6 m² m⁻²). Greater rainfall in Ping Kong (1300 mm) than in Chamela, may explain this higher LAI value.

Usually, a single LAI value is used to characterize ecosystem canopy development. However, LAI can vary considerably within the year, particularly in deciduous ecosystems. Since monthly LAI values are rarely assessed, it has been suggested that LAI should be supplemented with an indication of leaf duration to obtain a more precise parameter of canopy development (Medina and Klinge, 1983). Our results show that the ceptometer can be used to quantify seasonal LAI dynamics in dry tropical forests. At Chamela, leaves usually remain on trees during a 7-8 month period (June to January), but LAIs are higher than 4 m² m⁻² only during 2.5-3.5 months of the year. Leaves also change their functional properties during the growing season affecting processes such as photosynthesis, herbivory, gas exchange or rainfall interception. Further studies are needed to characterize seasonal changes in the quality of the foliage.
Acknowledgments

Laboratory and field work help from Alberto Hernandez, Rocío Esteban, Patricia Centeno, Julia Benitez and Ana Isabel Domínguez is gratefully acknowledged. We also thank Peter Vitousek, J. Douglas Deans and another anonymous referee for critically reviewing the manuscript; to Alfredo Pérez-Jiménez for unpublished information about site characteristics; and to Estación de Biología Chamela (Instituto de Biología-UNAM) for logistic support. Funding for this study came from DGAPA-UNAM, CONACYT and from the USDA-FS Coweeta Hydrologic Laboratory.

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