Large seasonal swings in leaf area of Amazon rainforests


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Notes:
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Contributed by Robert E. Dickinson, December 22, 2006 (sent for review June 5, 2006)

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.

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 × 106 km2) 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-peak difference) that is 25% of the average annual LAI of 4.7 (Fig. 1A). 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...
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. 1A). 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. 1B): 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, 11, 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. 2A). 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 about 58% of all rainforest-occupied pixels, whereas only 3% show the opposite change (Fig. 2B). Second, the homogeneous region roughly overlies the precipitation gradient (20) in the basin (see SI Materials and Methods and SI Fig. 4C), suggesting that the amplitude is, to a first approximation, independent of the duration and intensity of the dry season. For example, an amplitude of about 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 about 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
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 the transitional and seasonally dry forests in the southern Amazon.}

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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 1° 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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