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What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network

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ABSTRACT

We investigated the seasonal patterns of Amazonian forest photosynthetic activity, and the effects thereon of variations in climate and land-use, by integrating data from a network of ground-based eddy flux towers in Brazil established as part of the 'Large-Scale Biosphere Atmosphere Experiment in Amazonia' project. We found that degree of water limitation, as indicated by the seasonality of the ratio of sensible to latent heat flux (Bowen ratio) predicts seasonal patterns of photosynthesis. In equatorial Amazonian forests (5° N–5° S), water limitation is absent, and photosynthetic fluxes (or gross ecosystem productivity, *GEP*) exhibit high or increasing levels of photosynthetic activity as the dry season progresses, likely a consequence of allocation to growth of new leaves. In contrast, forests along the southern flank of the Amazon, pastures converted from forest, and mixed forest-grass savanna, exhibit dry-season declines in *GEP*, consistent with increasing degrees of water limitation. Although previous work showed tropical ecosystem evapotranspiration (*ET*) is driven by incoming radiation, *GEP* observations reported here surprisingly show no or negative relationships with photosynthetically active radiation (*PAR*). Instead, *GEP* fluxes largely followed the phenology of canopy photosynthetic capacity (*Pc*), with only deviations from this primary pattern driven by variations in *PAR*. Estimates of leaf flush at three

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non-water limited equatorial forest sites peak in the dry season, in correlation with high dry season light levels. The higher photosynthetic capacity that follows persists into the wet season, driving high *GEP* that is out of phase with sunlight, explaining the negative observed relationship with sunlight. Overall, these patterns suggest that at sites where water is not limiting, light interacts with adaptive mechanisms to determine photosynthetic capacity indirectly through leaf flush and litterfall seasonality. These mechanisms are poorly represented in ecosystem models, and represent an important challenge to efforts to predict tropical forest responses to climatic variations.

1. Introduction

The Amazon basin represents a major component of regional and global carbon and hydrological cycles. Globally significant variations in these cycles could be induced by climate change (Betts et al., 2004; Monteith, 1965), but predictions for the future of Amazon forests under climate change vary widely (Friedlingstein et al., 2006). Predictions of vegetation responses to long-term climate change are not easily tested, but common mechanisms also control response to short-term climatic variations, including seasonal variations. Thus, understanding seasonal and spatial variation of forest metabolism is an important basis for understanding ecological responses to climate generally. In contrast to temperate zones, where the seasonality of ecosystem metabolism is evident and straightforwardly dominated by the contrast between an active growing and a dormant season, the seasonality of photosynthetic activity of evergreen tropical forests is not so obvious.

The dominant seasonal rhythm in many Amazonian forests is that of rainfall, with a distinct dry season, when precipitation inputs fall below 100 mm $month^{-1}$, varying in length from 0 months (no dry season in the ever-wet northwestern Amazon) to 5 months in central eastern equatorial Amazonia, and in southwestern edge (Sombroek, 2001) (Fig. 1). The dry season brings a decrease in cumulus cloud cover and, in areas close to the equator with low variation in top-of-atmosphere solar energy, an increase in solar radiation at the surface. The dry season also brings increased smoke from biomass burning (Koren et al., 2004; Oliveira et al., 2007), shifting the composition of direct and diffuse radiation.

Many vegetation modeling studies have represented Amazon forests as water-limited, and so predicted dry season declines in transpiration and/or photosynthesis (Botta et al., 2002; Dickinson and Henderson-Sellers, 1988; Lee et al., 2005; Nobre et al., 1991; Tian et al., 1998). Early empirical studies near Manaus both supported (Malhi et al., 2002, 1998) and opposed (Shuttleworth, 1988) the water-limitation view. However, an accumulating suite of evidence is beginning to clarify the picture. Eddy flux measurements begun as part of the Large-scale Biosphere-Atmosphere Experiment in Amazonia (LBA) clearly show that evapotranspiration at some central Amazon sites is not water limited but largely driven by the availability of net radiation (da Rocha et al., 2004; Hutyra et al., 2007). Recently, integrated analysis across a network of towers confirms this behavior across much of the Amazon (Hasler and Avissar, 2007; Negrón Juárez et al., 2009; da Rocha et al., 2009; Fisher et al., 2009; Costa et al., 2010a,b). This evidence suggests that intact Amazon forests could be more resilient to variations in climate than most models have predicted. Deep tree roots (Nepstad et al., 1994) combined with hydraulic redistribution by roots (Oliveira et al., 2005) and increased availability of sunlight (Potter et al., 1998) have been suggested as explanations for these observations.

Remote sensing data from the moderate resolution imaging spectroradiometer (MODIS) suggest that intact forest photosynthesis increases as the dry season progresses across a large area of the central Amazon. The MODIS Leaf Area Index (*LAI*) product shows a widespread pattern of dry-season *LAI* increases that peak during the early to mid-dry season (Myneni et al., 2007), while the MODIS Enhanced Vegetation Index (*EVI*) shows equatorial Amazon forests continually "greening-up" throughout the dry season as availability of sunlight increases. By contrast, areas with extensive conversion of forests to pasture or agricultural management show the opposite "brown-down" trend (Huete et al., 2006). Remote sensing of regional-scale chlorophyll fluorescence (*Fs*) in the Amazon (by the new Japanese Greenhouse gases Observing SATellite, GOSAT, which may give a more direct index of photosynthesis than existing technologies (Frankenberg et al., 2011), suggests patterns broadly similar to those observed via EVI (*Fs* vs *EVI*, R^2 = 0.52) (Lee et al., 2013).

Tower-based estimates of photosynthetic flux derived from observations of net ecosystem exchange of carbon dioxide via eddy covariance method are perhaps the most reliable and direct measure of ecosystem scale photosynthesis to "ground truth" remote sensing indices and to test models. Individual tower studies have shown a range of results, including: (1) clear increases in dry season forest photosynthesis in the central eastern Amazon (Goulden et al., 2004; Hutyra et al., 2007; Saleska et al., 2003), (2) dry season decreases in the southwest Amazon (von Randow et al., 2004), and (3) no detectable seasonality in the far eastern Amazon (Carswell et al., 2002). These studies have pointed to a range of possible biophysical drivers for carbon assimilation, including length of dry season, cloud cover, access to deep water, and disturbance history, among others. Site-specific results suggest the need for a consistent, integrated analysis across sites and biomes of the seasonal patterns in eddy flux-derived ecosystem-scale photosynthesis to present a coherent picture of its spatial variability and possible drivers across the Amazon basin.

Our objective is to use eddy covariance (EC) data from a network of flux towers, installed as part of the 'Large-Scale Biosphere Atmosphere Experiment in Amazonia' (LBA) project (Keller et al., 2004), to address the question of what environmental and biological factors control the seasonality of photosynthesis in these tropical Amazonian ecosystem. We also sought to provide an integrated, consistently processed dataset, which could be used for comparison to model simulations of the LBA "Data-Model Intercomparison Project (LBA-DMIP). To this end, we conducted the first integrated analysis of basin-wide patterns of ecosystem photosynthesis across the Amazon. This effort is possible by the collaboration from a range of research groups who have contributed their observations to an integrated and unified database, known as Brasil flux network (da Rocha et al., 2009). The nine sites (Table 1) from this database are: four tropical forests and one converted pasture/agricultural site located along the main stem of the Amazon (equator to 3° S), one tropical dry forest and an adjacent converted site located in southern Amazonia (~10° S), one seasonally flooded ecotone (~10° S), and one non-Amazonian savanna in southern Brazil.

First, we describe the seasonal patterns of ecosystem photosynthetic fluxes, and canopy photosynthetic capacity across different Amazonian ecosystems, latitudinal gradients, and disturbance history. Then, we test hypotheses about control of photosynthesis by analyzing relationships between environmental drivers and overall photosynthetic fluxes and capacity. We initially focus on two main contrasting ideas drawn from the literature: that photosynthesis is limited by water availability, and that photosynthesis is limited by