Seasonal balance and vertical pattern of photosynthetically active radiation within canopies of a tropical dry deciduous forest ecosystem in Mexico

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Abstract: Major components of the flux density of global photosynthetically active radiation (PAR) were measured above and within canopies in a tropical deciduous forest on the Pacific coast of Mexico. At each of 69 locations grouped along a topographic sequence the PAR reflected from the top of the canopy, the vertical profile of transmittance, and the reflectance from the ground, were measured as many as four times in the year, including the extremes of the wet and dry seasons. With these observations an annual balance of the portion of PAR radiation reflected and absorbed by the canopy and ground was assembled and the detailed spatial and temporal dynamics of PAR within canopy layers were estimated. Canopy stature declined along the topographic sequence and the shape of the transmittance profiles reflected this. In locations of declining moisture availability the fraction of PAR absorbed by the ground increased and the fraction absorbed by non-foliar tissues decreased. Seasonal variation in canopy structure was the dominant influence on the partitioning of radiation – spatial variation was less important. Of a total annual PAR input of 15 200 mol m^{-2}, about 95% of incident PAR was absorbed, 50% by leaves, 25% by non-foliar tissues and 20% by the ground. The remaining 5% was reflected by the top of the canopy.

Key Words: absorbance, canopy structure, Chamela, light profile, transmittance, reflectance, seasonality

INTRODUCTION

Solar radiation incident on a plant canopy may be reflected, transmitted or absorbed. The partitioning of energy into these components depends on the position of the sun and atmospheric conditions but primarily on structural and optical characteristics of the canopy (Campbell & Norman 1998). The details of canopy radiation exchange have an important influence on productivity and climate at local and regional levels (Gash & Shuttleworth 1991, Zhang *et al.* 2001). To date, however, detailed knowledge about radiative characteristics of natural forests is scarce (Baldocchi & Collineau 1994, Parker 1995).

Canopy light environments vary on many spatial and temporal scales but are best understood for photosynthetically active radiation (PAR, 400–700 nm) at the level of the forest floor and on a diurnal pattern (Battaglia *et al.* 2003, Brown & Parker 1994,

Chazdon & Fetcher 1984, Gholz *et al.* 1991, Pearcy 1990). PAR is the energy source for carbon gain and its distribution in vegetation canopies influences the organization, photosynthetic and morphological characteristics of leaves (Givnish 1988, Ellsworth & Reich 1993). Vertical light profiles are in turn influenced by optical properties of leaves, leaf angle, leaf area and its vertical organization. These canopy characteristics determine the radiation exchange with the environment, and therefore have an important role in controlling leaf and soil temperature, microclimate (e.g., vertical gradients of air temperature and vapour pressure deficit), and many dependent biological processes (Aber & Federer 1992, Norman 1979).

The vertical pattern of light attenuation is rarely known because of the difficulties of making measurements in three dimensions. Most reported measurements have considered only one or few locations (Maass *et al.* 1995, Torquebiau 1988, Vierling & Wessman 2000, Vose *et al.* 1995, Wirth *et al.* 2001, Yoda 1978). Therefore, mean conditions are not well known and spatial variability is not generally assessable. Temporal observations are also

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uncommon, and when taken are often restricted to light transmission to the understorey at few locations (Brown & Parker 1994, Constabel & Lieffers 1999). Lack of such detail is problematic in highly seasonal situations, such as in tropical deciduous forests (TDF), where canopy structure undergoes extreme changes annually (Lee 1989).

TDF is characterized by a highly seasonal rainfall pattern, which controls many ecosystem processes (García-Méndez *et al.* 1991, Jaramillo & Sanford 1995, Martínez-Yrizar & Sarukhán 1990). TDF represents 42% of all intratropical vegetation (Murphy & Lugo 1995) and has been subjected to extensive conversion into cattle pasture and agricultural use, causing a major shift in ecosystem functioning (García-Oliva *et al.* 1994, Jaramillo *et al.* 2003, Maass 1995). Knowledge about spatial and temporal characteristics of the radiation balance and canopy structure is an important basis for understanding local and regional effects of changes in vegetation cover on ecosystem processes.

Here we describe the spatial and seasonal variation in reflection, attenuation and absorption of visible light within several TDF canopies and estimate the annual balance of PAR flux components. We concentrate on the vertical distribution of these components in canopies of contrasting structure along a gradient of moisture availability. Our approach is to combine probabilities of PAR fate in these canopies with information on the seasonal course of PAR input to estimate the seasonal and vertical disposition of PAR radiation.

METHODS

The study was conducted at the Estación de Biología Chamela in the Chamela-Cuixmala Biosphere Reserve (Ceballos *et al.* 1999). The field station is located 2 km inland from the Pacific coast of Mexico (19°30′N, 105°03′W). The climate is warm (mean annual temperature 24.6 °C; 1978–2000); the influence of tropical cyclones produces a highly variable and seasonal rainfall regime (Bullock 1986, García-Oliva *et al.* 2002). A 6–8-mo dry period extends from November to mid June; August and September are the wettest months. Mean annual precipitation is 788 mm (1977–2000, García-Oliva *et al.* 2002). Annual insolation is about 7900 MJ m^{-2} y^{-1} (Barradas 1991), but varies locally depending on slope, aspect and horizon (Galicia *et al.* 1999). The landscape is dominated by low-elevation (< 200 m asl) steep hills with convex slopes (López-Blanco *et al.* 1999). Soils are young, weakly developed Regosols (luvi-eutric) on a granite substrate (Cotler *et al.* 2002).

The TDF is a highly diverse and dense vegetation type with a well-developed understorey of shrubs (Lott 1993, Lott *et al.* 1987, Segura *et al.* 2003). A strong

seasonality in rainfall (Bullock 1986, García-Oliva *et al.* 2002) induces most species in the Chamela TDF to drop their leaves to resist drought (Bullock & Solís-Magallanes 1990). There is a markedly seasonal pattern of leaf cover (Bullock & Solís-Magallanes 1990), litterfall (Martínez-Yrízar & Sarukhán 1990) and leaf area index (Maass *et al.* 1995).

Structural and functional characteristics of the Chamela forest have been monitored continuously for more than 20 y on five contiguous small watersheds (Maass *et al.* 2002a). Topography has marked ecological effects in these watersheds. Species richness (Balvanera *et al.* 2002), LAI (Maass *et al.* 1995), litterfall (Martínez-Yrízar & Sarukhán 1990) and net primary production (Martínez-Yrízar *et al.* 1996) decline with increasing elevation. Also, soil P availability and mean foliar P concentrations are higher at the Lower than at the Upper site (Renteria *et al.* in press). Potential insolation depends strongly on slope, aspect and local horizon (Galicia *et al.* 1999).

The present study was conducted in one watershed, designated Watershed 1, 15 ha in area, between 60 and 160 m in elevation, and oriented E–W. The watershed was divided in three elevation sectors based on its geological structure (López-Blanco *et al.* 1999). One permanent plot (80 × 30 m) was located on each sector. The plots were oriented perpendicular to the drainage channel so that one half of each plot faced north and the other faced south. Each plot was subdivided into 24 10 × 10-m subplots, except in the Upper plot, which had 21. Litter traps (0.5-m-diameter circle with opening at 1 m above ground), located in the centre of each subplot, were used as the sites of the light measurements. Site characteristics of each plot, henceforth designated as Upper, Middle and Lower, are summarized in Table 1.

Chamela has a 'dense deciduous forest, 4–15 m tall, with a well developed understory of shrubs on the slopes' and 'taller semideciduous forest along larger arroyos' (Lott *et al.* 1987). In the Upper plot the most important species are: *Guapira macrocarpa*, *Plumeria rubra*, *Lonchocarpus constrictus*, *Bursera instabilis* and *Colubrina*

Table 1. Characteristics of the permanent plots located in the tropical deciduous forest in Watershed 1 in Chamela, Jalisco, Mexico. Minimum diameter for the stem census was 5.0 cm.

| | Sampling plots | | |
Parameter	Lower	Middle	Upper
Elevation (m asl)[1]	70	130	150
Slope range (°) [1]	16–30	8–16	8–16
Live stem density (ind ha^{-1})[3]	567	1273	886
Live basal area (m^2 ha^{-1})[3]	10.7	8.1	7.9
Average tree height (m)[2]	6.2	4.9	5.1
Maximum tree height (m)[2]	25.0	14.0	9.0
Leaf Area Index (m^2 m^{-2})[2]	5.4	3.8	3.3

[1] Galicia *et al.* (1999), [2] Maass *et al.* (1995), [3] Segura *et al.* (2003).

heteroneura; in the Middle plot, *Guapira macrocarpa, Lonchocarpus eriocarinalis, Plumeria rubra, Piptadenia constricta* and *Bursera instabilis*; and in the Lower plot, *Thouinidium decandrum, Guapira macrocarpa, Astronium graveolens, Trichilia trifolia* and *Casearia corymbosa* (A. Pérez-Jiménez, *pers. comm.*). Species names follow Lott (1993).

Light measurements

At each sampling location in each plot, we measured vertical profiles of PAR flux under clear skies near midday using quantum sensors (model LI-190SB, Li-Cor Inc., Lincoln NB, USA). Canopy light measurements were obtained with two access systems. In the Upper and Middle plots the sensor was mounted atop a telescoping pole that could be raised to 13.5 m (Crain Enterprises, Mound City IL, USA). Balloons with a lift capacity of 1.0 kg (of a type described in Parker *et al.* 1996) were used in the taller canopy of the Lower plot. In the balloon and pole transects, ten 0.4-s measurements of PAR were taken at each vertical position and the average recorded to a datalogger (CR21X, Campbell Scientific Inc., Orem UT, USA). The topmost light readings in each 2–3- min-duration profile were used to represent external conditions during the in-canopy sampling.

Balloon profile measurements began at 1 m above ground with a vertical resolution of 1 m. Profiles taken with the telescoping pole began at 0.5 m, with a vertical resolution of 0.5 m. Values recorded when the balloon or pole moved or tilted during data acquisition were deleted and new measurements were taken when the platform stabilized. All profiles passed through the entire canopy, with the top measurement taken above the local outer canopy. Measurements were made on four occasions in the wet and dry seasons of 2000–2001 in the Upper and Middle plots, but only twice in the Lower plot. The relative illumination at each height, h, here called the transmittance, T(h), was calculated as the ratio of the in-canopy measurement of PAR flux to the corresponding external value, PAR_{inc}.

Canopy reflectance and scattering

In May 2001 (end of the dry season) and November 2001 (end of wet) at each sampling location in the Upper and Middle plots we measured the upwelling PAR above the canopy around midday using an inverted quantum sensor. The ratio of the upwelling : downwelling PAR above the canopy is an estimate of canopy reflectance. In the taller forest in the Lower plot, canopy reflectance was measured once in the wet season at one location using the balloon system. In November 2001 we measured the upwelling PAR within each canopy level at half the locations in the Middle and Upper plots, by taking additional profiles with the sensor pointed downward. The ratio of upwelling : downwelling PAR within a canopy layer is an estimate of scattering.

The absorption of downwelling light by a layer was estimated as the difference in mean transmittance between layers. We also estimated the vertical distribution of light upwelling following reflection from the ground. We assumed the probability of light capture for each canopy layer was the same for upwelling and downwelling streams. Absorption at any layer was the probability of light capture times the fraction of light reaching that level. The remaining light propagates to the next level. This calculation was repeated upward through all layers. The remaining light emerging from the top of the canopy was the scattering portion of canopy reflectance.

Derived measures

For each plot we grouped the transmittance values by height and calculated statistics by height using the SAS system (SAS Inc. 1990 a,b). The following measures were derived from the mean transmittance profiles: the gradient of attenuation in both the outer canopy and in the understorey (typically to 5 m above the lowest measurement) and the height where T(h) = 1.0 (the local canopy top). In each plot we defined three vertical regions based on the pattern of the mean and variance of transmittance: where mean transmittance is high with low variability (the bright zone), where transmittance is most variable and the mean changes rapidly with height (transition), and where both the mean and variability are low (dim).

Understorey PAR at each sampling location

The light profiles provided only a single estimate of transmittance at the level of each litter trap. To quantify the local variability in these values, we measured understorey PAR flux with a TRAC system (3rd Wave Engineering, Nepean, Ontario, Canada) in the vicinity and at the height of each litter trap under clear conditions. This hand-held instrument acquires PAR at 32 Hz from quantum sensors facing both up and down (Chen 1996). Light was sampled at the height of, but around the periphery of, each litter trap – the sensor was kept level with reference to a bulls-eye level. Additional measurements at nearby open sites interspersed with the in-canopy observations were interpolated to estimate the simultaneous incident PAR flux. The ratio of the downwelling light at 1 m to the concurrent external value (sensor pointed up in both cases) is termed understorey transmittance. The upwelling : downwelling ratio at this level is termed the ground reflectance.
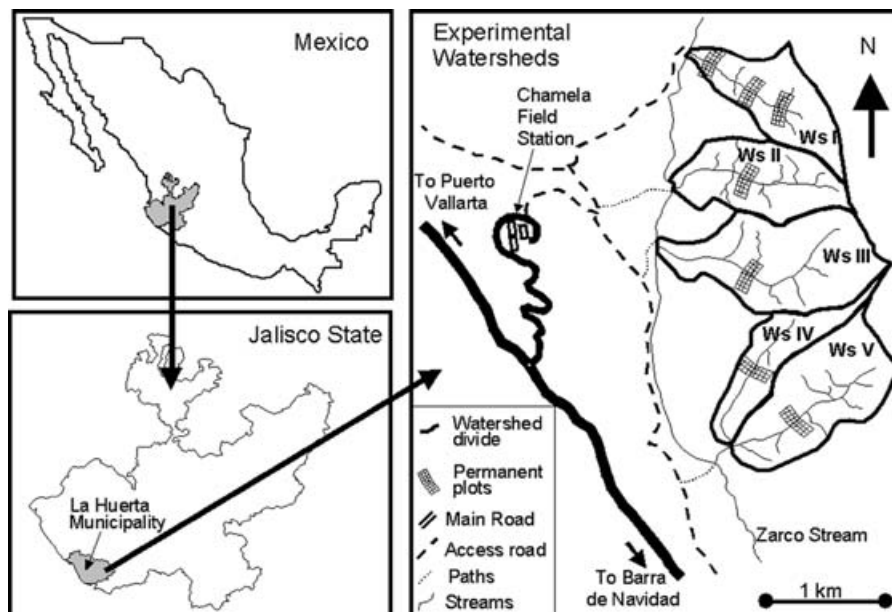
Figure 1. Location map of the study site, showing Jalisco state in Mexico, the Chamela region within Jalisco, the Chamela Biological Station, and the plots within the watersheds. This study was conducted on Watershed 1 (Ws I).

Canopy phenology

Observations of canopy leaf cover from a 42-mo phenological study by Bullock & Solís-Magallanes (1990) provided a basis for interpolating canopy profiles between sampling dates. We digitized the points in their figure 1B indicating the proportion of individual trees with at least some leaves and, by interpolation, obtained a general curve of annual foliage dynamics.

Radiation input

The seasonal variation of actual PAR flux incident to the top of the canopy was estimated from a 5-y study of shortwave and PAR radiation at a meteorological tower adjacent to the Middle plot (Barradas 1991). We digitized values of mean monthly PAR for this period from his Figure 4 and smoothed these to estimate daily totals of incident PAR.

Annual cycle of PAR components

Reflectance from the canopy (R_c), transmittance to 1 m (T_1), and ground reflectance (R_g) values were interpolated for each date and plot, weighted by the foliar cover. The fraction of incident PAR absorbed by the canopy was estimated from: $fAPAR_{can} = 1 - R_c - T_1 + (T_1 \times R_g)$. The last term is the PAR intercepted by the full canopy from ground reflection. The absorption by foliage, $fAPAR_{leaf}$, is estimated from the product of $fAPAR_{can}$ and the foliar cover. The absorption by the ground is estimated as:

$fAPAR_{ground} = T_1 \times (1 - R_g)$. These PAR components are similar to those defined by Gallo *et al.* (1985) for corn canopies.

RESULTS

Seasonal variation in incident PAR flux

The annual pattern of extraterrestrial radiation follows the solstices (Galicia *et al.* 1999); the flux incident to the Chamela canopy is greatest in April–May and reduced from July–January (Figure 2a). The difference is due to atmospheric factors, such as transmissivity, but primarily to cloudiness, which increases in the rainy season from July through January (Barradas 1991). From the 1984–1998 record of Barradas (1991) we estimate the annual PAR input at 15 200 mol m^{-2}. The PAR fraction of total solar radiation, about 0.41 on an annual basis, is lower than average under clear conditions and higher when cloudy or when transmissivity is low.

Foliar phenology

The Chamela canopy is closed from July through November, following this, leaf shedding of drought deciduous species causes a steady decline of leaf cover to a minimum, about 8%, in June (Figure 2b). A very rapid rise in leaf cover coincides with the onset of rains in May–June (Bullock & Solís-Magallanes 1990). Variability in the original data for January through March reflects some
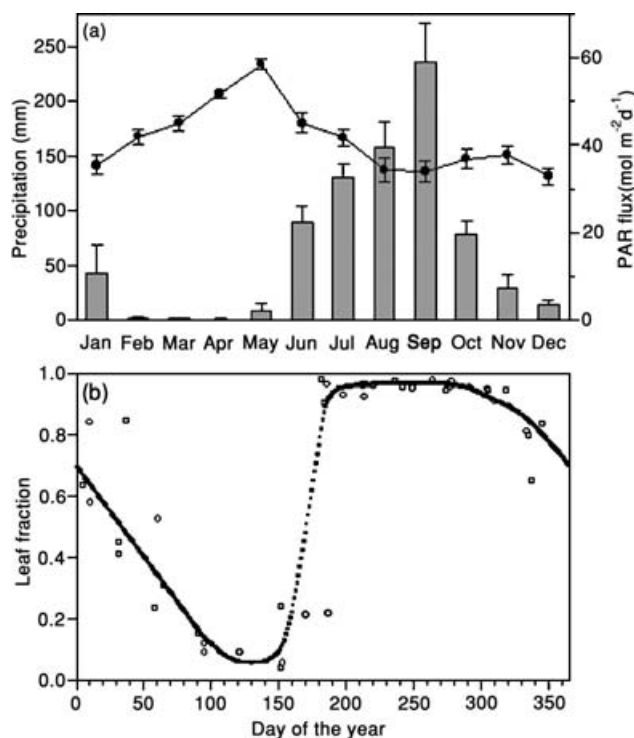
Figure 2. Long-term observations of seasonal patterns at Chamela, Jalisco, México. (a) mean monthly solar radiation at the top of the canopy with standard errors, shown with closed circles connected by a line (1978–2000, García-Oliva *et al.* 2002) and mean monthly rainfall presented in vertical bars (1984–1988, from Barradas 1991). (b) seasonal pattern of foliage presence in Chamela watershed 1 (closed circles), estimated from several years of phenological observations (open circles) reported by Bullock & Solís-Magallanes (1990).

atypical values for an extra flush of leaves responding to unusual rains in one year of their study (see also Maass *et al.* 1995).

Transmittance profiles

Large differences are evident between dry and wet seasons in the mean profile of PAR transmittance in all the plots (Figure 3). The vertical attenuation of PAR in the dry season is due to absorption by non-foliar tissues. In all cases, horizontal variability was greatest at those heights where the vertical change in the mean was steepest. The distribution of transmittance values was markedly non-normal at most levels in all seasons (Shapiro–Wilk test: $W > 0.21$, df > 8, $P < 0.05$ in the dry season; $W > 0.25$, df > 20, $P < 0.05$ in the wet season), except for some understorey levels in the dry season. The shape of the wet-season profiles changed with height, from a pronounced positive skew in the understorey to strongly negative skew in the overstorey. Similar patterns in the vertical variation in statistics of transmittance have been reported in other forests (Parker *et al.* 2002).

Differences among the plots in canopy structure are obvious in characteristics derived from the mean PAR profiles (Table 2). The mean height of full sunlight (H_{100}) varied inversely with plot elevation, following the pattern of maximum tree height (Table 2). The attenuation gradient was steeper in the wet season than in the dry season in all plots, by a factor of two or more. Vertical PAR attenuation was more gradual in the Lower plot than in the others, a reflection of its taller canopy. The mean understorey transmittance in the Middle and Upper plots declined somewhat as the wet season progressed (Table 2). Understorey transmittance increased markedly in the dry season, especially in the Middle and Upper plots. Vertical zonation of light environment was consistent by plot and season. In the wet season the transition zone of the Upper and Middle plots ranged from 3–9 m – in the Lower plot it was from 9–21 m. In the dry season, the transition zone extends to the ground in all plots – consistent, low transmittance (i.e., dim) conditions were not observed.

Canopy reflectivity and within-canopy scattering

Canopy reflectivity is inversely related to solar elevation at low solar angles but is relatively constant during

Table 2. Characteristics of PAR attenuation and transmittance derived from mean profiles in each plot and sampling visit. Outer canopy attenuation is the change in mean transmittance per unit height in the upper canopy. H_{100} is the height where transmittance was 1.0 (full sun) and T_1 is the mean transmittance at 1 m above ground. The three wet season entries correspond to dates of July 2000, November 2000, and August 2001, respectively, by row. The dry season entry corresponds to the May 2001 date.

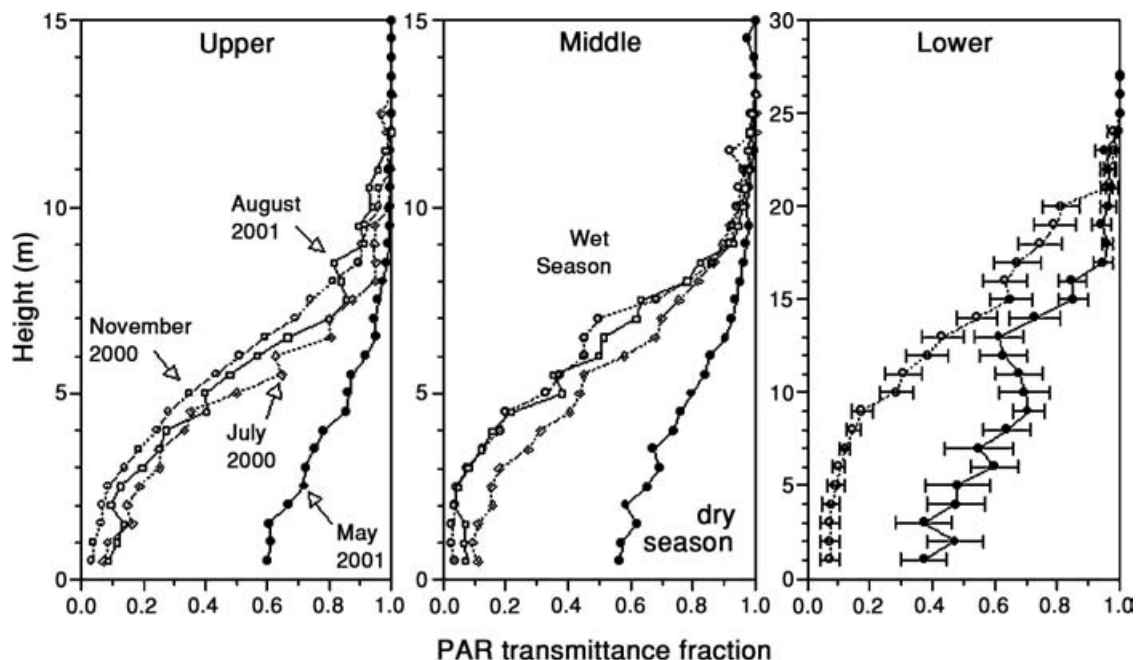| Characteristic	Lower Wet	Lower Dry	Middle Wet	Middle Dry	Upper Wet	Upper Dry
Outer canopy attenuation, m^{-1}	–	0.035	0.127	0.065	0.149	0.058
	0.061		0.159		0.152	
	–		0.152		0.152	
H_{100}, m	–	21.1 ± 3.7	9.4 ± 1.6	10.4 ± 2.2	8.0 ± 1.8	8.6 ± 2.1
	19.3 ± 3.6		9.7 ± 1.6		8.9 ± 1.4	
	–		10.4 ± 2.4		10.7 ± 1.7	
T_1, fraction	–	0.372 ± 0.124	0.093 ± 0.110	0.572 ± 0.194	0.085 ± 0.141	0.615 ± 0.154
	0.171 ± 0.144		0.024 ± 0.017		0.037 ± 0.036	
	–		0.067 ± 0.163		0.115 ± 0.163	

Figure 3. Seasonal differences in mean PAR transmittance profiles in the three elevation plots. The Upper and Middle plots have three sets of observations for the wet season but the Lower plot has only one. The vertical scale is different for the Lower plot. Representative standard error bars are given for the Lower plot.
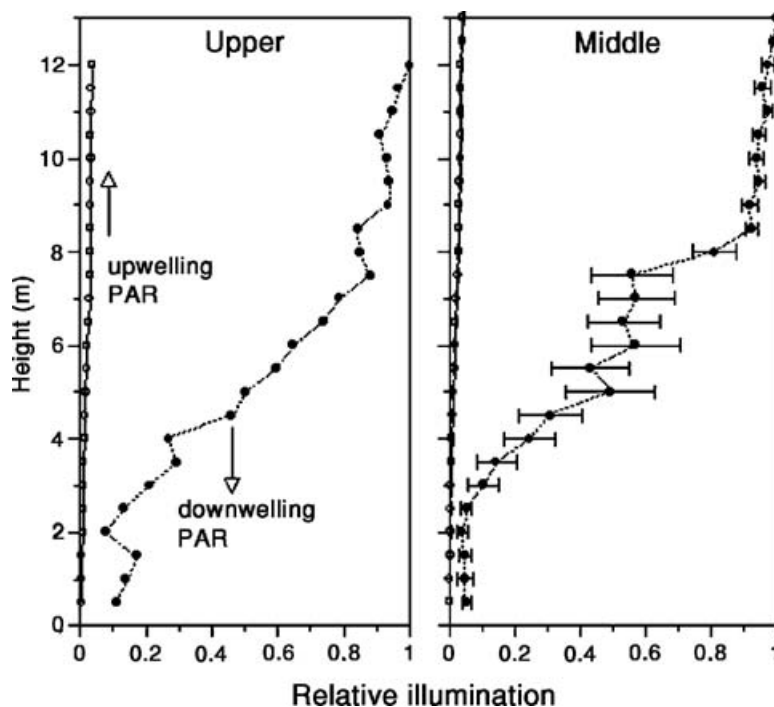

Figure 4. Within-canopy transmittance and reflectance measured at selected sites in two plots in November 2001. Representative standard error bars are given for the Middle plot – for the upwelling fraction, these are smaller than the symbols.

the middle of the day, when most PAR input occurs. Here we compare dry- and wet-season measurements of reflectivity made around solar noon.

During the wet season, the flux of upwelling light within each canopy layer was very small (Figure 4). When normalized to the incident downwelling light (within-canopy scattering), the upwelling fraction was nearly constant in all layers in both of the plots. The average ratio is about 0.04, that is, in any canopy layer about 4% of the incident light is recorded by a down-looking sensor.

Transmittance and ground reflectance

Measurements of understorey transmittance and ground reflectance made using the TRAC instrument revealed large differences between sites and between locations within sites and seasons. Mean dry-season transmittance ranged across sites from 0.362–0.847, while in the wet season it ranged 0.002–0.206. Conversely, the coefficient of variation ($CV = SD \times 100\%$ / mean) was low in the dry season (CV of 20–33%) but much higher in the wet season (67–110%). Ground reflectances were higher in the dry season (all around 0.11) than in the wet season (0.066–0.093). The pattern in the CV in ground reflectances paralleled that of transmittance: values were low in the dry season (20–33%) but higher in the wet season (66–132%).

The frequency distribution of both transmittance and ground reflectance was non-normal in both the wet and dry seasons (Shapiro–Wilk test, $P < 0.05$) and exhibited positive skew. Neither ground reflectances nor transmittances were related by site across seasons. The transmittance values at 1 m from the profile were not significantly correlated to mean TRAC transmittance at the same level. But dry-season transmittance was inversely related to ground reflectance (over all traps, $r = -0.56$, $P < 0.001$, $df = 68$). As a consequence, the product of $T_1 \times R_g$ was relatively uniform across traps in each season.

Major radiation components

The measured whole-canopy components of the PAR radiation balance include the reflectance at top, absorbance and scattering by each layer, transmittance to the ground and reflection from the forest floor (Figure 5). All major balance components differed significantly by season (ANOVAS with $df = 1$, for canopy reflectance: $F = 231$, $P < 0.0001$; understorey transmittance: $F = 788$, $P < 0.0001$; ground reflectance: $F = 10.3$, $P < 0.0017$). Season was the greatest influence on understorey transmittance: wet-season values of around 0.05 increased to 0.45–0.55 in the dry season. Ground reflectance was larger in the dry season than in the wet, especially in the Lower plot, where it doubled. Reflection from the ground back up to the canopy was low (< 0.005 of incoming) in the wet season, but much larger (0.05–0.06) in the dry season. Canopy reflectance of PAR in the dry season was nearly triple that during the wet season. The relative increase in midday PAR reflectivity from wet (2.8%) to the dry season (7.9%) was much greater than the corresponding change in midday shortwave albedo (14–21%) reported by Barradas (1991). The influence of plot was significant only for understorey transmittance (ANOVA; $F = 8.67$, $P < 0.005$, $df = 2$),
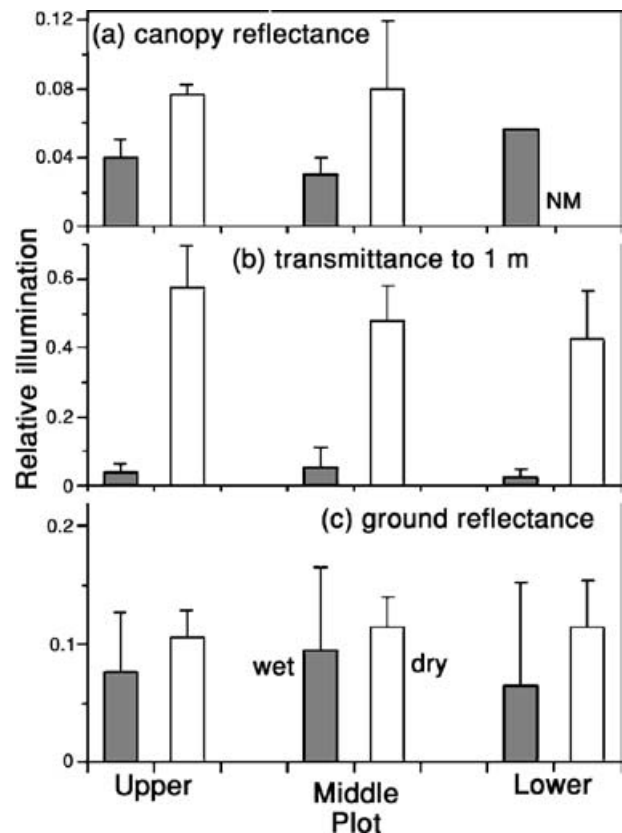

Figure 5. Mean PAR radiation components (a) canopy reflectance, (b) transmittance to 1 m, and (c) ground reflectance in the two extreme seasons across all three plots in Chamela Watershed 1. There is no estimate of variation for canopy reflectance in the Lower plot, as it was only measured at one location in the wet season ('NM' indicates no measurement in the dry season). Note that the vertical scales differ among panels.

which increased from the Lower (least-square mean 0.224) to the Middle (0.265) to the Upper plot (0.308), respectively.

Annual whole-canopy PAR balance

The annual dynamics of major components of canopy PAR balance is similar among the Chamela plots (Figure 6). The loss of energy input represented by canopy reflectance is greater in the dry season than in the wet, but is small overall. A large component is the absorption of PAR at the ground surface. Though smaller than canopy reflectance in the wet season, ground absorption is the largest dry-season component of PAR balance in the Upper; and Middle plots. The absorption of PAR by the canopy, $fAPAR_{can}$, is the largest component over the entire year, followed by canopy absorption when foliated, $fAPAR_{leaf}$. The difference between these is the absorption of PAR by non-leafy tissues, and to some extent, by canopy air.
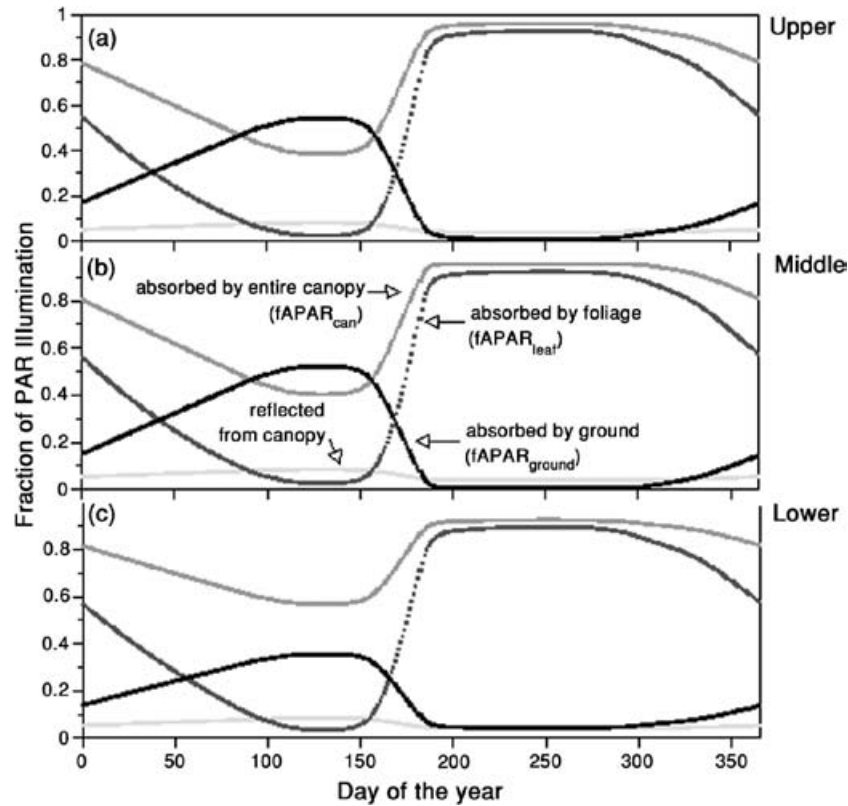
Figure 6. The seasonal dynamics of major components of PAR energy balance in canopies at three elevations in Chamela Watershed 1. Each panel gives daily values for canopy reflectance, absorbance by all canopy components, by foliage, and by the ground for the Upper (a), Middle (b) and Lower (c) plots. The dry season begins around day 320 and continues through day 160 of the following year.

The time-varying mix of radiation components is similar among plots. However, the annual fluctuations are greatest in the Upper plot and least in the Lower, especially for $fAPAR_{can}$ and $fAPAR_{ground}$. The annual pattern of $fAPAR_{leaf}$ is about the same in all plots.

When summed over a year, the components of PAR energy balance are similar among the plots (Figure 7). About 95% of incident PAR is absorbed, 50% by leaves, 25% by non-foliar tissues and 20% by the ground. The remaining 5% is reflected by the canopy. Ground absorption is higher and non-foliar absorption is lower in canopies in the moisture-limited plots.

The seasonal courses of PAR availability and PAR absorption by foliage within canopy layers are given for the three TDF canopies in Figures 8 and 9. The pattern of PAR availability is similar among the sites (Figure 8), when differences in canopy heights are taken into account. The seasonal variation is more pronounced than is the topographical difference, reflecting the strong phenology in LAI. The annual pattern of foliar PAR absorption (Figure 9) is not as smooth as that of PAR availability, as it depends on the seasonality of both incident PAR and LAI.
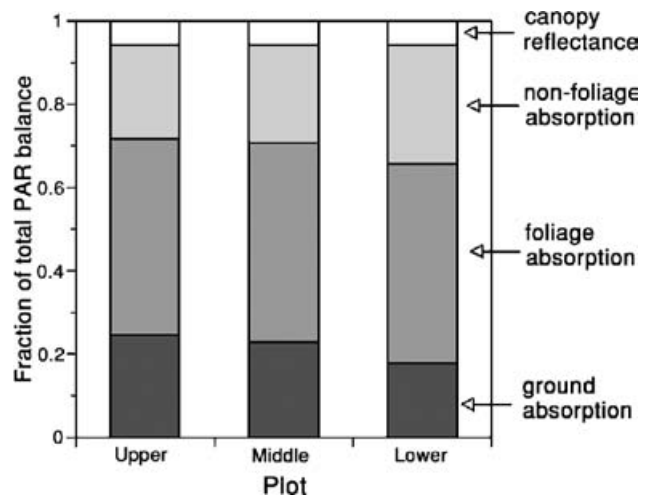

Figure 7. Summary of annual whole-canopy illumination components for the three plots at Chamela, Watershed 1.

DISCUSSION

In TDF the spatial variation and temporal dynamics of PAR components are associated with changes in canopy
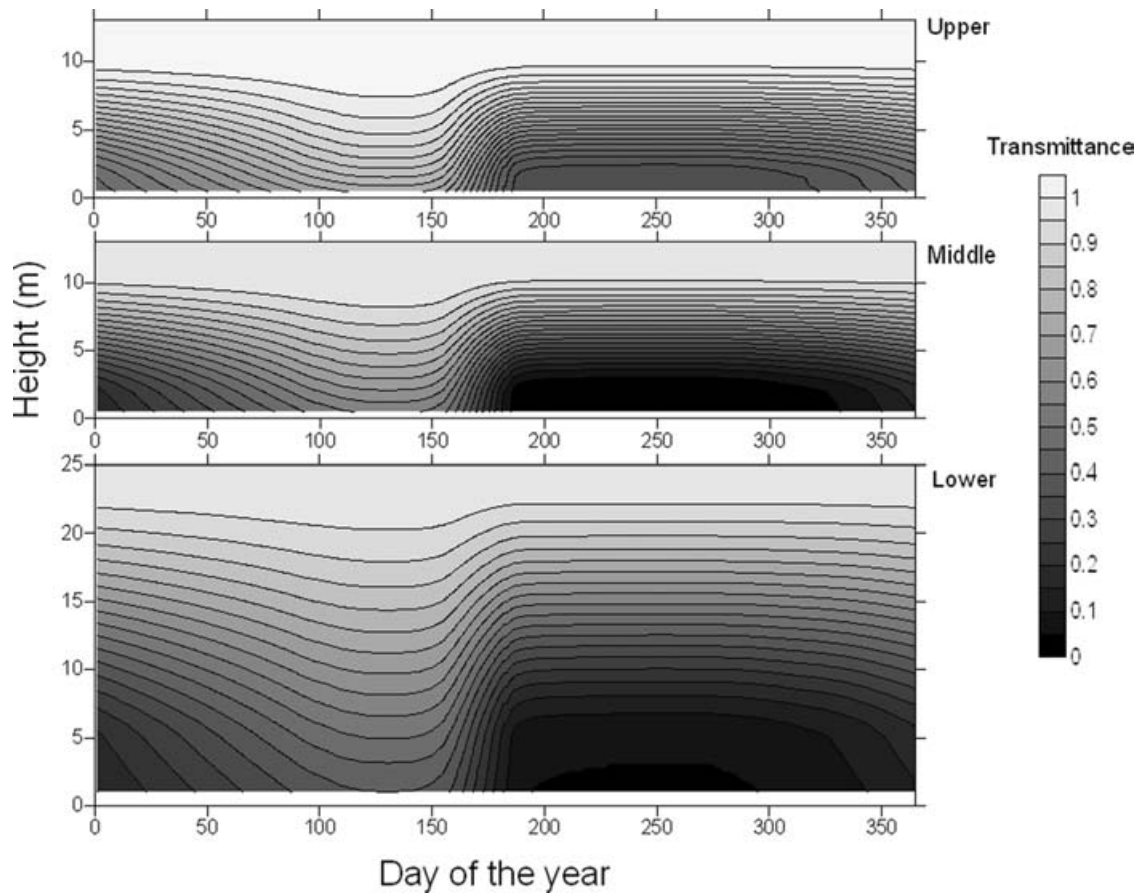
Figure 8. Vertical and seasonal change in canopy transmittance for the three plots at Chamela, Watershed 1. The units are fractional transmittance.

structure. In the Chamela forest, seasonal changes in leaf cover, and differences in canopy structure along a gradient of moisture availability had an important effect on the vertical patterns of PAR flux, major canopy PAR components and the annual whole canopy PAR balance. Only the understorey transmittance component differed among plots, which may reflect differences in LAI and species composition and phenology among sites (Bullock & Solís-Magallanes 1990, Maass *et al.* 1995, Segura *et al.* 2003). The total PAR budget balances and season and vertical courses were similar among plots.

Even in the leafless dry season, there was a significant vertical attenuation of PAR transmittance in the canopy, due to absorption by live and dead non-foliar tissues. Dead material (twigs, branches and boles) standing and hanging in the canopy is a conspicuous feature of the TDF. Maass et al. (2002b) have reported that two-thirds of above-ground dead phytomass is decomposing above 30 cm from the soil surface.

Understorey transmittance at Chamela is higher (0.025–0.115 wet season; 0.37–0.62 in the dry season) than for most closed canopy forests. Lee (1989) found similarly high understorey transmittances (0.10 in the wet season; 0.54 in the dry) in an Indian deciduous forest.

In tropical evergreen forests typically less than 1% of incoming radiation is transmitted (Baldocchi & Collineau 1994). It appears that understorey PAR availability may be higher in seasonal or deciduous forests, even in the wet season, than in tropical evergreen forests.

Canopy reflectance of PAR in the dry season (7.9%) was nearly triple that during the wet season (2.8%). Ground surface reflectivity also increased in the dry season, by as much as double compared with the wet season (0–3%)(Figure 5). However, in the deciduous period, the ground reflectivity is high and the canopy more transparent, so upwelling light was as much as 35–47% of canopy reflectance.

Spatially averaged PAR transmittance profiles differed among seasons. The pattern we observed in the Middle plot is similar to that from measurements made in one location (a meteorological tower) in this plot by Maass *et al.* (1995) with an integrating PAR line sensor (Sunfleck Ceptometer, Decagon Devices, Pullman Wa, USA) and by Barradas (1991) using quantum sensors. Furthermore, the mean profiles measured in the dry season at the meteorological tower in the Middle plot correspond closely to mean profiles obtained for that plot in the current study. However, the wet-season profiles of Maass *et al.* (1995)
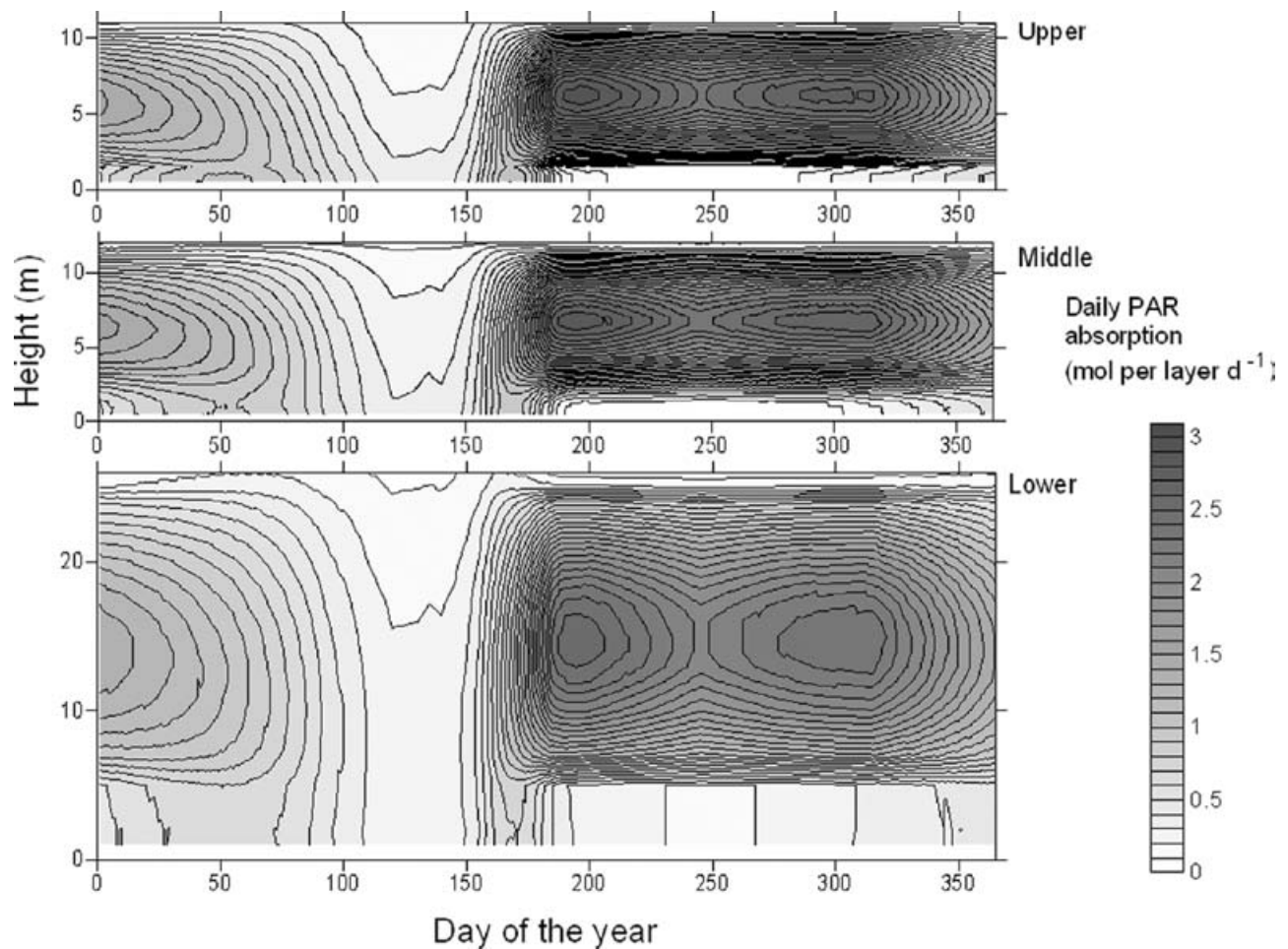
Figure 9. Vertical and seasonal change in foliar PAR absorbance for the three plots at Chamela, Watershed 1. The units are mol per layer d^{-1}.

are somewhat darker in the lower canopy and brighter in the upper canopy than the spatial average for the Middle plot reported here. This difference may be related to inter-annual variability in rainfall amount and timing (i.e., the start and end of the rainy season and the annual total). For much of the year however, the tower area appears to represent the vertical change in PAR light in the local canopy.

Ground reflectance and transmittance differed between seasons and among plots. The relative increase in midday PAR reflectivity from wet to the dry season was much greater than the corresponding change in midday shortwave albedo (14–21%) reported by Barradas (1991). The negative correlation between leaf cover at mid-month and mean monthly shortwave albedo ($r = -0.92$, $P < 0.01$, df $= 10$), supports the suggestion of Barradas & Adem (1992) that non-foliar surfaces may influence reflectivity. In this study ground surface reflectivity increased in the dry season, nearly doubling, likely because dry soils are lighter in colour and more reflective than wet ones (Barradas & Adem 1992, Idso *et al.*

1975). In the wet season ground reflectance was low and the canopy was nearly opaque, permitting little upwelling light to emerge (0–3% overall). However, in the deciduous period, the ground reflectivity was high and the canopy more transparent, so upwelling light originating from ground reflection contributed substantially to canopy reflectance.

The observations of PAR radiation reported here were restricted to clear skies, yet cloudy periods are common at Chamela (Barradas 1991). Chazdon & Fetcher (1984) and others have suggested that the diffuse light predominating under clouds can penetrate relatively deeper into the canopy than under clear skies. If true, then fractional understorey transmittance would have been underestimated under such conditions. However, as cloudy skies usually have lower insolation, absolute PAR fluxes to the forest floor would not be dramatically affected.

Though water availability is likely the dominant control on heterogeneity at Chamela (Balvanera *et al.* 2002), PAR components nonetheless have implications at a variety of scales. The regional radiation balance is

affected by the canopy of the forest, particularly through the control of reflected radiation (Dickenson 1983). Seasonal variation and anthropogenic modification in albedo can have substantial effects in large-scale climate predictions (Garratt 1993). For the ecosystem, PAR intercepted by foliage is the energy basis of photosynthesis and is important for accurate estimation of NPP from the method of light-use efficiency (Ruimy *et al.* 1999). More locally, the pattern of PAR interception within the canopy will determine plant access to energy for growth (Figure 9). At the level of the forest floor, the gradients in PAR and spectral differences will contribute to the establishment and growth of seedlings (Vázquez-Yanes *et al.* 1990).

The extreme seasonality of the Chamela TDF radiation balance illustrates the important distinction (Asner *et al.* 1998) between intercepted PAR (IPAR) and absorbed PAR (APAR). IPAR is the difference between the incident PAR and that exiting at the bottom of the canopy (i.e. $fIPAR = 1 − T_1$), whereas APAR additionally accounts for scattering from the canopy and ground (i.e. $fAPAR = 1 − R_c − fAPAR_{ground}$). Canopy PAR reflectance was low overall (5.5–5.7%) (similar to values reported by Dickenson 1983 and Parker 1997) but ground absorbance was large (18.1–24.7%). Consequently, fIPAR and fAPAR differ substantially in this forest: 0.725 vs. 0.423 for the Upper plot, 0.740 and 0.452 for the Middle, and 0.799 and 0.561 for the Lower.

Moreover, the annual absorption of PAR by ecosystem components at Chamela is not the simple product of mean probabilities and total incident radiation flux, because the seasonal patterns of incident PAR radiation and leaf cover differed. To better estimate actual foliar absorption in very seasonal forests it is essential to weight absorption components by leaf presence and incident fluxes on a short-term basis.

The present study shows that light environment in the undisturbed TDF varies among locations, between seasons and, very likely, among years. Land-use change in the region includes slash-and-burn pastures, intensive grazing, selective logging and extraction of non-timber products (García-Oliva *et al.* 1994, Jaramillo *et al.* 2003, Maass 1995). Regeneration following such changes depends not only on resprouting (Miller 1999), but also on the recruitment and their successful establishment of seedlings, which will be affected by the availability of light. Studies on light environment responses to transformations of the TDF are needed to understand light-controlling effects in forest recovery.

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