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SEASONAL CHANGE IN LEAF AREA INDEX AT THREE SITES ALONG A SOUTH AMERICAN LATITUDINAL GRADIENT

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Abstract. We measured Leaf Area Index (LAI) monthly, by light transmittance, on two 0.5 km to 1 km transects at each of three South American localities spanning a wide gradient in latitude and dry season severity. Our goals were: (1) to evaluate whether we could use a simple methodology to measure seasonal foliar changes in forest cover; (2) to examine the magnitude of seasonal changes within and between sites; and (3) to see how measured LAI patterns correlated with rainfall and litterfall phenology. Each site showed a predictable annual cycle in LAI. The magnitude of seasonal differences was directly related to the severity of the dry season. Median monthly LAI varied roughly inversely with rainfall: at all sites yearly minima occurred in the months of maximum rainfall, and maxima were recorded in the early to mid dry season. Transects with wet-season flooding had lower LAI than did more xeric transects. Litterfall patterns suggest that the major part of within-site seasonal LAI differences are due to deciduousness. This seemingly obvious result is counterbalanced by the many still unresolved interactions between climate, insolation, deciduousness, and seasonal light availability in tropical forest understories. *Accepted 17 July 2006.*

Key words: *Bolivia*, *foliage*, *French Guiana*, *Leaf Area Index*, *light*, *Peru*, *phenology*, *seasonality*, *tropical forest*.

INTRODUCTION

Leaf Area index (LAI), the vertically integrated surface of leaves per unit of ground area, can be a measure of several fundamental properties of forest vegetation, including photosynthetic productivity and structural complexity. Leaves are the primary sites of photosynthesis and transpiration, thus the LAI, which integrates the light interception by the canopy, is at the stand scale directly related to carbon and water exchange with the atmosphere. As a measurement of light interception, LAI likewise reflects plant growth. Understory light availability is the principal limiting factor of tree recruitment and growth within forests (Denslow *et al.* 1990). Largely for technical reasons, as outlined by de Wasseige *et al.* (2003), there have been few studies of seasonality of LAI in tropical forests (Maass *et al.* 1995, Wirth *et al.* 2001, de Wasseige *et al.* 2003, Kalácska, Sánchez-Azofeifa *et al.* 2005). There have been no long-term studies and few studies comparing different sites with a standard methodology (Kalácska, Sánchez-Azofeifa *et al.* 2005). However, a recently-developed simple technology for measuring LAI indirectly, by light transmission (LAIL: Cournac *et al.* 2002), has facilitated data collection so that in contrast to other methods, long transects of hundreds of points are easily sampled to yield data on a landscape scale that are useful for integrating with satellite imagery or forestry data for large areas.

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In 2001 we launched a collaborative effort (ECOFIT France, Amazon Conservation Association, LHE) to compare seasonal changes in LAI in three South American forests spanning 18 degrees of latitude and a gradient in the length and severity of the dry season. All three field sites have well-studied floras and research programs which provide the floristic data that is a necessary adjunct to LAI studies (Killeen and Schulenberg 1998, Bongers *et al.* 2001, Pittman *et al.* 2001). Our goals were to: (1) measure the annual patterns of change in leaf cover across large transects of forest, as indicated by measurements of LAI* (see below for use of the quantity defined as LAI* = *k*.LAI/0.88); (2) compare the patterns of intra-site differences between forests on different soil moisture regimes; (3) compare interannual patterns with rainfall patterns; and (4) compare annual patterns between sites with differing dry-season stress. We here report the results of four or more years of measurements.

STUDY SITES AND METHODS

Study sites. We measured light on two forest transects at each of three lowland sites in South America (Fig. 1, Table 1). At two sites, one transect was on better-drained, more xeric soils, and the other on a wetter, more mesic substrate. From south to north, the sites are as follows: (1) Los Fierros camp (LF), Parque Nacional Noël Kempff Mercado, Santa Cruz, Bolivia, is on the Brazilian Shield. The national park and field site lie across the transition zone between tall Amazonian humid forests, semi-deciduous forests, *cerrado* savannas, and seasonally flooded savannas. The habitats, flora, fauna, and geology are described in Killeen and Schulenberg (1998) and Panfil (2001). Transect LF2 is in tall, semi-deciduous forest on flat ground of a well-drained lower shoulder of the Huanchaca Massif, and comprises two parallel 500 m transects, 200 m apart, bordering an experimental plot in which all trees have been identified and measured (T. Kil-

TABLE 1. Study site characteristics. Coordinates measured by GPS (WGS 84). The plots on which tree species were enumerated were near or within the LAI* transects (LN, LF) or on the same terrace (LA). Δ Daylength = difference between shortest and longest photoperiod in the year, calculated with J.Lammi calculator (www.sci.fi/~benefon/sun.php3).

Site	Substrate	Transect length, km	Latitude	Longitude	Elevation, m
Les Nouragues M	upland	1.0			110
Les Nouragues H	upland	0.6	4.08778	–52.68028	120
Los Amigos 2	river floodplain	0.5	–12.4517	–70.24366	210
Los Amigos 1	upland	1.0	–12.50554	–70.12239	240
Los Fierros 3	stream floodplain	0.5	–14.5788	–60.83115	203
Los Fierros 2	upland	1.0	–14.55453	–60.93391	237

Site	Mean rainfall mm (years)	Months ≤ 60 mm average rainfall	Δ Daylength, minutes	Tree spp. ≥ 10 cm / ha	Individuals ≥ 10 cm / ha	Tree diversity, Fisher's α
Les Nouragues	2,939 (14)[d]	0	28	185[a]	540	99.4
Los Amigos	2,653 (5)	1	89	157[b]	492	79.7
Los Fierros	1,453 (9)[e]	4	104	96[c]	607	32.1

[a] Mean of 7 one-ha plots (Poncy *et al.* 2001)
[b] Mean of 2 one-ha plots on upland terrace (Pitman *et al.* 2001)
[c] Mean of 2 one-ha upland plots (Panfil 2001)
[d] Sum of average monthly rain, many data gaps.
[e] Rainfall measured at El Refugio Huanchaca, 30 km SW of LF.

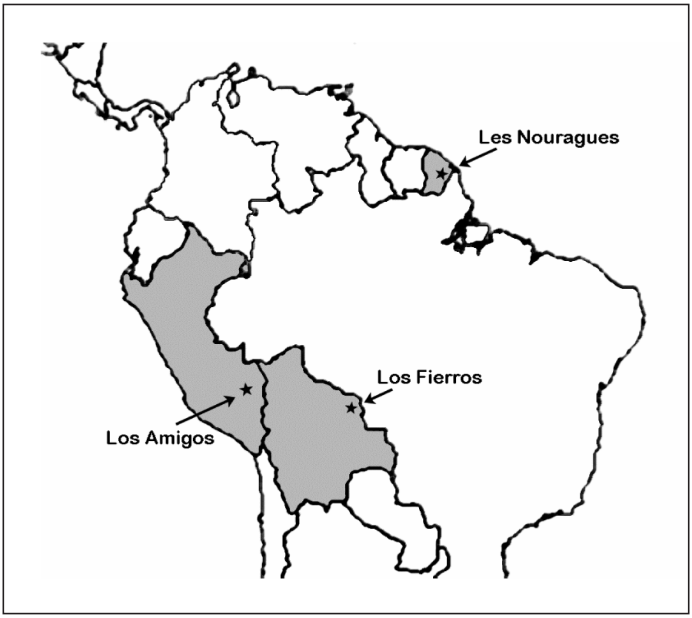

FIG. 1. Locations of the three study sites.

leen, unpublished). Transect LF3, about 15 km from LF2, is 90° to the LF airstrip, in tall, semi-deciduous forest in lowland streamside habitat susceptible to episodes of brief flooding, with temporary standing water during the wet season. (2) Centro de Investigación Río Los Amigos (LA), near the confluence of the Los Amigos and Madre de Dios rivers in Madre de Dios, Perú, is on Subandean Quaternary fluvial deposits that form high terraces bordering river floodplains. The transects are in continuous, tall, semi-evergreen Amazonian forest. Transect LA1 is in tall, mature forest characterized by brazil-nut groves (*Bertholletia excelsa*) on a high, well-drained terrace dissected by a few small streams within deep erosion gullies. Transect LA2, in low-lying floodplain of the Río Madre de Dios, is on permanently moist soil seasonally subject to temporary flooding and pools of standing water, but it is not *várzea* forest. This forest is a late stage of river-meander successional vegetation, likely several hundred years old (Foster 1990, Puhakka & Kalliola 1993, Emmons & Dubois 2003). The two LA transects are over 4 km apart. (3) Les Nouragues Field Station (LN), French Guiana, on the Guiana Shield, lies in continuous, tall evergreen forest. The station, climate, vegetation, and fauna are described in Bongers *et al.* (2001). Transect LNM is mostly of mature forest, but with signs of anthropogenic disturbance (likely of Amerindian origin >100 ybp). It is on the "Grand Plateau," a substrate of metamorphic rocks of the Paramaca series with clay soil. Transect LNH is on the "Petit Plateau," 500 m west of LNM, on granites and crystalline rocks of the Caraibe series partly covered with sandy-clay soil. Neither transect is subject to seasonal standing water. Dry-season length and severity vary inversely with latitude of the sites (Table 2), as do yearly photoperiod range and tree species richness (Table 1). LN is on the boreal seasonal cycle, while LA and LF are austral.

Light measurements. We marked measured transects with permanent tags at 10 m intervals, where we took light readings. We measured light with a simple LAIL apparatus (Cournac *et al.* 2002) that has been favourably compared with several other methods (Ferment *et al.* 2001). Transmitted light is recorded with a light-dependent resistor behind an economical off-the-shelf fish-eye lens (spy-hole optic). The method uses the Beer-Lambert law to calculate the attenuation of light by vegetation ($I = I_o e^{-k.LAI}$; where I = transmitted light, I_o = incident light, k = extinction coefficient). We directly derive a quantity which is not LAI, but rather k.LAI, where k is a geometric foliage light-extinction factor of order unity associated with leaf

TABLE 2. Pairwise comparison of monthly LAI* readings along each transect during a calendar year. Year 2002 for LN and LA; Apr-2001 to Mar-2002 for LF (no data for Jan or Aug). Wilcoxon signed-ranks test (Siegel, 1956), # = $p \geq 0.05$; * = $p \geq 0.01$, ** = $p \geq 0.005$, *** = $p \geq 0.001$, **** = $p \geq 0.0001$, blank cells ns. Above diagonal: LNH, LA1, LF2; below diagonal: LNM, LA2, LF 3.

Les Nouragues	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan		**	***			****	**	*				
Feb				****			****	#				
Mar				****	****		#	**				
Apr					#							
May	***	***	****	*								
Jun	#	*	*				****	***				
Jul			#					****				
Aug	***	***	**	****	****	****	****					
Sep								***		#		#
Oct	#			#	****	***	***		**		#	
Nov	****	***	****	#				****	**			**
Dec	#		#					****		****	**	

Los Amigos	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan						***	*					
Feb						****	****					
Mar				*			****	#				
Apr	**	**				***	#		*	#	*	*
May	***	***	*				****	#				****
Jun	***	**	#				**	****		****	****	
Jul	***	***	*			#		****		****	****	****
Aug	***	***	*						***	#	#	**
Sep	****	****	*			#						
Oct	***	***			#		**	#	***			#
Nov	**	***	*									
Dec				***	****	****	***	***	****	****	***	

Los Fierros	Feb	Mar	Apr	May	Jun	Jul	Sep	Oct	Nov	Dec
Feb								#	***	
Mar	****			****	#		**	****		
Apr	**	***			*	*	**	****	*	****
May	*	**			****		****		****	
Jun		****							***	
Jul		***	****	****	****					
Sep	****		#		****	****			****	
Oct		****	#	*			***			#
Nov	#	*			****	****	#	*		****
Dec		****	****	**			***		*	

angle. To be consistent with the conventional use of the dimensionless parameter LAI, we give our values as LAI*, defined as *k*.LAI/*k*, where $k = 0.88$ at 2 m, as reported for tropical humid forests (e. g., Wirth *et al.* 2001). Because our primary interest here is to measure relative, rather than absolute, values, it is not critical whether the actual value of *k* on our transects deviates slightly from 0.88. The sensor does not distinguish between light extinction by leaves and that by woody elements (woody area index, WAI); thus the measurement could be termed Plant Area Index (PAI: see Kalácska *et al.* 2005, and de Wassige *et al.* 2003, for discussions). Wirth & Reth (unpublished, cited in Wirth *et al.* 2001) estimated that extinction from WAI could equal 0.6 LAI in a deciduous German oak forest, while Kalácska, Calvo-Alvarado *et al.* (2005) calculated WAI as 0.4 ± 0.14 for late successional tropical dry forest in Costa Rica. The contribution of WAI to light extinction is constant for a given transect and thus does not effect our measurements of seasonal change, but its percent importance would increase with decreasing canopy foliage, such that the area of leaves would be increasingly over-represented with increasing leaf loss (Kalácska, Calvo-Alvarado *et al.* 2005). Emmons & Dubois (2002) discuss the method further; it has also been used in Madagascar (Cournac *et al.* 2004), Eastern Cameroon (Vincens *et al.* 2000), and Western Congo (Favier *et al.* 2004).

We made all light measurements between 11 h and 13 h, with the light sensor held at 2 m; only foliage above this level influenced readings. When taking readings we placed the sensor within an arm's length of the marker, positioned to avoid small transient sunflecks and closely overhanging foliage. Larger, persistent, structural sunspots and gaps were sampled normally. We corrected for partial cloud cover as detailed in Cournac *et al.* (2002). We did not sample on days with complete cloud cover. Particularly at LF (Bolivia), dense atmospheric smoke from anthropogenic burning often significantly decreased dry season solar radiation. We took control readings under open sky and removed any smoke effect from the measurement series for that day by normalizing full-sun readings to LAI* = 0. At the space and time scales of our project, we consider the ecosystem as more or less constant from year to year, and gaps due to treefalls are compensated by growth of other trees (turnover). If a tree fell at a measurement point along the transect, we took subsequent measurements at the same point.

LN (French Guiana) and LA (Peru) have year-round research staff, and measurements were taken on each transect once a month, as near to the same day of the month as weather permitted. LA transects were sampled in 25 months from Apr-01 to Jun-03, and on 12 additional months in 2004-5. LN was sampled in 39 months from Jul-01 to Dec-03. LF is unstaffed, is remote and difficult to reach in the wet season, and monthly measurements could only be taken on 8 (2001), 6 (2002), 3 (2003), 5 (2004), and 5 (2005) months of the study years. Continuous bad weather prevented sampling of one of the two LF transects in several wet season sessions, when dense clouds formed almost daily during the time window required for readings. LAIL readings have a small observer bias (Cournac *et al.* 2002); to minimize this, readings at a given site were made as often as possible by the same observer.

Analysis. Because the nature of the forest structure causes asymmetrical punctual readings (sunflecks, treefall gaps) with fixed magnitude near LAI* = 0, which are not associated with the general canopy leaf cover, we use the median as the statistic for comparison, to reduce the influence of unidirectional sunlight "noise." This gives LAI* values slightly greater than do the means, but it does not change any of the relative comparisons treated below. As light readings were taken at the same markers on each transect for each monthly sample, we use the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) for pairwise statistical comparison of monthly samples for each of the six transects. Each light-reading point subtends a unique foliage and plant species configuration. The Wilcoxon signed-ranks test uses both the direction and magnitude of differences between two samples, with no assumption about the sign of differences. Under *Ho*: the medians of the samples do not differ. As our samples are large (N = 50 - 100 points) the analysis gives *p* values (Siegel 1956). Tree diversity indices are estimated with Fisher's α, defined implicitly by the formula $S = a*\ln(1+n/a)$, where *S* is number of taxa, *n* is number of individuals, and *a* is the Fisher's α.

RESULTS

Large variations in the raw LAI* curves for individual transect samples reflect the inherent heterogeneity of forest canopy structure (Fig. 2). Peaks correspond to measurements taken under patches of dense foliage such as those caused by large palms, liana dominated forest, or multilayered tall canopies; and minima correspond to measurements taken in gaps created by treefalls or branchfalls, in low-canopy spots such as bamboo, or on sloping terrain. All transects included large treefall gaps with open sky above. Repeated runs of the same transect in different months show regularity in the patterns of peaks due to fixed structural elements of the forests, but all transects experienced new treefalls that changed the baselines during the course of the study, for example at the end of LF2 (Fig. 2, lower). On each transect most measurements fall near to an approximately horizontal line, suggesting that for any given transect in our set the forest

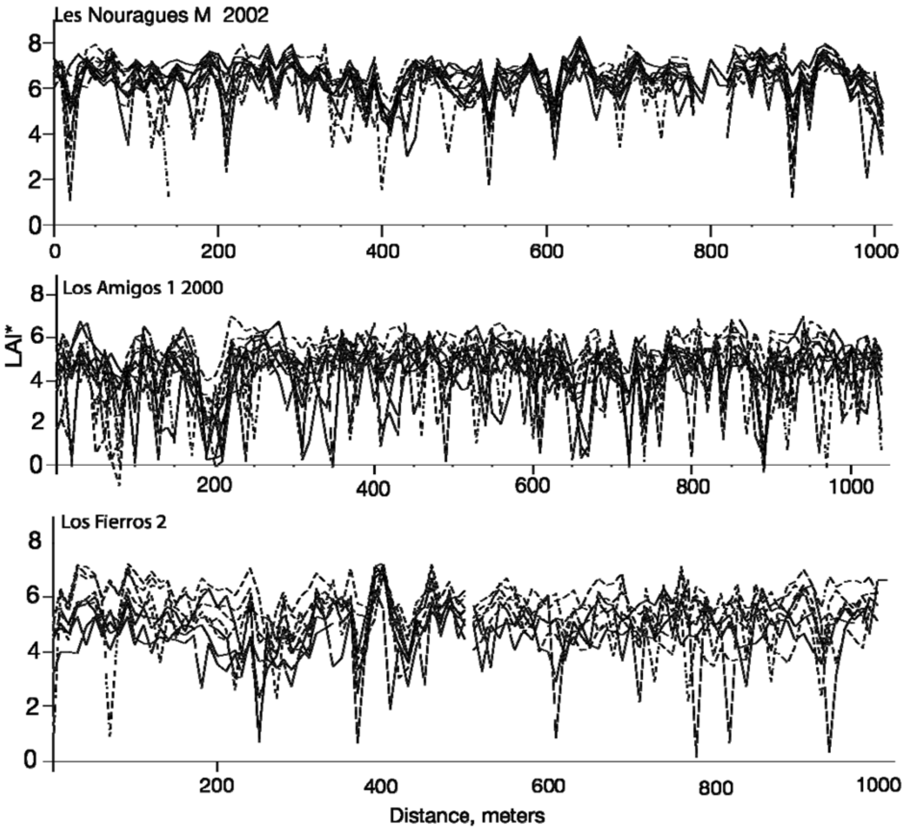

FIG. 2. Raw curves of LAI* transect data from the 1 km, upland forest transects at each site, including all samples from one calendar year (12 months for LN, LA, 8 months for LF). The shape of the top of the series reflects plant structure, the noise below the curves represents sunflecks and light gaps.

has a fairly uniform, "typical" foliage coverage, but that this differs between transects and sites (Fig. 2).

Seasonal patterns. Graphs of the median monthly LAI* values for each transect, for cycles of two dry and two wet seasons, show that all study sites exhibit seasonal differences in LAI* that are coherent from year to year (Fig. 3). The following general patterns emerge (Fig. 4A-C): (1) Site LN has a much greater median LAI* at all times (6-7) than the monthly maximum reached at LA or LF, while of the latter two, LF shows higher peak values and lower minima than LA; (2) forest on poorly drained ground at both LA and LF has a lower LAI* than forest on the well-drained substrate, with the most pronounced within-site disparity during the wet season; (3) LAI* generally tracks the inverse of rainfall, always peaking at early to mid dry season and reaching minimal values in wet-season months, but in LA and LF lesser peaks can sometimes occur during the wet season, in January or March; (4) a site's seasonal variation in LAI* increases markedly with increasing dry-season severity; (5) the mesic sites that are subject to standing water (LA2, LF3) show sharp decreases in LAI* relative to neighboring terra firme during months of exceptionally high rainfall.

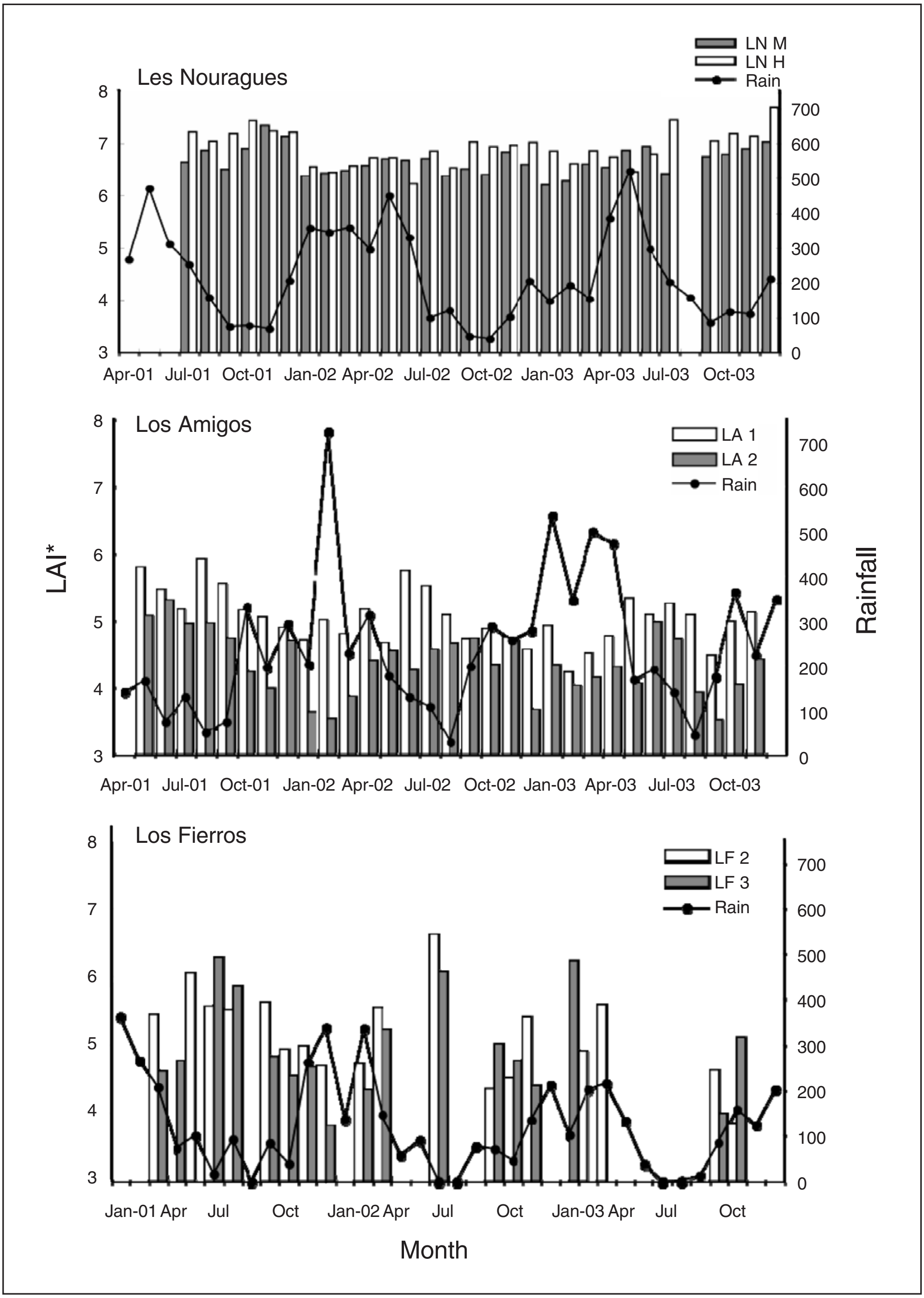

FIG. 3. Median monthly LAI* for two years on all transects, and local rainfall for those months (additional 2003-5 data not shown). Rainfall for LF was measured at El Refugio Huanchaca, 30 km from the transects.

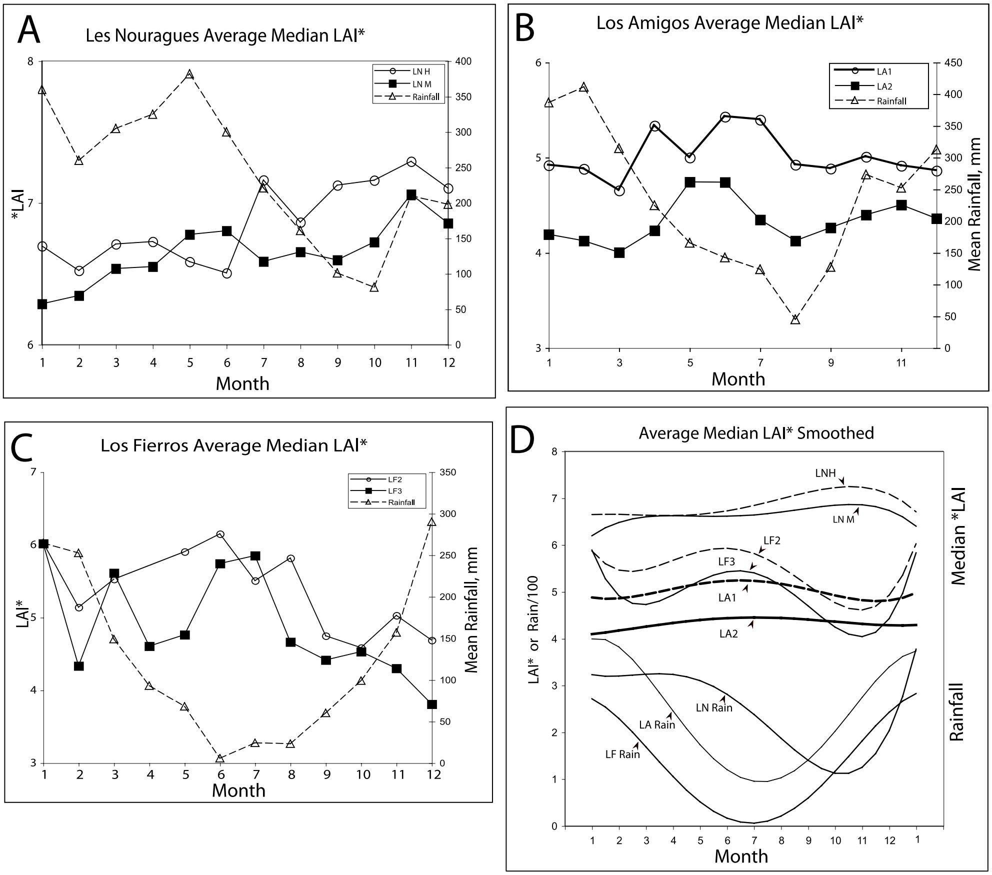

FIG. 4. Overall means of median monthly LAI*. A-C, raw data; D, the same data shown in A-C greatly smoothed with 4th order polynomial, January repeated to emphasize curves.

Overall patterns are easier to see in smoothed curves (Fig. 4 D), which likewise best visualize the inter-site differences in rainfall seasonality and dry-season severity. Although LN and LA have similar total annual rainfall (Table 1) LN has a shorter and wetter dry season than LA, and its boreal cycle is evident. Likewise, LF has a similar austral rainfall pattern to LA, but it is drier in every month of the year. Inter-annual rainfall differences appear associated with shifts in LAI* monthly patterns (Figs. 3, 5). These shifts result in considerable damping of annual fluctuations when data for several years are averaged (Fig. 4), so that the averaged medians exhibit smaller seasonal differences than do individual years.

Statistical comparison of the monthly results for one year shows that months of maximal and minimal LAI* differ significantly at LA and LF (Table 2), as do many other sets of months. Even small seasonal differences are often highly significant, such as those between August or October/November, and every other month on LNM. This is due to the generally high precision of LNM transect readings (Fig. 1). Nevertheless, despite a slightly larger maximum difference between seasonal medians, LNN has few months with significant differences in LAI* (Table 2). This might be due either to smaller sample size (60 vs. 100 points) or to genuinely insignificant seasonal differences.

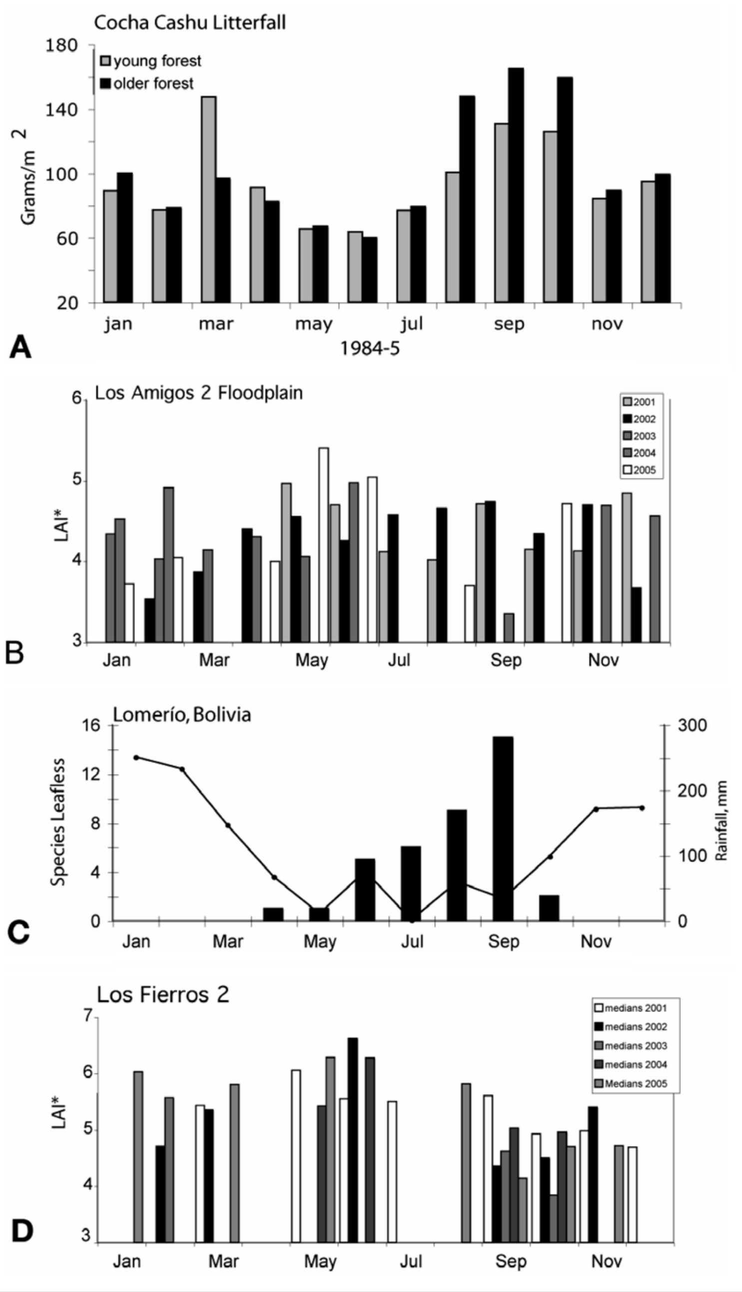

FIG. 5. A, litterfall data from floodplain forest at Cocha Cashu, near LA; 1984-5 months rearranged to fit a calendar year (after Cornejo & Lombardi 1993); B, multi-year LAI* monthly medians on LA2 (bars); C, number (of 39) timber-tree species leafless per month (bars), and rainfall (lines) for 1997, in semi-deciduous forest at Lomerío, Santa Cruz, Bolivia (after Justiniano & Fredericksen, 2000); D, multi-year LAI* monthly medians on LF2.

The distribution of monthly median LAI* values in LA2 floodplain can be compared with litterfall patterns in the Cocha Cashu floodplain 150 km NW (Cornejo & Lombardi 1993), while that at LF can be compared with phenology data for a forest farther south in the same region (Justiniano & Fredericksen 2000; Fig. 5). In Peruvian floodplain forest, both litterfall and LAI* data sets show bimodal annual patterns, with LAI* inversely related to litterfall and exhibiting the slight temporal shift expected if growth and functional expansion of new leaves follows peaks in leaf drop. The yearly May–September LAI* maximum coincides with the May–July early dry season minimum litterfall. At the August–October end of the dry season, peak litterfall coincides with declining LAI* that reaches a minimum in October. Although the data for Peruvian sites were taken 18 years apart at different sites, a remarkably consistent pattern is evident, suggesting that an important fraction of the intra-annual variation in LAI* is due to predictable seasonal patterns of leaf-fall.

Justiniano & Fredericksen (2000; Fig. 5) recorded foliar phenology by counting numbers of species with or without leaves for a sample of 39 timber tree species in a semi-deciduous forest at Lomerío, Bolivia, about 200 km south of Los Fierros. The sampled species gradually lost leaves throughout the dry season, with a quarter leafless by August and the maximum of half of species leafless in September. Only two species remained leafless in October. Although these data do not measure the forest-wide pattern, they clearly show sampled trees reaching maximum leaflessness at the end of the dry season. The data from Lomerío indicate a unimodal pattern of leaf abscission.

Rainfall is clearly associated with both inter- and intra-annual seasonal patterns, and also likely with the intra-site differences (Figs. 3–5). Site LA has the strongest edaphic difference between the two sampled transects, with LA2 on alluvial floodplain subject to saturation and standing water, and LA1 on a well-drained high terrace. During the extremely wet months of January–February 2002 and 2003 (regional historical precipitation maxima), the LAI* on mesic transect LA2 dropped dramatically relative to the LAI* for the same months on well-drained LA1 (Fig. 3).

Inter-site comparisons. The raw LAI* data curves are difficult to interpret or to compare with those from other transects (Fig. 2). Simple rank order sorting of the LAI* data (Fig. 6) uncovers several otherwise cryptic characteristics of the data sets. The sets of curves for a single annual cycle clearly show the higher overall LAI* in dry-season than in wet-season samples at our three sites, although the seasonal differences at LN are extremely small (Fig. 6). The lowest 20 % of the values (left tail) evidently includes all "light gap" and sun spot effects, while the middle 80 % form a smooth series of flat curves that remain approximately parallel from month to month. These we consider to represent the "typical" forest canopy for a transect. The highest 2–3 % of LAI* values (right tail) on some transects (LNM, LNH, LA1) represent a few spots of unusually dense structure, perhaps dense vine-tangles or interlacing palms and branches. The seasonal variation within a site is reflected in the vertical spread of readings at the midpoints of these curves. This spread increases with increasing dry-season severity, from tight at LN, to widely spread at LF (Table 3). The irregular, low LAI*, left tail of the rank-order curve has a shallower slope during low LAI* months when the canopy has fewest leaves. The more seasonal field sites, LA and LF, show more flattening of the left-tail curve than LN. This flattening should represent opening of the canopy by leaf loss, to form a graded series of degrees of canopy thinning that contrasts to the inverted L-shape (gap or no gap) structure of the curves from LN evergreen forest and maximum monthly LAI* curves of all sites.

A flat rank-order curve with steep ends implies a homogeneous canopy structure, as at LN, while a curve with a shallower initial slope indicates much canopy disruption and/or patchy distribution of deciduous trees, as in LA2. The LA2 floodplain has the shallowest rank-order curves of all transects, with the lowest maxima and flattest initial portion of all samples. The floodplain forest of LA2 is a dynamic

TABLE 3. Spread of LAI* values at the midpoint of rank-ordered curves representing one calendar year for each measured transect (Fig. 6).

Transect & mid-rank point	Max LAI*	Min LAI*	Max-Min LAI*
LNM 50	6.88	6.28	0.60
LNH 30	6.91	6.16	0.75
LA1 50	5.66	4.54	1.12
LA2 25	4.78	3.63	1.15
LF2 50	6.03	4.4	1.39
LF3 25	6.26	3.79	2.47

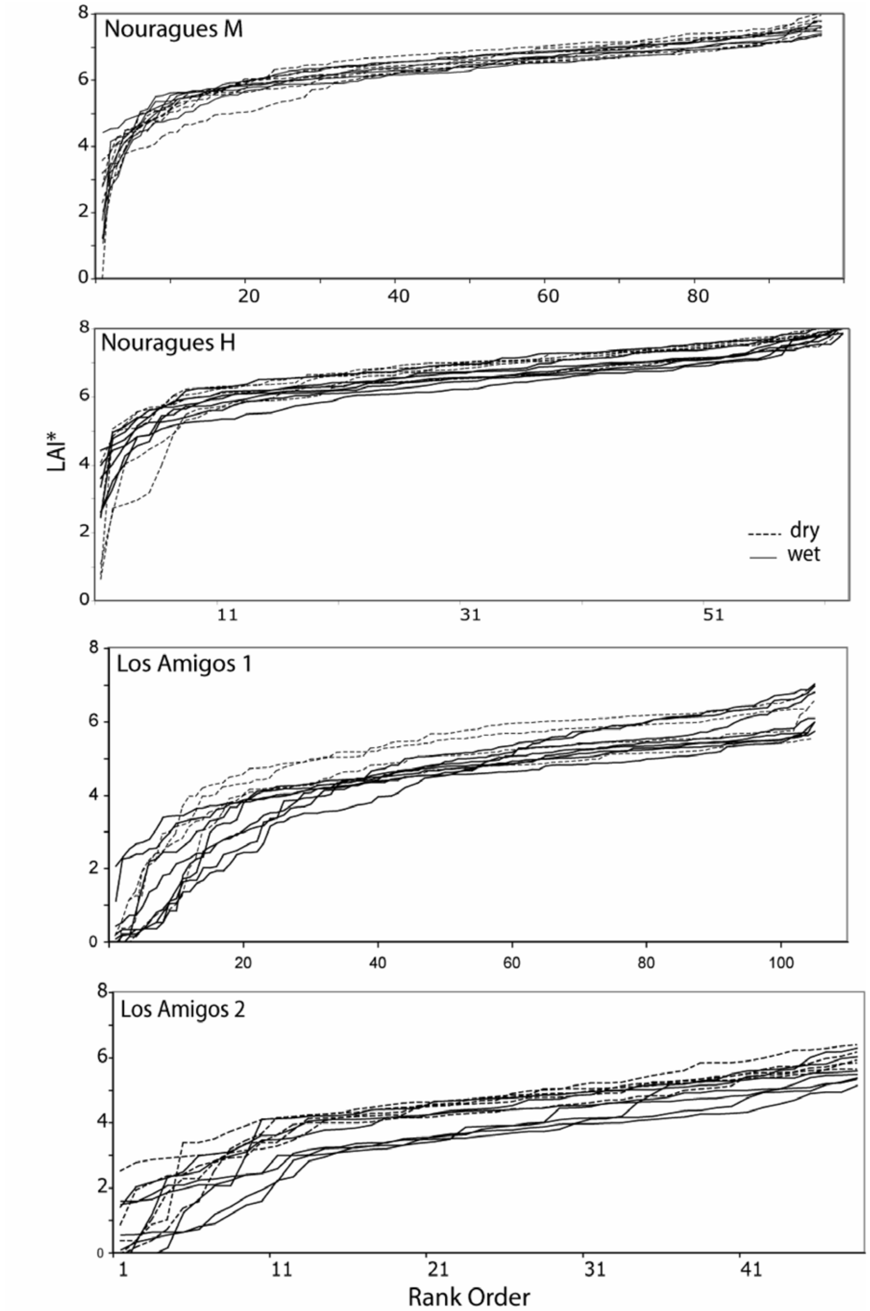

FIG. 6. LAI* data sorted by rank order, representing one calendar year from each transect, 12 months of 2002 for LN and LA; 8 months between March 2001–April 2002 for LF. Note that 3 transects have 100 sampling points, the others 50 or 60 points. Broken lines = dry season, solid lines = wet season.

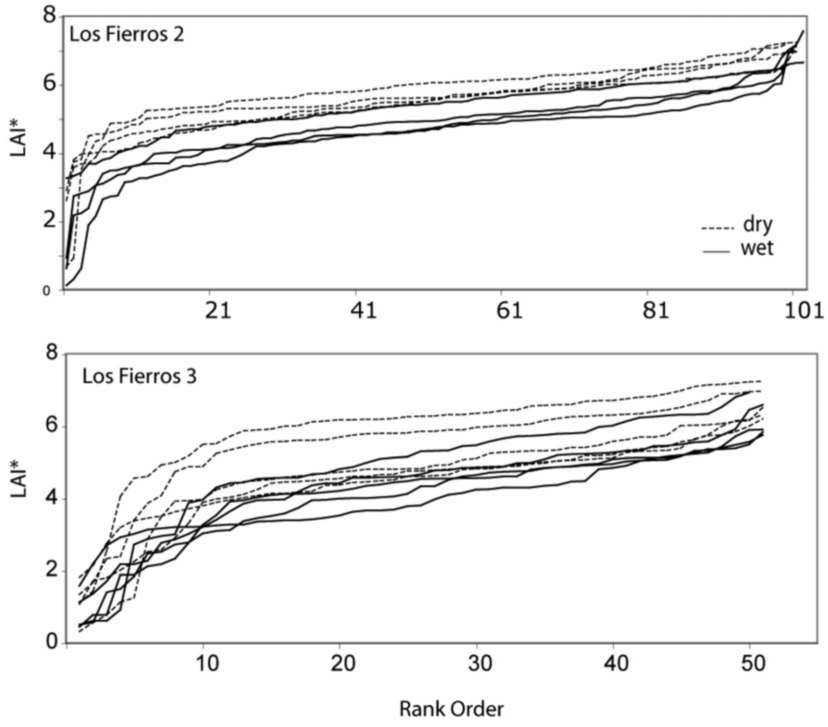

FIG. 6 (continued).

successional sequence on the active floodplain of a large meandering river (Puhakka & Kalliola 1993, Foster 1990). Trees readily uproot in the saturated ground and have higher turnover, with more light gaps, than forest on old, well-drained terraces.

DISCUSSION

Seasonal patterns. Water stress and photoperiod seem to be the main triggers of leaf abscission of tropical forest deciduous species, but the mechanisms triggering abscission are poorly understood, and drought alone does not always cause leaves to drop (Borchert & Rivera 2002, Rivera *et al.* 2002). Forest-wide phenological patterns reflected in our LAI* measurements result from the integrated individual responses of hundreds of tree species, and we do not propose that our results derive from any simple, universal phenological behavior. Except at LF, relatively few of the trees on a transect are simultaneously deciduous, so the overall patterns are unlikely to be dominated by a single category of response. Our measurements show seasonal periodicity in LAI* that varies inversely with monthly rainfall and litterfall, such that peak LAI* values are reached at early to mid dry season: May–July for LF, July–August for LA, and October–November for LN (Figs. 3, 4). In the more seasonal sites LA and LF, values decline slowly, as if through gradual leaf-loss, to reach minima one to three months after the beginning of the rainy season.

It initially seems counter-intuitive that foliage is minimal when there is no water-stress, and maximal during months of drought. Several factors could account for this seemingly paradoxical finding. We surmise that: (1) at our study sites, ground-water stores are sufficient to prevent leaf abscission due to water-stress of susceptible species until the mid to late dry season (see Nepstad *et al.* 1994); and (2) that later dry season deciduousness of emergent trees is counterbalanced by mid-layer and subcanopy leaf retention, so that overall, LAI* is high in mid dry season, after which there is a gradual net leaf-loss that continues to the end of the dry season or the beginning of the rains.

From a functional standpoint, dry season loss of high canopy foliage can provide a seasonal light increase for understory trees, which can benefit by retaining or increasing their foliar surfaces as the emergent trees go bare. In their study of the phenology of 453 individuals of 39 tree species in Lomerío, Bolivia, Justiniano & Fredericksen (2000) found that 17 canopy species were deciduous (63%) and 10 (37%) evergreen while only two understory tree species (17%) were deciduous and 10 (83%) were evergreen. Rainfall influenced the phenology: during a year with little rain from May to July (1996), peak leaflessness was in August, while in a year with June and August rains (1997), leaflessness peaked in September (Justiniano & Fredericksen 2000), suggesting that leaf abscission of most trees was triggered by water-stress. In late September in strongly deciduous forest patches near LF, there is a marked Spring, where despite high temperatures and a total drought, the low understory and herb layer bursts into leaf and bloom in the sunlight below a thin canopy. In late September–October the bare emergents flush with tiny new leaves forest-wide, even when no rain has fallen for months. Such Spring flushing in tree species of semi-deciduous tropical forests worldwide has been shown to be triggered by annual photoperiod differences of as little as 30 min (Rivera *et al.* 2002). Wirth *et al.* (2001) noted that augmented understory irradiance due to seasonal canopy deciduousness could change growth conditions for understory plants, such that the gap- non-gap paradigm for seedling growth might be too simplistic.

The January–March rainy season at the two more seasonal sites, LA and LF, is characterized by afternoon convectional cloud cover, with some days of total overcast; in some months it is difficult to find days clear enough for LAI* measurement. The yearly minimum LAI* during wet-season months likely corresponds to months of minimum insolation. In March–April there is massive, forest-wide mid- and understory leaf flushing at LF and LA, but the new leaves droop vertically for several weeks, and many are red or whitish, with little photosynthetic capacity. These subsequently become functional in May–June, when they contribute to the yearly May–July LAI* maximum. Wet-season cloudiness greatly reduces available radiation, and the seasonal patterns that we observe of maximal LAI* values in June–July are consistent with LAI*, and hence primary production, coinciding with full dry-season months of maximal insolation, but before maximal desiccation of ground water (September–October). Both rainfall and insolation are thus likely to interplay to produce the seasonal LAI* patterns that we here document. A study of a deciduous canopy tree species in Panama showed that wet-season clouds significantly decreased both growth and net CO_2 uptake, and proposed that CO_2 uptake is more limited by light than by water (Graham *et al.* 2003). Wright and van Schaik (1994) hypothesized and presented evidence that tropical forest foliar phenologies are selected to produce leaves to coincide with maximal irradiance. Our results support this hypothesis.

Recent investigation of carbon flux in a central Amazonian forest found that: “Carbon was lost in the wet season and gained in the dry season, which was opposite to the seasonal cycles of both tree growth and model predictions.” (Saleska *et al.* 2003). Our results do in fact confirm that at our study sites carbon gain should be maximal in the early dry season and gradually decrease through the wet season, in step with LAI*, as suggested by the results of Saleska *et al.* (2003).

Not all tropical forests show similar LAI patterns. Like ours, seasonal LAI changes recorded at a Mexican dry forest locality showed an inverse relationship between rainfall and LAI, with maximum LAI at the beginning of the dry season and minimal LAI during the rainiest months (Maass *et al.* 1995). However, on a 50 x 50 m plot on BCI, Panama, Wirth *et al.* (2001) found highest LAI in wet season measurements, so perhaps BCI has a different foliage cycle. As sampling on BCI was restricted to one wet-season and two dry season months, we cannot easily compare our results with theirs. Furthermore, their small plot size may have caused measurements to be influenced by the seasonal behavior of a few individual large trees, rather than reflecting forest-wide patterns. Seasonal LAI data from a large plot (2 x 2 km) in the Central African Republic (CFA) show a clearly different pattern than ours, with LAI directly related to rainfall, decreasing with decreasing dry-season rains, and increasing regularly with monthly rainfall increases in the wet season (de Wasseige *et al.* 2003). These differences between the LAI seasonal patterns at different localities or on different continents may be due to differences in groundwater availability or seasonal insolation, but we are still a long way from understanding them.

Apart from deciduousness, other factors that could cause seasonal LAI* differences include changes in leaf angle or heavy predation of leaves by arthropods. Leaves are most likely to droop (and intersect less light, lowering LAI*) if they are either weighed down by water after rain or lose turgidity under water-stress; leaves in the top canopy layer may change angle in response to the heat of direct insolation (Graham *et al.* 2003). Predation can sometimes nearly defoliate trees, and might reach levels easily detectable with our meter. Species-rich forests are likely to show small overall defoliation by arthropods, but Emmons has observed massive generalized seasonal leaf predation on Borneo. We cannot evaluate the magnitude of such effects on our data.

The sites cross a latitudinal gradient from 04° N to 14° S, and one can therefore ask whether some of the observed LAI* variation could be due to seasonal solar radiation differences. Because we take light measurements around noon, it is easy to compute that the largest yearly variation of clear sky light intensity is < 22%. This produces a maximum LAI* error of 0.25, much smaller than the amplitude of the observed seasonal excursions. The true error is certainly smaller because this first-order geometric effect is attenuated by diffusion due to nebulosity and canopy penetration. We are thus confident that the pattern of inter- and intra-site differences is due to foliar phenology and not to seasonal, latitude-dependent geometric variations of solar intensity.

Within-site patterns. As shown by Borchert and Rivera (2002) and by Armbrüster *et al.* (2004), phenology and LAI are sensitive to local edaphic conditions and irregular rainfall variations. At the most seasonal site, LF, the wetter transect had higher LAI* in some dry months than did the more xeric transect, notably in June–July 01, when almost no rain fell (Fig. 3). This is the predicted result when drought stress triggers leaf abscission (Borchert & Rivera 2002).

In contrast, in most months, the wetter of the two transects at LA and LF not only had lower LAI* values than did well-drained upland transects, but intrasite transects sometimes showed slightly different seasonal patterns. Wetter transects showed greater reduction in LAI* at mid wet season than did drier transects (Fig. 3; note Jan 2002), and in 2001 at LF and 2002 at LA, the wetter transect developed its maximum LAI* two months later in the dry season than did the more well-drained site. The lowest LAI* occurred when the soils were saturated with standing surface water. Water-saturation is a stress factor that in some species can take months to overcome as the soil dries out (Armbrüster *et al.* 2004). The sharp drop in LAI* of saturated or flooded forests during months of heavy rain likely reflects a negative effect on foliage of root hypoxia, low nutrient availability, and/or mycorrhizal insufficiency (Armbrüster *et al.* 2004). A field for further research is whether foliage suppression by unusually heavy rains is subsequently reflected in low or delayed flowering or fruit productivity, as suggested by Foster (1982).

Inter-annual patterns. Although at each site there was a generally repeating annual pattern from year to year, the correspondence was not at all perfect. Examination of the rainfall and LAI* (Fig. 3) shows that anomalies in rain are sometimes closely mirrored (inversely) by the LAI*. We are continuing measurements, and hope to arrive at a better understanding of the associations between rainfall, litterfall, tree phenology, and LAI* values.

Inter-site differences. The differences in tree species densities at the three sites (Table 1) may influence seasonal patterns: in richer forests, the presence of more species should dampen the influence of the deciduousness of individual species or groups of species with similar phenological attributes. Because, due to edaphic and historical factors, the forests within any region vary greatly in both floristics and structure we hesitate to generalize to forest-wide values from only two transects at a site. However, we have measured at least 5 km of additional, independent transects in "tall" forests at all three study areas, and these show a considerable within-site similarity in LAI* magnitude and pattern (all sites have forests with other patterns, such as palm, bamboo, liana, or swamp forests).

The LN Guianan forests have a more uniformly closed and layered canopy structure and much higher average LAI* in all months than do those at LA and LF (Fig. 2). In contrast, during peak leaflessness, LF semi-deciduous forests are sometimes so open that it is difficult to position the measuring apparatus so that no sunspot falls on it. Paradoxically, these more deciduous Bolivian forests nonetheless reach higher average LAI* at peak values than do the more evergreen Peruvian forests of LA (Fig. 4D). To compensate for a shorter annual productivity period in the seasonal Bolivian forests, seasonally deciduous species may spread a greater foliage area during their foliage peak than the more evergreen canopy trees at LA. Strong dry season insolation may facilitate a pulse of high productivity before groundwater stores are depleted.

Conclusions. The simple LAIL methodology can yield useful comparative data that provide new insight into seasonal and spatial LAI dynamics. The method makes it easy to sample large areas quickly, so that it is feasible to undertake long-term studies with small investments of manpower and money. Our results have uncovered patterns of seasonality that are consistent with data from other sources on litterfall and carbon flux. The LAIL methodology is highly sensitive to small differences and could be used to detect climate change by long-term monitoring. We are currently studying analysis techniques that should allow us to use LAIL-generated data to characterize and model forest structure.

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