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Seasonal leaf dynamics in an Amazonian tropical forest

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ABSTRACT

The ecological consequences of climate change for large tropical forests such as the Amazon are likely to be profound. Amazonian forests strongly influence regional and global climates and therefore any changes in forest structure, such as deforestation or die-back, may create positive feedback on externally forced climate change. Monitoring, modelling and managing the impacts of anthropogenic climate change on forest dynamics is therefore an important objective of forest researchers, and one that requires long-term data on changes at the level of community, populations and phenotypes. In this paper we provide the most comprehensive study yet on the seasonal dynamics of various leaf traits: leaf area index (LAI), leaf mortality (LM), leaf biomass (LB), leaf growth rate (LG), and leaf residence time (TR) from 50 experimental plots in a forest site at Belterra, Pará State, Brazil. From this study we estimate annual mean leaf area index (LAI) to be 5.07 m^2 m^{-2} and annual mean leaf dry biomass to be 0.621 kg m^{-2}. The typical leaf grew at 0.049 kg m^{-2} $month^{-1}$ and remained on the tree for 12.7 months. We compare these results to other similar studies and critically discuss the factors driving leaf demographics in Amazonia.
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1. Introduction

Anthropogenic changes in temperature and rainfall patterns are predicted to significantly influence vegetation dynamics and the spatial distribution of different biomes with accompanying changes in albedo and evapotranspiration which, in turn, feedback into global climate systems (e.g. Foley et al., 2003). The feedback between climate and vegetation dynamics is, of course, universal but may be particularly important in certain ecosystems, such as tropical forests, because of their enormous size and correspondingly vast stores of carbon. Unsurprisingly then, much attention has focused on the role of the Amazon, the Earth's largest remaining area of continuous rainforest, in global change research. For example, Amazonian forests are thought to store 120 ± 30 Pg C of biomass carbon (Malhi et al., 2006).

In a recent review, Malhi et al. (2008) identified several ways in which the Amazon may influence global and regional climate cycles: first, widespread deforestation can have a positive feedback on externally forced climate change. It is thought that the Amazon had lost about 837,000 km^2 of forest by 2001 (Soares-Filho et al., 2006) and has lost a staggering 25,000 km^2 $year^{-1}$ to deforestation throughout the 1990s (Achard et al., 2002). Second, intact forests, especially those in fertile western Amazonia may represent a carbon sink. Third, some models have predicted that continuing loss of forest may interfere with regional precipitation cycles and cause a qualitative change to a drier climate regime across the region (Costa and Foley, 2000; Senna et al., 2009). Finally, deforestation induced changes in aerosol loading may also influence regional patterns of precipitation.

Monitoring and modelling the local and global effects of climate changes on the ecology of the Amazon rainforest is clearly essential for the development of effective mitigation and adaptation strategies and for effective forest management. It is equally clear that realistic climate models crucially depend on accurate data on vegetation dynamics and should ideally include information on several biophysical variables of the vegetation. One of the greatest barriers to the development of truly predictive simulations is the difficulty in obtaining detailed and realistic information on parameters such as plant cover, growth rate, biomass, etc. This gap in information is especially apparent in the Amazon rainforest where issues of scale and the technical challenge of estimating a complex interrelated suite of ecological metrics have hampered the development of sufficiently sophisticated assessment and monitoring programmes.

Understanding the vegetation dynamics of forests requires an in-depth knowledge of changes in roots, stems, branches and leaves over time, and how these tree characteristics vary in relation to important environmental variables. Assessing the leaf dynamics of forest trees is especially challenging since turnover is often high

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and there is abundant variation in leaf phenotypic characteristics between and within individuals, populations and species (Malhado et al., 2009). Moreover, the allometric relationship between tree size and leaf area is poorly known for many species making scaling-up problematic. Tree ecologists with an interest in leaf dynamics have typically concentrated on assessing a limited number of variables, most notably leaf area index (LAI). For example, Caruzzo and da Rocha (2000) estimated LAI using hemispheric photographs, collected in two areas situated in the Jarú Biological Reserve, and reported average values of 4.79 ± 1.27 m^2 m^{-2} (=m^2 leaf per m^2 ground) and 4.96 ± 1.3 m^2 m^{-2}. In a spatial study, Roberts et al. (1996) using litterfall methodology reported LAI values of: Ji-Parana—4.63 m^2 m^{-2}; Manaus—6.1 m^2 m^{-2}; and Marabá—5.38 ± 0.43 m^2 m^{-2}. Myneni et al. (2007) built on this work to investigate temporal dynamics by assessing LAI of the Amazon tropical forest using remote sensing data for the period between 2002 and 2005. They observed a seasonal amplitude of 1.2 m^2 m^{-2} in LAI, which corresponds to a 25% variation compared to the annual mean of 4.7 m^2 m^{-2}. Doughty and Goulden (2008) also explored LAI seasonally. They took *in situ* measurements (over almost 3 years) of the amount of PAR intercepted by the canopy and reported LAI values from 6 m^2 m^{-2} in August 2001 to 10 m^2 m^{-2} in March 2004. These results overestimate most of the values in the literature, and may be a consequence of the methodology used (interception of direct radiation using the entire PAR spectrum), which is contaminated by radiation in the green waveband reflected by the leaves.

Field observation on seasonal patterns of leaf dynamics in the Amazon forest is limited and, to our knowledge, there are very few reports in the literature of important variables such as leaf residence time, biomass accumulation, biomass partitioning, and mortality rate. In this study we attempt to fill this important gap by describing the results of an in-depth study on the temporal patterns of leaf area index (LAI), leaf mortality (LM), leaf biomass (LB), leaf growth rate (LG), and leaf residence time (TR) for an experimental Amazonian rainforest site at Belterra, Pará State, Brazil.

2. Methods

All leaf measurements were taken at the experimental site known as "km 67" (2°51′S and 54°58′W) of the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) project, located in the Tapajós National Forest (FLONA Tapajós). This site is situated in an area of Amazonian primary tropical forest belonging to the municipality of Belterra, Pará state, Brazil. The forest is mostly evergreen with a few deciduous species. The canopy is characterized by large emergent trees up to 55 m tall, with a closed canopy at approximately 40 m; there are few indications of recent anthropogenic disturbance other than hunting trails. Abundant tree species include the tauari (*Couratari guianensis*), matamatá (*Eschweilera* sp.), maçaranduba (*Manilkara huberi*), andiroba (*Carapa guianensis*), tachi (*Sclerolobium paniculatum)*, abiu (*Pouteria* sp.), breu (*Protium decandro*), and louro (*Licaria guianensis*). Soils are nutrient-poor clay oxisols with low organic content. The monthly incident photosynthetically active radiation (PAR) values vary from 640 to 850 μmol m^{-2} s^{-1} (Senna et al., 2005). The annual mean precipitation is 1911 mm, the mean temperature is 25 °C, and the dry season extends from July to November (Juárez et al., 2009). We established 50 plots (Fig. 1) around the micrometeorological site of the LBA Experiment in Amazonia. Within each plot, monthly measurements were taken between December 2003 and November 2004.

Leaf area index (LAI) measurements were taken using three LAI-2000 Plant Canopy Analysers (Li-Cor, 1992). This technique is referred to as the indirect non-contact method and represents the

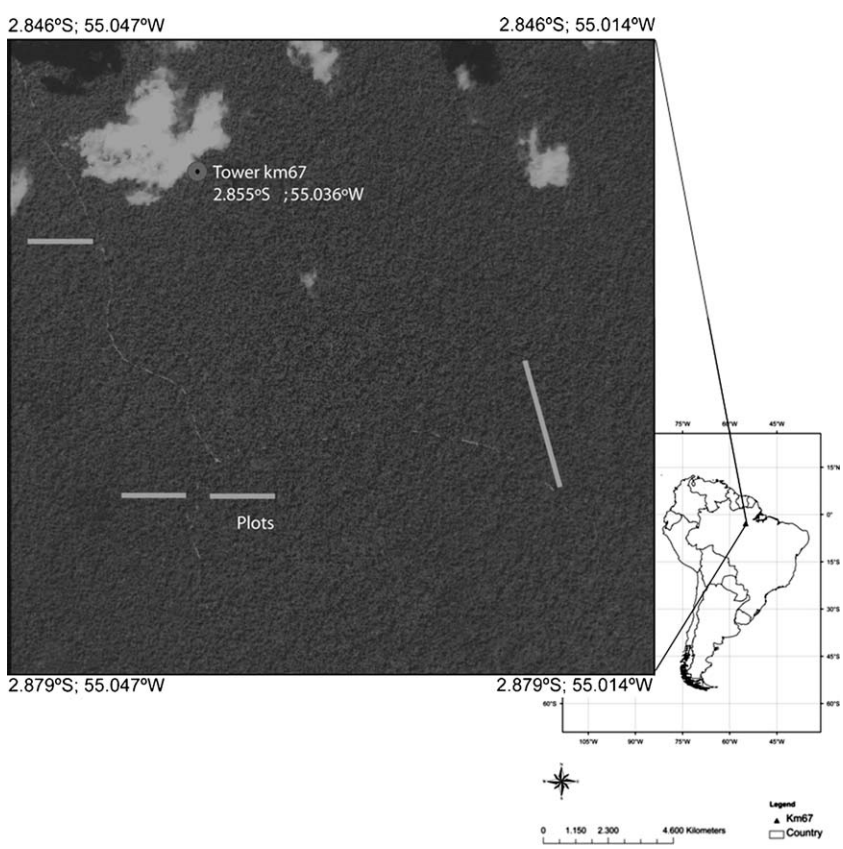

Fig. 1. Location of the study area (plots) in Tapajós National Forest, Belterra, State of Pará, Brazil. This is an Ikonos image showing the layout of 4 transects. The longest transect (25 m × 500 m) shows the location of 20 (25 m × 25 m) plots. The other 3 transects (25 m × 250 m) contain 10 plots per transect. Each plot has 5 subplots (not shown).

projected area of leaves taking into account individual leaf inclinations (Scurlock et al., 2001). One of the instruments was installed on the top of a tower to measure the diffuse radiation on the top of the canopy, while the other two measured diffuse radiation at about 1 m high. The Plant Canopy Analyser measures diffuse radiation with a light sensor, in the 320–490 nm range, where the radiation scattering by leaves is minimal. LI-COR software was used to determine the canopy transmittance and the LAI (m^2 leaf per m^{-2} ground) per subplot using an instrument-specific formulation.

Litterfall measurements were taken by 250 litter baskets (0.25 m^2 each) installed in each subplot. Leaf litter was collected every month and the leaves were separated, dried in an oven for 24 h, and then weighed. Leaf mortality (LM) (kg dry biomass m^{-2} $month^{-1}$) at each plot was calculated as the average of the 5 subplot measurements.

Leaf biomass LB (kg m^{-2}) was calculated by dividing LAI by specific leaf area (8.16 m^2 leaves/kg dry leaf biomass measured at a site 16 km away from the study sites) (Figueira et al., 2002). Although this figure for specific leaf area is at the low end of the range of values reported for this parameter in Roberts et al.' (1996) review of physiological traits of Amazonian forests (8–27 m^2/kg for sites in Manaus and Marabá), most of their sites are strongly skewed towards lower values (cf. Fig. 3, p. 292) suggesting that the figure used in the current study is robust.

Leaf growth LG (kg m^{-2} $month^{-1}$) at each plot was calculated through a mass balance of leaves at each plot, i.e., $LG_t = (LB_t - LB_{t-1})/\Delta t + LM_t$, where Δt is the time interval between measurements (1 month). There is an inherent error in all LAI measurements due to the indirect nature of the measurements. This error might influence leaf biomass calculation and will therefore be transferred to the leaf growth rate results.

Finally, leaf residence time (TR) was calculated as the ratio between the annual mean leaf biomass and the annual mean leaf mortality ($TR = \overline{LB}/\overline{LM}$). LAI and LM measurements were initially taken at each subplot and then averaged to calculate the plot value. LB, LG and TR were calculated at the plot level.

3. Results

3.1. Leaf area and biomass

Annual mean leaf area index (LAI) for the 50 plots was 5.07 m^2 m^{-2} (±0.17 S.E.) (Table 1). There was no strong pattern of seasonal variation in LAI (Fig. 2a) and this is reflected in the slight increase in the LAI values from August to December. Moreover, there was very low monthly variation in LAI (Fig. 2a) which is reflected in only 0.4 m^2 m^{-2} difference between the month with the highest LAI (December, with 5.23 m^2 m^{-2}) and the month with the lowest LAI (April with 4.8 m^2 m^{-2}). This value represents only 8% of the annual mean of 5.07 m^2 m^{-2}.

Annual mean leaf biomass for the 50 plots is 0.621 kg m^{-2} (±0.020 S.E.) (6.21 Mg ha^{-1}) (Table 1). The annual pattern of leaf biomass (Fig. 2b) follows LAI seasonal patterns (Fig. 2a).

Table 1
Annual mean averages of leaf area index (LAI), leaf dry biomass (LB), leaf growth (LG), leaf mortality (LM), and leaf residence time (TR) with corresponding standard errors (S.E.).

	LAI (m^2 m^{-2})	LB (kg m^{-2})	LM (kg m^{-2} $month^{-1}$)	LG (kg m^{-2} $month^{-1}$)	TR (month)
Mean	5.07	0.621	0.049	0.046	12.7
S.E.	0.17	0.020	0.004	0.025	

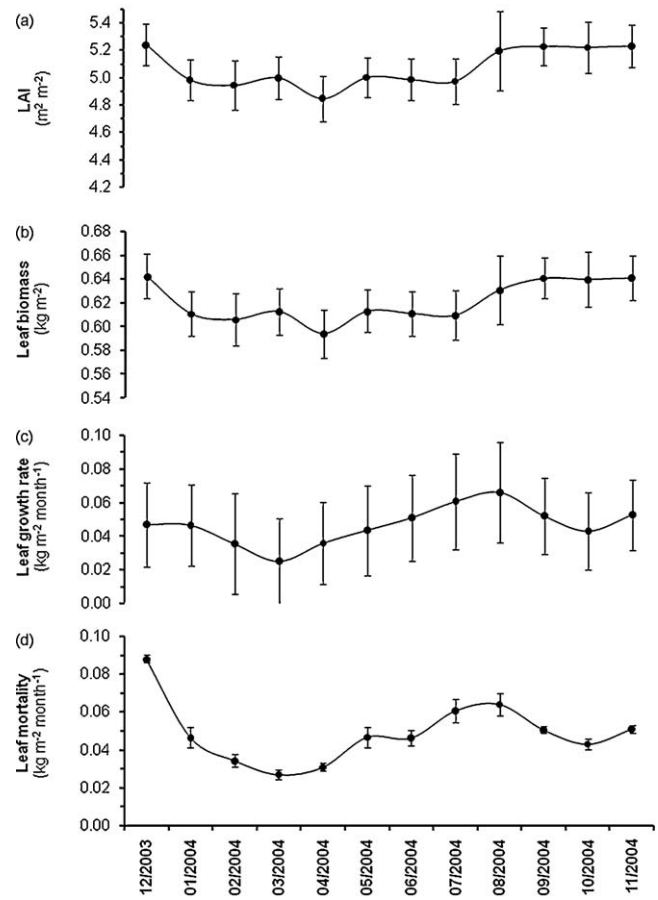

Fig. 2. Monthly variation in leaf dynamics from December 2003 to November 2004: (a) mean seasonal variation of leaf area index; (b) mean seasonal variation of leaf biomass; (c) seasonal variation of leaf growth rate; (d) seasonal variation of leaf mortality. The dry season runs from June to November. Error bars indicate 95% confidence intervals.

3.2. Leaf dynamics

We were able to quantify four separate parameters in the life-cycle of a leaf: growth rate, mortality rate, residence time and litterfall. Leaf growth rate in the period occurred at an average rate of 0.046 kg m^{-2} $month^{-1}$ (Table 1, Fig. 2c). Leaf residence time at this site is 12.7 months (Table 1). We estimated total annual litter fall to be 0.588 kg m^{-2} (±0.044 S.E.) (5.88 Mg ha^{-1}). Annual mean leaf mortality for the 50 plots was 0.049 kg m^{-2} $month^{-1}$ (Table 1). The temporal pattern of leaf mortality was more complex than biomass or LAI and was characterized by a high peak in mortality in December (the end of the dry season), followed by a second gentle increase that peaked at the start of the dry season around June to August (Fig. 2d).

4. Discussion

Leaf area index (LAI) and its dynamics is one of the key parameters for modelling forest growth and, by extension quantifying the role of forests in global carbon cycles (Clark et al., 2008). It is therefore critical for model parameterization that accurate methods for direct leaf measurements are developed (MacFarlane et al., 2007), and that these data are rapidly made available to the scientific community. This need is especially apparent in the Amazon rainforest which, as the largest remaining continuous area of tropical moist forest in the world, is thought to play a crucial role in global climate and carbon cycles (Malhi et al., 2008).

The figure reported here for mean annual leaf area index for the 50 plots was 5.07 $m^2\ m^{-2}$ which is remarkably similar to the reported LAI of 4.9 $m^2\ m^{-2}$ for 61 published observations in tropical forests by Asner et al. (2003). More generally, Scurlock et al. (2001) reported that LAI ranged from 3.80 to 7.10 $m^2\ m^{-2}$ in Tapajós forests (both primary and logged forests) using data from the Worldwide Historical LAI data set. Our figure is also very similar to the groundbreaking landscape scale measurement in Costa Rican rainforest by Clark et al. (2008). In this study they used a modular tower and stratified random sampling to harvest all foliage from forest floor to canopy top across 500 ha of old growth forest and estimated LAI to be 6.00 ± 0.32 (mean ± S.E.). More recently, Juárez et al. (2009) used hemispherical photograph methodology to calculate LAI reporting a mean value of 5.07 $m^2\ m^{-2}$—identical to that reported here. Furthermore, Brando et al. (2008), using LI-COR 2000, reported a mean value for LAI of approximately 5.9 $m^2\ m^{-2}$ (derived from Fig. 5, p. 1844) using 6 years of data. Although it has been reported elsewhere that LAI-2000 might systematically under-estimate LAI (Asner et al., 2003), our results are broadly similar to measurements reported on both global and local scales.

Interestingly, we found no significant seasonality in our LAI measurements and the difference in magnitude between the highest (December) and lowest (April) months was only 0.4 $m^2\ m^{-2}$. This figure is about a third of the LAI amplitude reported by Myneni et al. (2007) who, using remotely sensed data from the period 2000–2005, observed a LAI amplitude of 1.2 $m^2\ m^{-2}$ corresponding to 25% of the annual mean of 4.7 $m^2\ m^{-2}$. A similar result was also found by Doughty and Goulden (2008). Likewise, Juárez et al. (2009) working in Tapajós National forest also report a much higher LAI amplitude than in the current study. This discrepancy in results is interesting and may partly reflect the evergreen nature of tropical forests in contrast to well-studied temperate forests. However, given that one of the studies – Juárez et al. (2009) – was also in a tropical forest and purported to show a clear seasonal pattern in LAI this explanation is not sufficient. Possible reasons for this observed discrepancy could be yearly fluctuations in leaf parameters (Juárez et al. study ran from 2000 to 2002) or even differences in experimental methods—Juárez et al. (2009) calculate LAI using analysis of histograms from hemispherical photographs. Clearly, further studies are needed to confirm these seasonal differences and to compare the effectiveness and accuracy of different methods of quantifying LAI.

The measurement of leaf biomass is also important for understanding carbon cycles since it is an important and potentially variable component of total vegetation biomass. Our value of 6.21 Mg ha^{-1} annual mean leaf dry biomass for the 50 plots is once again similar to those reported in the literature. Specifically, McWilliam et al. (1993) report a value of 6.3 ± 0.5 Mg ha^{-1} for Amazonian *terra firme* forest near Ducke Reserve, Manaus, Brazil. However, it should be noted that both the value reported here and the McWilliam et al. (1993) estimate are approximately 2–4 Mg ha^{-1} lower than other studies from Amazonia or measurements taken from rainforest in Puerto Rico (reviewed in McWilliam et al., 1993).

To fully understand the dynamics of the Amazonian canopy and the carbon contained therein it is also necessary to accurately quantify the life-history of leaves. This is because it is the interaction between leaf growth, leaf life span (residence time), and temporal dynamics (e.g. seasonality) of leaf production that controls plant productivity (Janzen, 1975). In the current study we found that a typical leaf grew at an average of 0.05 kg m^{-2} $month^{-1}$ and remained on the tree for 12.7 months. This latter figure is much higher than the 6-month value that Smith et al. (1998) found for leaves from *terra firme* forest in the Curuá-Una Forest Reserve in eastern Pará, Brazil.

Our estimate for total annual litterfall (5.88 Mg ha^{-1} $year^{-1}$) is very similar to recently reported values (5.74 Mg ha^{-1} $year^{-1}$, Chave et al., 2009) in a macrogeographic study in South America. However, it is slightly lower than those recorded in other Amazonian primary forest sites: range 9.4–12.4 Mg ha^{-1} $year^{-1}$ (Jari landholding, Pará, Barlow et al., 2007); 6.6–9.5 Mg ha^{-1} $year^{-1}$ (Tapajós National Forest; Nepstad et al., 2002); and 8.8–9.5 Mg ha^{-1} $year^{-1}$ (Manaus area, Vasconcelos and Luizão, 2004) and in other humid tropical forests (see Sundarapandian and Swamy, 1999). In an evergreen rainforest, the relationship between yearly litterfall and LAI is not as direct as it is in mid-latitude deciduous forests. Higher levels in leaf mortality in an evergreen rainforest may imply either a higher LAI, a lower specific leaf area or a lower residence time. Unfortunately, these studies did not make simultaneous measurements of all these variables. Unlike LAI and leaf biomass, litterfall shows a distinct seasonality and occurs at greater rates in the dry season, as has been reported in others studies (e.g. Sundarapandian and Swamy, 1999; Barlow et al., 2007). The second, higher peak in leaf mortality that occurs in December might be due to other more stochastic factors such as variation in wind velocity. More generally, even though litterfall peaks during the dry season, there is typically a relatively high degree of monthly variability (cf. Mesquita et al., 1998 p.171).

5. Conclusions

In this study we estimate annual mean leaf area index (LAI) to be 5.07 $m^2\ m^{-2}$ and annual mean leaf dry biomass to be 0.621 kg m^{-2}. The typical leaf grew at 0.049 kg m^{-2} $month^{-1}$ and remained on the tree for 12.7 months. An accurate analysis of vegetation needs to take into consideration the annual variability of the system and the seasonal results reported here significantly contribute towards filling these gaps. The data reported here provide important parameters in ecological and modelling studies, as it is now possible to seasonally parameterize leaf growth, instead of the previously assumed regular growth. It is also clear that there is great variability in the demographics of canopy leaves in rainforest trees both within the Amazon and between the Amazon and other tropical rainforests. Quantifying this variability at multiple spatial scales is an immense technical and logistic challenge. However, this challenge will need to be met if scientists are to develop accurate and precise global models of the interaction between climate and forests.

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