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What drives long-term variations in carbon flux and balance in a tropical rainforest in French Guiana?

Maricar Aguilos[a], Bruno Hérault[b,c], Benoit Burban[a], Fabien Wagner[d], Damien Bonal[e,*]

[a] INRA, UMR "Ecologie des Forêts de Guyane" AgroParisTech-CIRAD-INRA-CNRS-Université de Guyane-Université des Antilles, Campus Agronomique, 97387 Kourou, Guyane Française, France
[b] CIRAD, UMR "Ecologie des Forêts de Guyane" AgroParisTech-CIRAD-INRA-CNRS-Université de Guyane-Université des Antilles, Campus Agronomique, Kourou, Guyane Française, France
[c] INPHB Institut National Polytechnique Félix Houphouët-Boigny, BP 1093, Yamoussoukro, Cote d'Ivoire
[d] National Institute for Space Research (INPE), São José dos Campos, SP 12227-010, Brazil
[e] Université de Lorraine, AgroParisTech, INRA, UMR Silva, 54000, Nancy, France

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ABSTRACT

A thorough understanding of how tropical forests respond to climate is important to improve ecosystem process models and to reduce uncertainties in current and future global carbon balance calculations. The Amazon rainforest, a major contributor to the global carbon cycle, is subject to strong intra- and interannual variations in climate conditions. Understanding their effect on carbon fluxes between the ecosystem and the atmosphere and on the resulting carbon balance is still incomplete. We examined the long-term (over a 12-year period; 2004–2015) variations in gross primary productivity (GPP), ecosystem respiration (RE) and net ecosystem exchange (NEE) in a tropical rainforest in French Guiana and identified key climatic drivers influencing the changes.

The study period was characterized by strong differences in climatic conditions among years, particularly differences in the intensity of the dry and wet seasons, as well as differences in annual carbon fluxes and balance. Annual average GPP varied from 3384.9 $g\,C\,m^{-2}\,yr^{-1}$ (95% CI [3320.7, 3445.9]) to 4061.2 $g\,C\,m^{-2}\,yr^{-1}$ (95% CI [3980.1, 4145.0]). RE varied even more than GPP, with a difference of 933.1 $C\,m^{-2}\,yr^{-1}$ between the minimum (3020.6 $g\,C\,m^{-2}\,yr^{-1}$; 95% CI [2889.4, 3051.3]) and maximum (3953.7 $g\,C\,m^{-2}\,yr^{-1}$; 95% CI [3887.6, 4019.6]) values. Although NEE showed large interannual variability (nine-fold), from –65.6 $g\,C\,m^{-2}\,yr^{-1}$ (95% CI [–4.4, –126.0]) to –590.5 $g\,C\,m^{-2}\,yr^{-1}$ (95% CI [–532.3, –651.6]), the forest remained a carbon sink over the 12-year period.

A combination of global radiation (Rg), relative extractable water (REW) and soil temperature (Ts) explained 51% of the daily variations for GPP, 30% for RE and 39% for NEE. Global radiation was always the best predictor of these variations, but soil water content and temperature did also influence carbon fluxes and balance. Seasonally, Rg was the major controlling factor for GPP, RE and NEE during the wet season. During the dry season, variations in carbon fluxes and balance were poorly explained by climate factors. Yet, REW was the key driver of variations in NEE during the dry season.

This study highlights that, over the long-term, carbon fluxes and balance in such tropical rainforest ecosystems are largely controlled by both radiation and water limitation. Even though variations in Rg have a greater impact on these fluxes, water limitation during seasonal droughts is enough to reduce ecosystem productivity, respiration and carbon uptake. The reduced precipitation expected in tropical rainforest areas under future climatic conditions will therefore strongly influence carbon fluxes and carbon uptake. This study also highlights the importance for land surface or dynamic global vegetation models to consider the main drivers of carbon fluxes and balance separately for dry and wet seasons.

1. Introduction

Tropical forests account for 34% of global terrestrial gross primary productivity (GPP) and have the highest productivity per unit area (Beer et al., 2010) of all living ecosystems. Among these tropical forests, the Amazon basin occupies a central position as it represents half of all

* Corresponding author at: INRA, UMR Silva - 1434 Université de Lorraine-AgroParisTech-INRA, 54280 Champenoux, France.
E-mail address: damien.bonal@inra.fr (D. Bonal).

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tropical vegetation biomass (Saatchi et al., 2011) and is being threatened by human activity and climate extremes. The Amazon basin has seen increased climatic variability over recent decades and has suffered exceptional droughts (overview in Bonal et al., 2016). The large-scale mortality associated with the extreme drought in 2005 was equivalent to the release of carbon accumulated by all rainforests over several decades (Gloor et al., 2012). During the extreme drought year in 2010, the Amazon basin (burned forested part excluded) shifted from the net carbon sink typical of wet years to a carbon neutral status (Gatti et al., 2014). Even though tropical rainforests do show strong resistance to drought (Baker et al., 2013; Saleska et al., 2007), the impact of repeated droughts over a short period of time has clearly modified the tropical forest ecosystem's response to severe water shortage (Feldpausch et al., 2016). These issues compelled us to try to better understand the impacts of a changing climate on rainforest ecosystems, particularly on GPP, ecosystem respiration (RE) and net ecosystem exchange (NEE).

Any changes in climate significantly disturb terrestrial carbon pools and contribute to the large interannual variability in atmospheric CO_2. However, just how sensitive the terrestrial carbon budget is to climatic drivers in the tropics remains uncertain (Bonal et al., 2016). There is a recurring debate about whether Amazonian forests are more water-limited (Gatti et al., 2014; Morton et al., 2014; Tian et al., 2000) or more light-limited (Arias et al., 2011). Some studies suggest that photosynthesis increases during extremely dry conditions due to higher solar radiation (Hutyra et al., 2007; Saleska et al., 2003; Carswell et al., 2002). However, two partial throughfall-exclusion experiments conducted in the Amazon region found that proxies for forest productivity declined under drought conditions (Brando et al., 2008). Process-based biogeochemical models also predict that moisture limitation during the dry season should put a strong constraint on canopy carbon uptake in tropical forests (Morton et al., 2014; Lee et al., 2013; Saleska et al., 2003; Restrepo-Coupe et al., 2017), but previous observations have not supported this paradigm in the Amazon (Hutyra et al., 2007) or in other tropical areas (Xiao et al., 2013). These conflicting results highlight the importance of using long-term series of flux values that have been accurately measured at ecosystem level to represent biophysical processes in land surface or dynamic global vegetation models (Zeri et al., 2014; Restrepo-Coupe et al., 2017). Resolving this issue is critical to reducing uncertainties in the currently estimated carbon balance of tropical forests and in determining the plausible response of Amazonian forests to climate change (Gatti et al., 2010).

In ecosystem-level studies, NEE is the parameter measured, following the eddy-covariance methodology (Baldocchi 2003); however, GPP and RE are the actual ecosystem-level processes that respond to biological and environmental cues. Variations in NEE with climate are complex because RE and GPP may respond differently to climate conditions. GPP is mainly controlled by radiation, air temperature, vapor pressure deficit, the amount of root water uptake, the amount of leaves in the canopy (leaf area index) (Zhang et al., 2010) and the distribution and function of these leaves in different parts of the canopy (Brando et al., 2010). RE is mainly controlled by air and soil temperature, soil water content (Baker et al., 2013) and substrate availability (Reichstein et al., 2002); it is thus partly coupled to GPP (Hutyra et al., 2007). While examining the mechanisms involved in GPP and RE is critical, determining the relationships between the two factors and their climatic drivers is equally important because the climate–carbon feedback cycle could significantly influence future climate warming (Zeng et al., 2005).

While eddy covariance towers can provide estimates at a high temporal resolution, the number of stations is limited in Amazonian, African and Asian tropical rainforests. Furthermore, with one exception (Zeri et al., 2014), long-term data acquisition in these different regions is lacking (Bonal et al., 2016). The "Guyaflux" tower, located in French Guiana's Amazonian forest (Bonal et al., 2008), has been recording eddy covariance data continuously since the end of 2003 and has endured through several climatic anomalies. The present study makes use of the 12 years of data (2004–2015) acquired at this station and is the longest time-series of eddy covariance data for tropical rainforest ecosystems ever published.

We investigated the following questions: (1) How did carbon fluxes and balance behave over the 2004–2015 period? (2) What drives the long-term variations in ecosystem productivity, respiration and the resulting net carbon uptake? (3) Which of the two, light or water, holds the primary key to such variability, or are both involved? We hypothesized that, in view of the varying climate conditions which occurred during the study period, the observed ecosystem may alternate carbon sink or carbon source periods on an annual basis. We further hypothesized that light would be a limiting factor during wet periods, while soil moisture would have the most control over carbon fluxes during the dry season.

2. Methods

2.1. Study site

This study was conducted in French Guiana, South America (5°16′54″N, 52°54′44″W), in a wet tropical climate with large seasonal variations in rainfall (Bonal et al., 2008). The site receives its highest incident extraterrestrial radiation in March and September. September also corresponds to the beginning of the long dry season, during which a gradual decrease in radiation is observed. Decadal average annual rainfall at the study site was 3041 mm and average annual air temperature was 25.7 °C.

Bonal et al. (2008) present detailed information about the Guyaflux site where the flux tower stands; we recall certain key points from their study here. The site is located in the northernmost part of a region on the Guiana Plateau characterized by a succession of small, elliptical hills rising to 10–40 m a.s.l. The soils are mostly nutrient-poor acrisols (FAO-ISRIC-ISSS, 1998). The flux tower stands in an area of more than 400 ha of undisturbed forest. The 55-m high, self-supporting metallic tower makes it possible to acquire eddy flux data over around 100 ha of undisturbed forest in the direction of the prevailing winds. The top of the tower is about 20 m higher than the overall canopy and most meteorological and eddy flux sensors are mounted 3 m above the tower.

The forest around the tower has a tree density of about 620 trees ha^{-1} (trees with a dbh > 10 cm). Mean diameter of the trees at breast height (dbh) is 40.1 cm and mean tree height is 35 m, with emergent trees exceeding 40 m. Tree species richness is about 140 species ha^{-1}.

2.2. Meteorological and flux monitoring

The data used in this study were obtained with the same equipment as those in Bonal et al. (2008). Microclimate and eddy covariance data have been recorded continuously at the site since December 2003 following the Euroflux methodology described in Aubinet et al. (2000). The present study covers a 12-year period, from 2004 to 2015. Air temperature and humidity (HMP45, Vaisala, Helsinki, Finland), bulk rainfall (ARG100, EM lmt, Sunderland, UK), wind direction and speed (A05103-5, Young, Traverse City, MI, USA), and global, infrared incident and reflected radiation (CNR1, Kipp & Zonen, Bohemia, NY, USA) were measured above the canopy. We used temperature sensors (CS107, Campbell Scientific Inc., Logan, UT, USA) to measure soil temperature (Ts, °C) and frequency domain sensors to measure volumetric soil water content at 0.05 m depth (SWC, $m^3\,m^{-3}$) (CS615 or CS616, Campbell Scientific Inc.). It should be noted that soil temperature data are missing for 2015 due to technical problems with the sensor. All meteorological data were collected at 1 min intervals and compiled as 30 min averages or sums with CR23X, CR1000 or CR3000 dataloggers (Campbell Scientific Inc.). Vapor pressure deficit above the canopy (VPD, kPa) was calculated based on air temperature and humidity measurements. Only a few minor equipment breakdowns or power cuts caused any loss of meteorological data over the 2004–2015