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Large Seasonal Swings in Leaf Area of Amazon Rainforests

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Despite early speculation to the contrary, all tropical forests studied to date display seasonal variations in the presence of new leaves, flowers, and fruits. Past studies were focused on the timing of phenological events and their cues but not on the accompanying changes in leaf area that regulate vegetation–atmosphere exchanges of energy, momentum, and mass. Here we report, from analysis of 5 years of recent satellite data, seasonal swings in green leaf area of ≈25% in a majority of the Amazon rainforests. This seasonal cycle is timed to the seasonality of solar radiation in a manner that is suggestive of anticipatory and opportunistic patterns of net leaf flushing during the early to mid part of the light-rich dry season and net leaf abscission during the cloudy wet season. These seasonal swings in leaf area may be critical to initiation of the transition from dry to wet season, seasonal carbon balance between photosynthetic gains and respiratory losses, and litterfall nutrient cycling in moist tropical forests.

remote sensing | tropical forests phenology | vegetation climate interaction

The trees of tropical rainforests are known to exhibit a range of phenological behavior, from episodes of ephemeral leaf bursts followed by long quiescent periods to continuous leafing, and from complete intraspecific synchrony to complete asynchrony (1). Several agents (e.g., herbivory, water stress, day length, light intensity, mineral nutrition, and flood pulse) have been identified as proximate cues for leafing and abscission in these communities (1–8). These studies were focused on the timing of phenological events but not on the accompanying changes in leaf area. Leaves selectively absorb solar radiation, emit longwave radiation and volatile organic compounds, and facilitate growth by regulating carbon dioxide influx and water vapor efflux from stomates. Therefore, leaf area dynamics are relevant to studies of climatic, hydrological, and biogeochemical cycles.

The sheer size and diversity of rainforests preclude a synoptic view of leaf area changes from ground sampling. We therefore used data on green leaf area of the Amazon basin (≈7.2×10^6 km^2) derived from measurements made by the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the National Aeronautics and Space Administration's (NASA's) Terra satellite [see ref. 9 and supporting information (SI) *Materials and Methods*]. These data were expressed as one-sided green leaf area per unit ground area [leaf area index (LAI)].

Results

Seasonality in LAI Time Series. Leaf area data for the Amazon rainforests exhibit notable seasonality, with an amplitude (peak-to-trough difference) that is 25% of the average annual LAI of 4.7 (Fig. 1*A*). This average amplitude of 1.2 LAI is about twice the error of a single estimate of MODIS LAI, and thus is not an artifact of remote observation or data processing (see *SI Materials and Methods*). The aggregate phenological cycle appears timed to the seasonality of solar radiation in a manner that is suggestive of anticipatory and opportunistic patterns of leaf flushing and abscission. These patterns result in leaf area leading solar radiation during the entire seasonal cycle, with higher leaf area during the shorter dry season when solar radiation loads are high and lower leaf area during the longer wet season when radiation loads decline significantly. This seasonality is roughly consistent with the hypothesis that in moist tropical forests, where rainfall is abundant and herbivore pressures are modest, seasonal increase in solar radiation during the dry season might act as a proximate cue for leaf production (1, 2, 4).

In a community dominated by leaf-exchanging (10) evergreen trees, leaf area can increase if some of the older leaves that are photosynthetically less efficient because of epiphylls and poor stomatal control are exchanged for more numerous new leaves. Leaf area can decrease if the new leaves are less numerous than

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Abbreviations: LAI, leaf area index; MODIS, Moderate Resolution Imaging Spectroradiometer.

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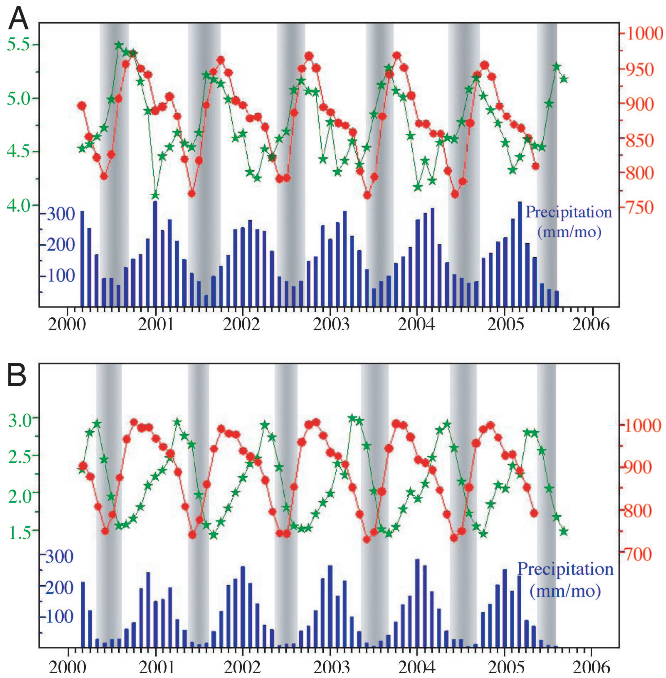

Fig. 1. Time series of monthly LAI from the Terra MODIS instrument (green), monthly maximum of hourly average surface solar radiation from the Terra Clouds and the Earth's Radiant Energy System (CERES) and Geostationary Operational Environmental Satellite 8 (GOES-8) instruments (red), and monthly merged precipitation from the Tropical Rainfall Measuring Mission (TRMM) and other sources (blue). (*A*) Time series based on data averaged over all Amazon rainforest pixels, as identified in the MODIS land cover map (SI Fig. 4*B*), south of the equator. The start of the data record is March 2000 and the end points are September 2005 (LAI), May 2005 (solar radiation), and August 2005 (precipitation). The shaded areas denote dry seasons, defined as months with precipitation <100 mm or less than one-third the precipitation range [0.33·(maximum–minimum) + minimum]. The solar radiation data are for all sky conditions and include direct and diffuse components. (*B*) Same as *A* except that the data are from savanna and grassland pixels adjacent to the Amazon basin in Brazil and south of the equator (SI Fig. 4*B*). The shaded areas denote dry seasons, defined as months with precipitation <50 mm. Information on the data is given in *SI Materials and Methods*.

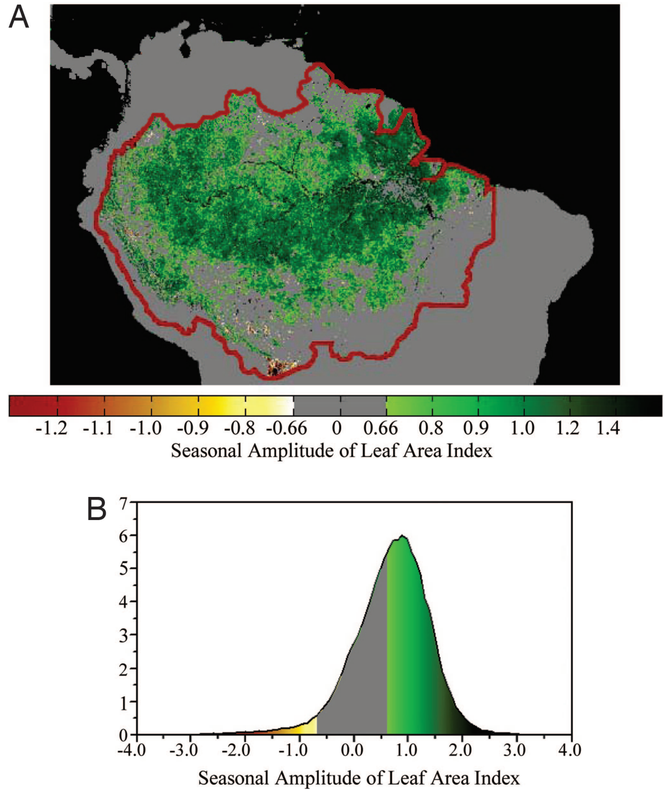

Fig. 2. Seasonal amplitude of LAI. (*A*) Color-coded map of LAI amplitudes greater than 0.66 or less than −0.66; this threshold (|0.66|) is the smallest LAI difference discernable with the MODIS LAI data set (see *SI Materials and Methods*). In regions with dry seasons longer than 3 months, the amplitude is calculated as the difference between the maximum 4-month average LAI in the dry season minus the minimum 4-month average LAI in the wet season. Where the dry season is three or fewer months, the amplitude is calculated as the difference between the dry-season average LAI and the minimum 4-month average LAI in the wet season. The dry and wet seasons are defined based on the precipitation data set at 15′ spatial resolution (see *SI Materials and Methods*). Thus, the seasons vary spatially and interannually. (*B*) Distribution of LAI amplitude for all Amazon rainforest pixels. The color scheme is similar to that in *A*.

the older ones that are dropped. If such exchanges are staggered in time among the individuals over a large area, for example due to asynchrony (7), they can result in a gradually increasing spatially averaged leaf area over a period of several months during the ascending phase of the seasonal cycle, and a gradually decreasing leaf area during the descending phase, while maintaining the evergreen character of the rainforest (Fig. 1*A*). These patterns of net leaf flushing and abscission also generate higher leaf litterfall in the dry season relative to the wet season, as reported in refs. 11–13. Such a leaf strategy will enhance photosynthetic gain during the light-rich dry season (14–19), provided the trees are well hydrated (2), and reduce respiratory burden during the cloudy wet season.

Leaf area changes in the adjacent grasslands and savannas in Brazil are concordant with rainfall data (Fig. 1*B*): higher leaf area in the wet season and lower leaf area in the dry season. This expected behavior imbues confidence in the opposing seasonality of deep-rooted and generally well hydrated (2), but light-limited (2, 4, 17, 18), rainforests inferred from the same LAI data set.

Geographic Details of Leaf Area Changes. The satellite data provide geographic details of leaf area changes in the Amazon (Fig. 2*A*). The region with a distinct seasonality of leaf area spans a broad contiguous swath of land that is anchored to the Amazon River, from its mouth in the east to its westernmost reaches in Peru, in the heart of the basin. This pattern is notable for at least two reasons. First, for its homogeneity; a higher dry-season leaf area relative to the wet season is observed in ≈58% of all rainforest-occupied pixels, whereas only 3% show the opposite change (Fig. 2*B*). Second, the homogeneous region roughly overlies the precipitation gradient (20) in the basin (see *SI Materials and Methods* and SI Fig. 4*C*), suggesting that the amplitude is, to a first approximation, independent of the duration and intensity of the dry season. For example, an amplitude of ≈1 LAI unit is observed in areas with two to five dry months in a year. Ostensibly, these forests maintain high leaf area (19, 21) and remain well hydrated during the dry season in nondrought years (see *SI Materials and Methods* and SI Fig. 5) via their deep root systems (2, 22) and/or through hydraulic redistribution (23, 24), which is also verified through a recent model study (see *SI Materials and Methods*: *Modeling GPP Seasonality of Amazon Rainforests by Constraining Rooting Depths*). Similar changes are not seen in ≈40% of the rainforest pixels, some of which represent transitional and drier rainforests to the south and east.

Correlation Among Changes in Leaf Area, Solar Radiation, and Precipitation. To associate quantitatively the changes in leaf area, solar radiation, and precipitation, we correlated the successive

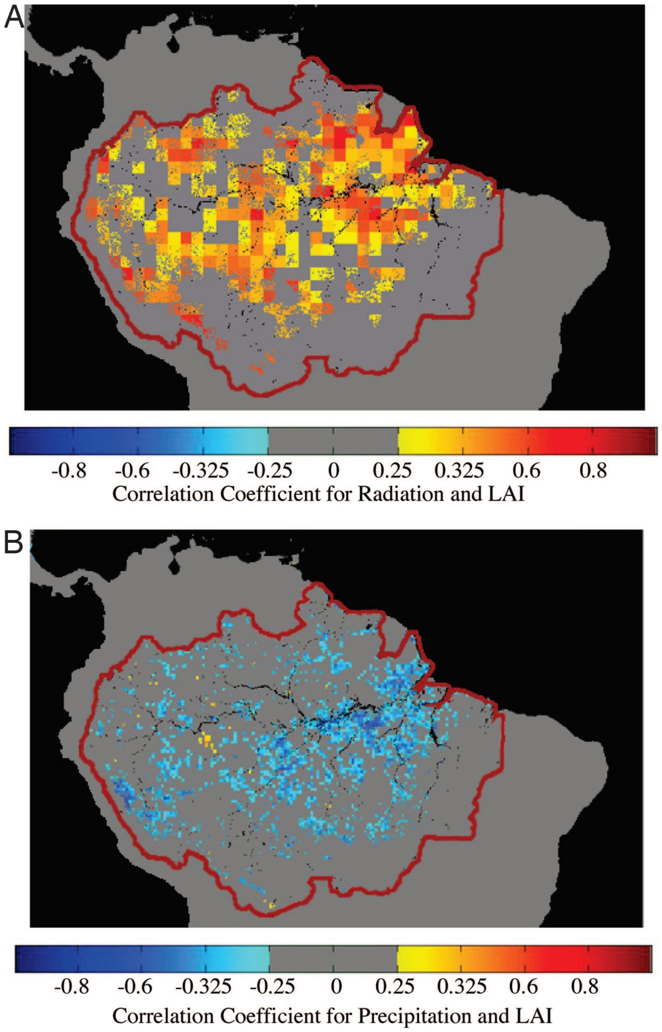

Fig. 3. Correlation coefficients. (*A*) Correlation between first differences of LAI and solar radiation. The first differences of LAI [ΔLAI(t)] are calculated as LAI($t + 1$) − LAI(t), where t is months in the timeline March 2000 to May 2005. The number of data points is 62 for each pixel. Correlation coefficients greater than 0.25 or less than −0.25 are shown ($P < 0.05$). The analysis was performed for rainforest pixels with LAI amplitudes greater than 0.66 or less than −0.66; this threshold (|0.66|) is the smallest LAI difference discernable with the MODIS LAI data set (see *SI Materials and Methods*). (*B*) Correlation between first differences of LAI and precipitation.

monthly differences of these variables, first by using the spatially averaged data shown in Fig. 1*A* and second by using pixel-level data. Changes in LAI are both positively correlated with changes in solar radiation ($P < 0.0001$) and negatively correlated with changes in precipitation ($P < 0.0001$), but the correlations between leaf area and radiation changes are larger and, at the pixel level, more numerous (Fig. 3 and SI Fig. 6). The negative correlations between LAI and precipitation are likely an indirect effect of the changes in cloudiness and radiation associated with precipitation changes (17). These results, together with past phenological studies, support the idea of an evolved pattern of endogenously controlled vegetative phenology that is timed to the seasonality of solar radiation (2, 10).

Discussion

The consistency between leaf area, solar radiation, and precipitation data from various satellite instruments is especially noteworthy. However, the strong seasonality in cloud cover and tropospheric aerosol loading may introduce seasonally opposing artifacts in MODIS leaf area. In the Amazon region there is significant cloudiness, which varies greatly between the wet and dry seasons. This seasonality in cloud cover can bias the results if cloud-contaminated retrievals are not screened out from the analysis. To minimize the impact of clouds, we used a coarse-resolution (8 km and monthly) data set that was derived by averaging the best-quality LAI values from the standard 1-km, 8-day MODIS data set (see *SI Materials and Methods*). Although some of the coarse-resolution LAI values were based on fewer high-quality estimates in the wet season, this did not bias the inferred seasonal LAI amplitudes.

The high aerosol content in the dry season, from biomass burning, natural biogenic emissions, and soil dust resuspension (25), can result in artificially low LAI values unless the reflectance data are corrected for aerosol effects. The MODIS processing system was found to correct well for such effects (see *SI Materials and Methods* and SI Fig. 7). The LAI values may have been underestimated by ≈5% from any residual aerosol effects. This effect is small and of opposite timing relative to the observed seasonality. Other possible sources of bias, such as reflectance saturation at high leaf area and changes in the light scattering and absorption properties of leaves due to aging and epiphylls (26), were found to be small and with the wrong timing to significantly alter our estimates of the amplitude of LAI seasonality (see *SI Materials and Methods*).

A robust validation of leaf area seasonality recorded in the MODIS satellite data requires a large number of leaf area measurements. These are presently lacking for the obvious reasons of cost, site accessibility, and the difficulty and questionable accuracy of ground sampling techniques. Nevertheless, the available data and published evidence support early to mid-dry season leaf area enhancement (21, 22), although further testing of this phenomenon is needed. The mechanism by which leaf area increases through the early dry season and decreases through the wet season (cf. Fig. 1) is partially supported by published observations on litterfall seasonality (11–13), but data on accompanying leaf emergence and expansion are lacking.

There is emerging evidence that the rainforest plays a critical role in initiating the onset of the wet season in the Amazon (ref. 27; see also *SI Materials and Methods*). An increase in surface evapotranspiration at the end of the dry season appears to be the primary cause of increased buoyancy of surface air, which consequently increases the probability of atmospheric convection and rainfall. The 25% increase in LAI over nearly 60% of the Amazon rainforest during the dry season reported in this article therefore suggests a potentially important role of vegetation in controlling the initiation of the wet season.

The seasonal dynamics and interplay between canopy photosynthesis and ecosystem respiration will likely be altered by this unexpected seasonality in leaf area (11, 14–19, 28), with attendant consequences for litterfall nutrient cycling (29). However, depending on other environmental and ecological constraints associated with vapor pressure deficits, temperatures, water and nutrient availability, etc., the dry-season increase in leaf area and sunlight may or may not result in enhanced photosynthetic activity. The transitional and seasonally dry forests in the southern Amazon do not show enhanced dry-season greening, which may indicate that these forests could be water-limited. A similar response can be envisioned for the more humid forests in drought years, especially those associated with strong El Niño events. Therefore, it is important to further investigate the significance of these changes in regard to climatic, hydrological, and biogeochemical cycles, and whether such swings in leaf area also exist in the moist forests of Africa and Asia.

Materials and Methods

A continuous record of data on green leaf area from the MODIS onboard NASA's Terra satellite was used to track leaf area changes over the Amazon basin from March 2000 to September 2005. An 8-km monthly LAI data set obtained by averaging the cloud-free main algorithm LAI estimates available in the standard 1-km, 8-day data set was used in this study. Monthly precipitation data at 15′ spatial resolution for the period January 1998 to August 2005, and monthly solar radiation data at 1° spatial resolution for the period March 2000 to May 2005, were also used. A detailed description of these data sets and of the validation of the MODIS LAI data set are given in *SI Materials and Methods* and SI Table 1.

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