

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Asynchronism in leaf and wood production in tropical forests: a study combining satellite and ground-based measurements

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Received: 15 April 2013 – Accepted: 25 April 2013 – Published: 16 May 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

The fixation of carbon in tropical forests mainly occurs through the production of wood and leaves, both being the principal components of net primary production. Currently field and satellite observations are independently used to describe the forest carbon cycle, but the link between satellite-derived forest phenology and field-derived forest productivity remains opaque. We used a unique combination of a MODIS EVI dataset, a climate-explicit wood production model and direct litterfall observations at an intra-annual time scale in order to question the synchronism of leaf and wood production in tropical forests. Even though leaf and wood biomass fluxes had the same range (respectively $2.4 \pm 1.4 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ and $2.2 \pm 0.4 \text{ MgC ha}^{-1} \text{ yr}^{-1}$), they occurred separately in time. EVI increased with the magnitude of leaf renewal at the beginning of the dry season when solar irradiance was at its maximum. At this time, wood production stopped. At the onset of the rainy season when new leaves were fully mature and water available again, wood production quickly increased to reach its maximum in less than a month, reflecting a change in carbon allocation from short lived pools (leaves) to long lived pools (wood). The time lag between peaks of EVI and wood production (109 days) revealed a substantial decoupling between the irradiance-driven leaf renewal and the water-driven wood production. Our work is a first attempt to link EVI data, wood production and leaf phenology at a seasonal time scale in a tropical evergreen rainforest and pave the way to develop more sophisticated global carbon cycle models in tropical forests.

1 Introduction

Tropical forests have a primordial role in the terrestrial carbon (C) cycle. On one hand, 55% of the total forest C stocks are stored in live biomass, deadwood, litter and soil of tropical areas ($471 \pm 93 \text{ PgC}$). On the other hand, carbon sequestration in tropical intact forests represents about half ($1.19 \pm 0.41 \text{ PgC yr}^{-1}$ for the period 1990–2007 Pan

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



et al., 2011; Baccini et al., 2012) of the total sink in global established forest. Most carbohydrates are produced by photosynthesis in leaves and redistributed to plant tissues or lost during chemical processes such as respiration (Kozlowski, 1992). Accumulation of carbohydrates in woody tissues during secondary growth constitutes the main component of carbon sequestration in trees. Tree growth occurs in two ways. Primary growth corresponds to the length extension of shoots from the apical meristems, where the leaves grow, and to root development. Secondary growth gathers all the biological mechanisms behind cambial activity and stem growth in thickness (Kozlowski, 1992). In this paper, we will use seasonal tree diameter growth as a proxy of seasonal variations in wood production and leaf phenology to assess leaf production, extension and fall. Wood and leaf production are the main components of net primary production and constitute the long lived pool (wood) and the short lived pool (leaves) of carbon in the trees (Malhi and Grace, 2000; Malhi et al., 2011). We will study their seasonality and the temporal decoupling between them.

Seasonality of leaf phenology in tropical rainforests has been observed either from (i) field measurements of litterfall and leaf production (Chave et al., 2010; Zalamea and Gonzalez, 2008; Bonal et al., 2008; Sabatier and Puig, 1986) or (ii) satellite data (Huete et al., 2006; Asner et al., 2000, 2004; Caldararu et al., 2012; Pennec et al., 2011). The latter studies characterize leaf phenology through variations in different vegetation indices, i.e. Leaf Area Index (LAI), Normalized Difference Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI) (Justice et al., 1998). These indices are computed based on measurements of surface reflectance by sensors embarked on satellites. The drivers of leaf phenology in tropical rainforests are still studied, but recent results suggest that irradiance is the main driver throughout Amazonia (Bradley et al., 2011). Flushes of new leaves with increased photosynthesis capacity were observed in the heart of the dry season and closely coincided with seasonal peaks in solar irradiance (Myneni et al., 2007; Brando et al., 2010; Huete et al., 2006; Saleska et al., 2003; Caldararu et al., 2012; Wright and Vanschaik, 1994; De Weirtdt et al., 2012).

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Seasonal rhythms of secondary growth, i.e. wood production, in tropical forests have been highlighted in most long-term permanent plots (Nepstad et al., 2002; Stahl et al., 2010; Wagner et al., 2012), even under very stable climate conditions (O'Brien et al., 2008; Clark et al., 2010). This seasonality is obviously linked to the intra-annual variation of cambial activity that has been reported in various environments, from dry (Worbes, 1999; Enquist and Leffler, 2001; Lisi et al., 2008) to flooded forests (Schongart et al., 2002), but also in more mesic environmental conditions (Fichtler et al., 2003; Clark et al., 2010). Most current studies performed in tropical rainforests have highlighted three major climate drivers of secondary growth: rainfall, solar irradiance and air temperature. (i) Rain or lack of rain is often implicitly viewed as the main driver of rainforest dynamics (Phillips et al., 2009), as annual net primary production (NPP) generally positively correlates with the annual amount of precipitation (Tian et al., 1998). Recently, Wagner et al. (2012) showed that rainfall seasonality plays a key role in the forest's response to climate variability. (ii) Irradiance is obviously directly linked to plant photosynthetic capacity, in turn driving carbon uptake and plant growth (Graham et al., 2003). (iii) Recent studies suggest that tropical tree mortality may increase significantly with increasing night-time temperature, while seasonal tree growth appears surprisingly very sensitive to 1–2 °C variations in mean annual night-time temperature (Clark et al., 2010). Some works suggest that reductions in photosynthetic rate may occur at temperatures above 30 °C and are driven by reductions in stomatal conductance in response to higher leaf-to-air vapour pressure deficits (Lloyd and Farquhar, 2008), rather than by a direct down regulation of biochemical processes during CO₂ fixation.

Few studies have simultaneously analyzed the diverse components of net primary production in tropical forests and the dynamics of non-structural carbohydrates (NSC) (Wurth et al., 2005; Rocha, 2013). In Panama, higher NSC concentrations were found across all species and organs in the dry season (Wurth et al., 2005). This increase was attributed to drought-constrained growth, the photosynthesis being less impeded than tree growth by drought. In French Guiana, carbohydrates production was more variable at times as photosynthesis decreased in the dry season (Stahl et al., 2013).

Very recently, significant advances in understanding tree growth and within-tree C cycling have been made in temperate forests (Richardson et al., 2013). NSC were found to be both highly dynamic and about a decade old. A two-pool (fast and slow cycling reserves) model structure gave reasonable estimates of the size and mean residence time of the total NSC while greatly improving model predictions of inter-annual variability in woody biomass increment.

While field measurements of productivity, reported as biomass gain or growth in diameter at breast height (DBH), showed an increase in the wet season (Wagner et al., 2012; Grogan and Schulze, 2012; Nepstad et al., 2002; Clark et al., 2010), satellite measurements of productivity, reported in terms of increasing canopy photosynthetic capacity, were correlated with leaf production and peaked in the dry season (Huete et al., 2006; Brando et al., 2010; Anderson, 2012). In this study, we use a unique combination of three independent datasets to resolve this apparent absence of synchronism in leaf and wood production in tropical forests. First, 3 yr of intensive field measurements of diameter growth of 256 tropical trees were used to calibrate a wood production model. Next, litter production was surveyed every 25 days in the same period in the same forest area. Finally, leaf production was estimated using EVI data from the Modis sensor of the satellite Terra. We hypothesized that this apparent paradox of biomass productivity in tropical forests reflects a time overlap in the use of carbohydrates in tropical trees. We addressed two specific questions: (i) whether field and satellite data converge in describing the biological functioning of tropical forests, and (ii) how these two sources of information explained seasonal variations in tropical forest productivity. To our knowledge, this study is the first attempt to link leaf phenology, wood production and EVI data at a seasonal time scale.

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2 Methods

2.1 Field data

Seasonal changes in trunk circumference were monitored in 256 trees from 74 species using home-made steel dendrometer bands, distributed in 3 inventory plots (Stahl et al., 2010; Wagner et al., 2012) in Paracou, French Guiana (5°18' N, 52°23' W), a lowland tropical rainforest (Gourlet-Fleury et al., 2004). Changes in trunk circumference were censused every c. 40 days from 2007 to 2010 (mean = 39, sd = 19.8). Trunk bark thickness has been measured on 255 of the 256 studied trees (methods described in Stahl et al., 2010). In the same 3 inventory plots, 12 litter traps (0.67 m × 0.67 m = 0.45 m²) were placed 1.5 m above the ground at each corner of each plot. Trap contents were collected every 25 days on the same day and oven-dried at 60°C for 3 days until constant weight before being weighed to the nearest 0.1 g (Bonal et al., 2008).

2.2 Satellite data

We used Enhanced Vegetation Index (EVI) satellite data from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor onboard the satellite Terra (EOS AM, NASA) (Justice et al., 1998). Vegetation indices measure canopy greenness, a composite property of canopy structure, leaf area, and canopy chlorophyll content (Myneni et al., 1995). EVI is an index of canopy photosynthetic capacity (Huete et al., 2006). We obtained EVI from the Global MOD13Q1 datasets provided every 16 days at 250 m spatial resolution. The EVI maintains sensitivity even for high LAI canopies by relying on near-infrared canopy reflectance, which is less prone to saturate with moderate resolution pixels (Gao et al., 2000; Huete et al., 2002, 2006). We used all 16 day composite EVI data from 4 January 2007 to 2 February 2011 included. In addition, we used a typology of French Guiana forest defined from SPOT-4/VEGETATION product (Gond et al., 2011) to analyze EVI variation between forest types. This typology is relied to

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the data set from the VEGETATION sensor onboard the SPOT-4 satellite (1 km spatial resolution).

2.3 Climate data

We used the CRU-TS3.1 and CRU-TS3.10.01 monthly climate datasets for the period 2007–2010 of the Climate Research Unit (CRU) at the University of East Anglia (Mitchell and Jones, 2005). These datasets are calculated on high-resolution grids ($0.5 \times 0.5^\circ$), which are provided by more than 4000 weather stations distributed around the world (4 in French Guiana). Here we used cloud cover (cld), precipitation (pre), daily mean, minimal and maximal temperatures (respectively tmp, tmn and tmx), vapour pressure (vap) and potential evapotranspiration (pet). For the calculation of potential evapotranspiration (pet), the method used is the Food and Agricultural Organization's (FAO) grass reference evapotranspiration equation (Ekstrom et al., 2007; Allen et al., 1994). It is a variant of the Penman Monteith method using the gridded tmp, tmn, tmx, vap and cld. These data were estimated using linear approximation for the grid and the time of the Modis image. Additionally, for the graphic representation, we used global radiation, mean temperature and relative extractable water (REW) measured or computed at Paracou (details of the sensors and computation of REW in Wagner et al. (2012) and Bonal et al., 2008). REW is a daily value between 0 and 1: when REW = 1, the amount of extractable water by the tree is at its maximum, and when REW = 0, no water is available for trees. Mean monthly temperature of CRU data have a coefficient of correlation of 0.962 with mean monthly temperature measured in Paracou.

2.4 Data analysis

2.4.1 Wood production versus stem hydration

Changes in tree circumference are commonly used to characterize seasonal or annual variations in secondary growth. However, accelerated changes in circumference

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



increments during the onset of the wet season can be caused by bark swelling as they become hydrated (Stahl et al., 2010). Similarly, bark shrinking during dry periods can mask any secondary growth and even lead to negative growth increments (Stahl et al., 2010). To disentangle the effect of climate seasonality vs. bark hydration on secondary growth and wood production, we compared the monthly biomass increments (see Eq. (2) for the computation of biomass from tree diameter) of two groups of trees corresponding to the first and the last quantile of trunk bark thickness. Both groups showed synchronous and highly correlated variations (Pearson correlation coefficient of 0.80) in biomass increment (Fig. 1), suggesting that secondary growth is driven by cambial activity.

2.4.2 Modeling wood production

We converted measured changes in circumference into wood production using the model of Molto et al. (2013). This model uses the diameter at breast height of the tree i at the time t ($DBH_{i,t}$) to estimate the current height in meters ($H_{i,t}$), Eq. (1).

$$\log(H_{i,t}) \sim \log(\beta_1 \times (DBH_{i,t}/(\beta_2 + DBH_{i,t}))) \quad (1)$$

Where $DBH_{i,t}$ is in cm, $\beta_1 = 40.3$, $\beta_2 = 9.43$. Then the wood production ($AGB_{i,t}$) was computed using the estimated height ($\hat{H}_{i,t}$), the diameter ($DBH_{i,t}$) and the wood specific gravity of the tree (WSG_i), Eq. (2).

$$\log(AGB_{i,t}) \sim \beta_3 + \beta_4 \log(DBH_{i,t}) + \beta_5 \log(\hat{H}_{i,t}) + \beta_6 \log(WSG_i) \quad (2)$$

Where $DBH_{i,t}$ is in cm, $\hat{H}_{i,t}$ is in m, $\beta_3 = -2.91$, $\beta_4 = 2.19$, $\beta_5 = 0.756$, $\beta_6 = 0.187$. For 158 of the studied trees, WSG_i had been measured in a companion study (see methods in Stahl et al., 2010). For the remaining 98 trees, we assigned the mean WSG of its species from the data of Stahl et al. (2010). If the WSG_i of the species was still missing, then we used the databases from Baraloto et al. (2010) and Rutishauser et al. (2010) to complete them.

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The wood production at the time t ($\Delta\text{AGB}_{i,t}$) was computed as the difference of AGB_{*i*} between t and $t - 1$. The mean wood production of our sampled population for each time t was computed with the number of trees (n_t) at the time t .

$$\Delta\text{AGB}_{i,t} = \text{AGB}_{i,t} - \text{AGB}_{i,t-1}$$

$$\Delta\text{AGB}_{\text{paracou},t} = \frac{\sum_{i=1}^{n_t} \Delta\text{AGB}_{i,t}}{n_t} \quad (3)$$

We calibrated a monthly wood production model with the mean wood production of our sampled population and the climate variable of the CRU dataset for the pixel of Paracou in a linear framework. To match the time scale of the Modis data, climate data and the mean wood production of Paracou ($\Delta\text{AGB}_{\text{paracou},t}$) were linearly interpolated to the modis time m ($\Delta\text{AGB}_{\text{paracou},m}$).

$$\log(\Delta\text{AGB}_{\text{paracou},m} + 1) \sim \alpha_0 + \alpha_1 \times \text{pre}_m + \alpha_2 \times \text{pet}_m + \alpha_3 \times \text{tmp}_m + \alpha_4 \times \text{tmn}_m + \alpha_5 \times \text{tmx}_m + \alpha_6 \times \text{cld}_m + \alpha_7 \times \text{vap}_m \quad (4)$$

Where $\Delta\text{AGB}_{\text{paracou},m}$ is the wood production for the modis time m , α_0 is the intercept of the model, $\alpha_{1,\dots,7}$ are the parameters of the climate drivers and the error of the model assumed normal. We modelled the logarithm of growth instead of growth itself because our data showed a strong heteroscedasticity.

In a second step, we applied this model to predict the wood production ($\overline{\Delta\text{AGB}_{p,m}}$, Eq. 5) for Modis pixel p with the CRU climate variable at the modis time m .

$$\overline{\log(\Delta\text{AGB}_{p,m} + 1)} \sim \alpha_0 + \alpha_1 \times \text{pre}_{p,m} + \alpha_2 \times \text{pet}_{p,m} + \alpha_3 \times \text{tmp}_{p,m} + \alpha_4 \times \text{tmn}_{p,m} + \alpha_5 \times \text{tmx}_{p,m} + \alpha_6 \times \text{cld}_{p,m} + \alpha_7 \times \text{vap}_{p,m} \quad (5)$$

2.4.3 Image processing

Using MRTtools, EVI, VI_Quality and pixel_reliability were extracted from the Modis MOD13Q1 granule in .hdf, resized to latitude of 2–6° N and longitude of –55 to –51° W,

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



and converted to GeoTIFF images. On these images, we selected only the Modis pixels containing forest, as defined by the five forest classes of Gond et al. (2011): low dense forest, high forest with regular canopy, high forest with disrupted canopy, mixed high and open forest, and open forest and Euterpe palm forest. We determined the validity of each 16 day composite EVI value of a land pixel using the methodology used and described in Samanta et al. (2010, Auxiliary materials). The selection was made by excluding Pixel Quality Flags, Clouds, Cloud Shadows, Aerosol Climatology and High Aerosols. Pixels with the following quality flags were deemed “valid” (all other quality flags were ignored). The “MODLAND_QA” flag must be equal to 0 (good quality) or 1 (check other Quality Assessment flags, QA). “VI usefulness” flags must be equal to 11 or less. “Adjacent cloud detected”, “Mixed clouds” and “Possible shadow” flag values must be equal to 0. The “Aerosol quantity” flag must equal 1 (low aerosol) or 2 (average aerosol).

We estimated the value of EVI for the pixels excluded in the previous selection, $EVI_{\rho_{\text{excluded}},m,\text{type}}$. The estimation was made by assigning to the pixel missing an EVI value the mean EVI value of the n neighbor valid pixels of the same forest type (type) in a square of side 40 km, weighted by the inverse distance (dist), Eq. (6).

$$EVI_{\rho_{\text{excluded}},m,\text{type}} = \frac{\sum_{i=1}^n EVI_{\rho_{\text{valid}},m,\text{type}} \times (1/\text{dist}_n)}{\sum_{i=1}^n (1/\text{dist}_n)} \quad (6)$$

2.4.4 Seasonality analysis

To detect, estimate and test seasonal patterns in the EVI time series, we used temporal regression models from the package R season (Barnett and Dobson, 2010). The model is fitted using a sine and cosine term that together describes the sinusoid. These parameters are added to a generalized linear model to explain EVI data and test the existence of a seasonal pattern. The existence of a seasonal pattern was determined by the zero-test based on Snedecor’s F statistic. We computed cross correlation coefficients between EVI, $\Delta AGB_{\text{paracou},m}$, leaffall, global solar radiation, REW and temperature to

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



determine the maximum correlation and lagged times between the time series. For the construction of the time series, we used the mean of EVI and ΔAGB at each of the Modis times, and all the variables were linearly approximated at a daily scale. The level of statistical significance was computed by a bootstrap procedure. We randomly reordered the values of one of the time series, computed and stocked the cross correlation coefficients and repeated this operation 1000 times. Then the cross correlations of the original variable was compared to the distribution of the cross correlations with the randomly reordered variable. The null hypothesis of uncorrelated original variables was rejected at a level of 0.05% if the cross correlation of the original variables was outside the (0.025, 0.975) quantiles of the empirical distribution of the randomly reordered cross correlations.

All analyses were performed using the R project software (<http://www.r-project.org/>).

3 Results

The wood production model did reproduce well the general trend of the data ($R^2 = 0.72$, RMSE = 0.385), Table 2. The modeled wood production showed a strong seasonality (Fig. 3a). At the beginning of the rainy season, wood production increased quickly. However, production began to decline before the end of the wet season, in the middle of July. A decline in wood production was observed during the transition between the wet and the dry season (July to September) and during the dry season (September to December).

The EVI signal also exhibits a strong seasonality, and this signal has a similar pattern of variation among all five different types of forests found in French Guiana (Figs. 2 and 3b). The cosinor test indicated a significant seasonality for all the EVI pixels of French Guiana as well as for each forest type with $P < 0.05$ (Table 3). The amplitude of the sinusoid is 0.03 with a phase (high point) in November and a low point in May. The temporal pattern represents an increase in EVI during the dry season with a maximum

reached at the onset of the wet season (December to January) followed by a slow decrease during the wet season.

At the onset of the dry season, EVI increased when the peak of litterfall was observed (Fig. 3c). Peaks of EVI occurred 1 month after litterfall peak (31 days, Table 4). The peak of litterfall occurred when global radiation was maximum (Fig. 3e), and the peaks of litterfall and radiation occurred in a period of less than 1 month (Table 4). During the heart of the dry season (October to November), EVI was at its maximum and wood production at its minimum (Fig. 3). EVI and wood production have a significant negative cross correlation; the maximum negative correlation occurred with a lag of 1.5 months (Table 4). Meanwhile in October to November, relative extractable water (REW), an index of soil water availability for tress (Wagner et al., 2010a, 2012), reached its lowest values (Fig. 3d). As previously observed in Wagner et al. (2012), REW is highly and directly correlated to wood production (Table 4).

At the beginning of the wet season (December to January), EVI remained high, but wood production sharply increased to reach its maximal value in less than 2 months. The increase of wood production followed the trend of increasing REW in the early wet season (Fig. 3d). Peaks of EVI and wood production showed a positive correlation with a lag of 3.5 months (109 days, Table 4). During the rainy season (February to June), wood production as well as EVI values slowly decreased. In July, we observed a strong decline in wood production, while EVI started to increase. Then EVI reached its maximum, and the annual cycle started again. The link between wood production and EVI exhibited a regular annual hysteresis (Fig. 4). The highest wood production was observed for relatively high values of EVI during the early wet season. Surprisingly, EVI showed a substantial inter-annual variability (Fig. 4).

4 Discussion

The mean annual productivity of leaves at Paracou is $2.4 \pm 1.4 \text{ MgCha}^{-1} \text{ yr}^{-1}$ (Bonal et al., 2008; De Weirdt et al., 2012). This value has to be compared to the mean

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



biomass fluxes due to wood production at Paracou, i.e. $2.2 \pm 0.4 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (Rutishauser et al., 2010; Wagner et al., 2010b). Here, we showed that these two biomass fluxes, which have the same range in terms of C amount, occurred separately in time. In the following paragraphs, we discuss the dynamics and potential drivers of these fluxes and of the interactions between them.

4.1 Leaf phenology

The so-called greening of the forest observed with EVI data was related to the leaf production but did not constitute a direct indicator of wood production (Fig. 4). At Paracou, as expected for an evergreen tropical forest, leaf litter is produced throughout the year, indicating that the trees have sufficient carbon supply and adequate climate to produce new leaves even at the beginning of the dry season when litterfall peaks (Fig. 3c). Leaves are an important, but often neglected, part of the short-term forest carbon balance (Malhi and Grace, 2000). In this study, litterfall averaged $2.4 \pm 1.38 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (Bonal et al., 2008; De Weirtdt et al., 2012), a little more than half of the $4.351 \pm 0.955 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ (Chave et al., 2010) observed, on average, for old-growth tropical rainforests in Amazonia. However, these values of leaf production represent very short-term carbon pools and, contrary to wood production, cannot be directly connected to long-term variation of the biomass stock. Indeed, all leaves produced are expected to fall after a while, and there is therefore no biomass storage in the medium term. Recent works throughout Amazonia have estimated a large range of leaf residence time, from 6 to 36 months, with a lifespan distribution suggesting a pronounced annual regularity. The average leaf lifespan increases from Eastern Amazon, where leaves are typically short lived, to the evergreen Central Amazon Basin.

The ecological significance of a so-called “forest-greening” (Huete et al., 2006) in French Guiana (Table 3) is leaf production, which mainly occurs in the dry season when old leaves are replaced. Recent works have highlighted that EVI was sensitive to view-illumination effects due to the variation of the solar zenith angle during the dry season

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



in a location close to Xingu Indigenous Park in Brazil, 13°12' 22" S and 52°20' 59" W (Galvao et al., 2013; Moura et al., 2012). Nevertheless, we assume that this potential bias is reduced in our study due to a closer distance to the equator (5°18' N). Our results confirm the link between intra-annual variations of EVI and field observations of leaf phenology (Fig. 3) and suggest that most leaves are shed when new ones appear. These variations in phenology and index of canopy photosynthetic capacity from satellites measurements coincided with seasonal peaks in solar irradiance in Amazonia (Wagner et al., 2012; Bonal et al., 2008; Huete et al., 2006; Saleska et al., 2003; Wright and Vanschaik, 1994; Sabatier and Puig, 1986; Pennec et al., 2011; De Weirdt et al., 2012). Even if leaf fall is important throughout the year, it reaches its maximum when the peak of irradiance occurs in Paracou (Bonal et al., 2008; Sabatier and Puig, 1986; Loubry, 1994). Moreover, the EVI signal is synchronous among all forest types of French Guiana (Fig. 2), which suggests that irradiance could be the general driver of leaf fall in French Guiana. Recently, the extreme 2005 drought in Amazonia was suspected to impact leaf production (Saleska et al., 2007). In the end, no statistical correlation has been found so far between drought severity and greenness changes (Samanta et al., 2010). The phenological consequences of long-term changes in solar radiation or alterations in diffuse/direct components still remain an open question in tropical forests (Lewis et al., 2004). However, we know that the frequency of drought events should increase (Solomon et al., 2007, 2009), and as a consequence cloudiness should decrease while irradiance should increase (Nemani et al., 2003; Arias et al., 2011). Further analysis is needed to understand the link between leaf dynamics and climate in order to decipher if the trigger of leaf fall is the peak of irradiance, an intrinsic biological clock, another climate driver sensitive to climate change, or all these factors combined. The use of multiple sites with different phase between high rainfall and high irradiance could help disentangle physiological and climate effects on leaf and wood production.

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



4.2 Wood production

The seasonality of wood production was consistent with observations from other tropical forests, even those tropical forests without any month with precipitation below 100 mm (Clark et al., 2010; Grogan and Schulze, 2012; Wagner et al., 2012; Nepstad et al., 2002). This intra-annual seasonality cannot be considered as the sole result of bark shrinkage and swelling (Fig. 1). Indeed, both trees with low (1–3 mm, 71 trees) and high (8–39 mm, 67 trees) bark thickness exhibited similar seasonal variations in wood production, indicating that variations in cambial activity explained most of the variations in circumference. Here, we showed that wood production presents a complex link with the so-called “forest greening”. First, wood production decreased when EVI increased during the transition between the wet and the dry season (June to September). Second, wood production increased in the early wet season, while EVI remained constant at its highest values. Finally, wood production slowly decreased during the wet season, while EVI seriously dropped (Fig. 4). The asynchronism between leaf and wood production could reflect a time lag in the use of carbohydrates (3.5 months, Table 4) synthesized during the whole year but allocated into short lived pools (leaves) in the dry season and into long lived pools (wood) only during the wet season, as already observed in the forest of Parque Natural Metropolitano, Panama (Wurth et al., 2005). The time lag between peaks of EVI and wood production (109 days, Table 4) indicated the mean time needed for leaves to become fully mature.

Three main climate variables have been demonstrated to impact intra-annual wood production: (i) soil water availability, (ii) irradiance, and (iii) temperature. (i) Our results show that the highest wood production is observed after the greening in the early wet season, when water availability is high (Fig. 3) when new leaves have just matured and when the ecosystem photosynthetic capacity is at its maximum (Stahl et al., 2013). Soil water availability strongly impacts productivity as directly observed in tropical forests (Wagner et al., 2012; Nath et al., 2006; Baker et al., 2003) and as deduced from experimental forest droughts (Nepstad et al., 2002; Lola da Costa et al., 2010). (ii) Our results

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



suggest that seasonal changes in radiation may exert more influence on leaf phenology than changes in rainfall and an indirect effect on wood production (Fig. 3). This is consistent with the results of Huete et al. (2006), which indicated a strong influence of radiation on leaf phenology. However, our results do not support a predominant role of radiation in forest productivity expressed as wood production (Fig. 3). Some authors have further suggested that high values of irradiance could drive the leaf production cycle, as observed in seasonal and aseasonal forests (Zalamea and Gonzalez, 2008; Myneni et al., 2007; Hutyra et al., 2007). (iii) Correlation of wood production and temperature is difficult enough to observe at our site, as temperatures remain rather high (daily mean temperature never less than 23 °C) and seasonal variations in these temperatures remain rather limited (Fig. 3f). At La Selva (Clark et al., 2010), annual growth was found to be sensitive to variations of 1–2 °C in mean annual night-time temperature. Investigating the effects of temperature on the physiology of tropical forest trees (Chambers and Silver, 2004; Lloyd and Farquhar, 2008) is, today, of primary importance, given increases expected over the next century (Solomon et al., 2007; Malhi et al., 2009).

4.3 Does leaf production impact wood production?

Our results highlight a synchronism between old leaves falling, new leaf production and reduced or stopped wood production (Fig. 3). A few months later (3.5 months, Table 4), maximal wood production correlates with high value of water availability and high EVI signal (Fig. 3). Seasonal variations in wood production also exist even in a very constant environment without a dry season, like in La Selva, Costa Rica (Clark et al., 2010), supporting the idea of an annual regulation not induced by drought. In the same way, Tapajós National Forest ecosystems maintain high transpiration and photosynthesis in the dry season while wood production declines (Verbeeck et al., 2011; Figueira et al., 2011). Some studies have reported that (i) evergreen species in seasonally dry environments accumulate carbohydrates during the dry season because photosynthesis continues while wood production ceases (Wurth et al., 2005) and (ii)

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



deciduous species accumulate carbohydrates at the onset of the dry season to support respiration costs when they are leafless (Poorter and Kitajima, 2007; Janzen and Wilson, 1974). Indeed, the cost of wood production is high (to produce 1 g of trunk of *Eucalyptus regnans*, more than 1 g of glucose is needed Kozlowski, 1992). Contrarily to wood production, the cost of new leaf production, flowering or fruiting does not necessarily deplete NSC pools (Wurth et al., 2005). Even species flushing and fruiting during the dry season show high values of NSC, indicating that growth during the dry season is not carbon limited. In temperate forests, Michelot et al. (2012) showed for two deciduous species, *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl., and an evergreen conifer, *Pinus sylvestri*, that the timing, duration and rate of wood production are related to leaf phenology and the dynamics of NSC. They found that leaf phenology, NSC storage and intra-annual growth were clearly different between species, highlighting their contrasting carbon allocation. Very recently, the seasonal dynamics and ages of stemwood NSC in temperate forest trees has been assessed by Richardson et al. (2013). These authors found that NSC were both highly dynamic and about a decade old. Their model with a two-pool structure (fast and slow cycling reserves) gave reasonable estimates of the size and mean residence time of the total NSC pool and greatly improved model predictions of inter-annual variability in woody biomass increment. We should acknowledge that the existence itself of long-term and short-term cycles in NSC are largely ignored among researchers studying tropical trees. Such ecophysiological approaches are urgently needed to improve our understanding of intra-annual net primary production.

5 Conclusions

Tropical forest productivity assessed either by inventory-based observations or satellite-based studies does not rely on similar biological processes (Anderson, 2012). Inventory-based studies catch wood production through secondary growth, while satellite studies based on EVI catch only a part of NPP related to leaf production. We pointed

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

out the 3.5 month time lag between leaf production and wood production that probably reflects the change of carbon allocation in tropical trees during the year. Some work remains before we can understand what controls this time lag. To decipher whether this time lag is driven by endogeneous biological or by exogeneous climate drivers, pantropical analyses of inter-annual biomass production data coupled with EVI data and global climate data are needed. The use of multiple sites with different phases between high rainfall and high irradiance could enable researchers to disentangle physiological and climate effects on leaf and wood production. Furthermore, some authors have recently developed a new method for the remote estimation of chlorophyll content and have shown that fluorescence is a direct indicator of photosynthetic activity (Meroni et al., 2010; Delegido et al., 2011). In the near future, these new techniques for the study of plant status by remote sensing will be available for airborne and space-borne sensors as well (e.g., the ESA-FLEX scientific mission European Space Agency, 2008) and should give direct measurements of the chlorophyll content and activity. As current IPCC scenarios predict an intensification of the dry period for the Guiana shield and the Amazon during the 21st century (Solomon et al., 2007, 2009; Harris et al., 2008), further research is needed to decipher what shapes the forest productivity pattern. In the context of global change, a response to this question is urgently needed to predict the carbon balance of tropical forests for the next uncertain centuries.

Acknowledgements. Funding provided by the project Climfor (Fondation pour la Recherche sur la Biodiversité) and from the project Guyasim (European structural fundings, PO-Feder). This work has also benefited from an “Investissement d’Avenir” grant managed by Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-0025). This study has been possible thanks to the important field work realized at Paracou by B. Burban, J.-Y. Goret, J. Cazal, F. Bompoy, J. Sermage and S. Thibaudeau.

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



European Space Agency: ESA SP-1313/4 Candidate Earth Explorer Core Missions – Reports for Assessment: FLEX – FLuorescence EXplorer, Tech. rep., published by ESA Communication Production Office, Noordwijk, The Netherlands, available at: http://esamultimedia.esa.int/docs/SP1313-4_FLEX.pdf, 2008. 8264

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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ratana, P., Privette, J. L., Morissette, J. T., Vermote, E. F., Roy, D. P., Wolfe, R. E., Friedl, M. A., Running, S. W., Votava, P., El-Saleous, N., Devadiga, S., Su, Y., and Salomonson, V. V.: Large seasonal swings in leaf area of Amazon rainforests, *P. Natl. Acad. Sci. USA*, 104, 4820–4823, doi:10.1073/pnas.0611338104, 2007. 8249, 8262

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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Zelazowski, P., Alvarez Davila, E., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., Honorio, C., E., Keeling, H., Killeen, T. J., Laurance, W. F., Pena Cruz, A., Pitman, N. C. A., Nunez Vargas, P., Ramirez-Angulo, H., Rudas, A., Salamao, R., Silva, N., Terborgh, J., and Torres-Lezama, A.: Drought sensitivity of the Amazon rainforest, *Science*, 323, 1344–1347, doi:10.1126/science.1164033, 2009. 8250

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Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 1.** Description of the climate data for the period 2007–2009.

symbol	climate variable	unit
pre	precipitation	mm
cld	cloud cover	%
pet	potential evapotranspiration	mm
tmp	mean temperature	°C
tmn	minimal temperature	°C
tmx	maximal temperature	°C
vap	vapour pressure	hPa

BGD

10, 8247–8281, 2013

Asynchronism in leaf
and wood production
in tropical forests

F. Wagner et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 2.** Model parameters, standard errors and t values of the biomass production model.

	Estimate	Std. Error	t value	$\text{Pr}(> t)$
(Intercept)	8.8610	2.4690	3.59	0.0016
pre	-0.0004	0.0004	-1.05	0.3051
pet	-0.0125	0.0078	-1.59	0.1244
tmp	0.7350	1.2418	0.59	0.5597
tmn	-0.3149	0.6208	-0.51	0.6167
tmx	-0.6439	0.6325	-1.02	0.3193
cld	-0.0191	0.0072	-2.66	0.0140
vap	0.0639	0.0683	0.94	0.3593

BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Table 3. Seasonality of EVI estimated with cosinor analysis for the forest types of French Guiana.

Forest type	<i>N</i>	amplitude	phase	low phase	<i>P</i> value
low dense forest/included savanna	224	0.031	Month = Dec, day = 6	Month = Jun, day = 7	< 0.05
high forest with regular canopy	1455	0.032	Month = Nov, day = 23	Month = May, day = 24	< 0.05
high forest with disrupted canopy	125	0.028	Month = Nov, day = 10	Month = May, day = 11	< 0.05
mixed high and open forest	916	0.035	Month = Nov, day = 24	Month = May, day = 25	< 0.05
open forest and Euterpe palm forest	217	0.026	Month = Nov, day = 6	Month = May, day = 7	< 0.05
all forest types	2937	0.032	Month = Nov, day = 22	Month = May, day = 23	< 0.05

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

Table 4. Cross correlation between wood production (Δ AGB), enhanced vegetation index (EVI), relative extractable water (REW), leaffall, mean temperature (tmp) and global radiation (Rg). cor+ and cor- are maximum and minimum cross correlation coefficient, IC+ and IC- their confidence interval and lag cor+ and lag cor- their respective time lag corresponding to the maximum or minimum coefficient of correlation in days. If the correlation coefficient falls in the 95 % interval, we cannot reject the null hypothesis of uncorrelated variables.

var ₁	var ₂	cor+	IC+	lag cor+	cor-	IC-	lag cor-
Δ AGB	EVI	0.71	-0.059–0.059	109.00	-0.54	-0.06–0.057	-47.00
Δ AGB	leaffall	0.32	-0.059–0.054	-95.00	-0.66	-0.056–0.059	29.00
Δ AGB	REW	0.80	-0.06–0.064	-17.00	-0.39	-0.058–0.052	121.00
Δ AGB	tmp	0.26	-0.051–0.052	-140.00	-0.59	-0.058–0.06	-8.00
Δ AGB	Rg	0.27	-0.052–0.055	-166.00	-0.56	-0.064–0.063	10.00
EVI	leaffall	0.36	-0.061–0.06	31.00	-0.51	-0.061–0.06	-61.00
EVI	REW	0.59	-0.057–0.054	-131.00	-0.54	-0.056–0.062	30.00
EVI	tmp	0.30	-0.062–0.06	38.00	-0.45	-0.057–0.057	-127.00
EVI	Rg	0.36	-0.056–0.06	48.00	-0.43	-0.057–0.061	-93.00
leaffall	REW	0.41	-0.057–0.061	67.00	-0.54	-0.058–0.059	-45.00
leaffall	tmp	0.41	-0.059–0.062	-46.00	-0.24	-0.06–0.054	75.00
leaffall	Rg	0.36	-0.061–0.062	-20.00	-0.20	-0.064–0.059	126.00
REW	tmp	0.31	-0.054–0.055	-119.00	-0.63	-0.06–0.058	0.00
REW	Rg	0.28	-0.052–0.055	-124.00	-0.49	-0.06–0.063	22.00
tmp	Rg	0.66	-0.056–0.06	0.00	-0.22	-0.059–0.056	182.00

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

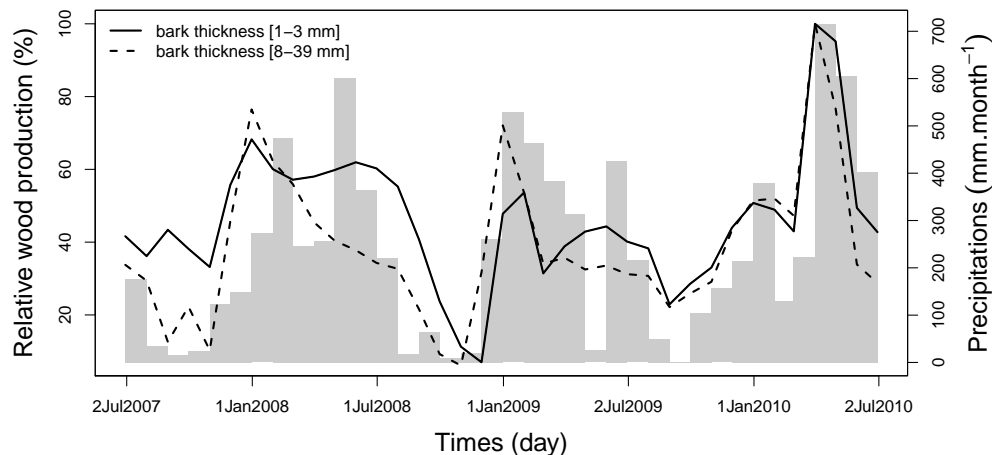


Fig. 1. Monthly variation of wood production (percentage of maximum value) for the 71 trees in the first quantile of bark thickness (1–3 mm, low thickness, solid line) and the 67 trees in the last quantile of bark thickness (8–39 mm, high thickness, dashed line).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



BGD

10, 8247–8281, 2013

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

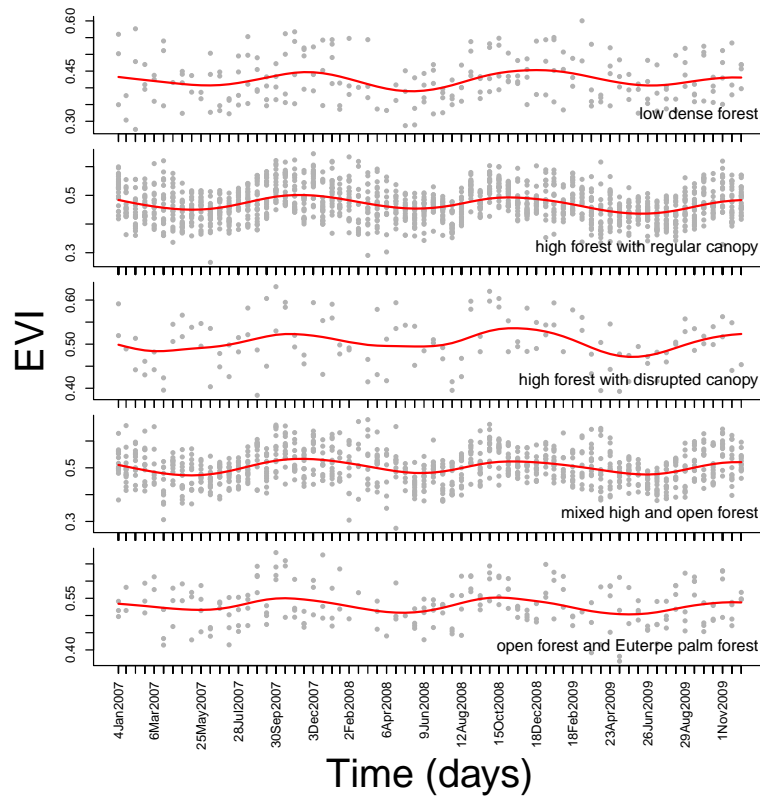


Fig. 2. Evolution of EVI values across French Guianan forest types. Each point reflects one pixel-time couple.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

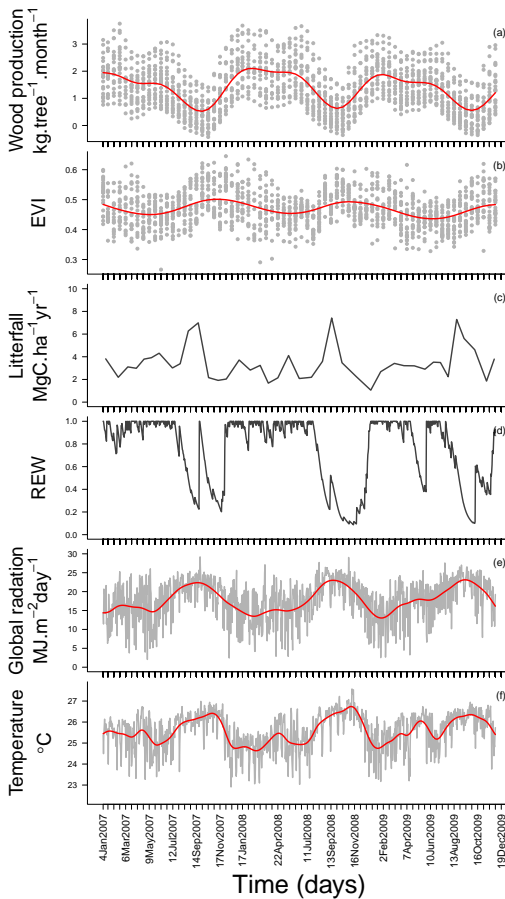



Fig. 3. Evolution of wood production, EVI, litterfall production, relative extractable water (REW, Wagner et al., 2010a), global radiation and mean daily temperature in the Paracou experimental site.

Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

[Title Page](#)

[Abstract](#) [Introduction](#)

[Conclusions](#) [References](#)

[Tables](#) [Figures](#)

[◀](#) [▶](#)

[◀](#) [▶](#)

[Back](#) [Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



Asynchronism in leaf and wood production in tropical forests

F. Wagner et al.

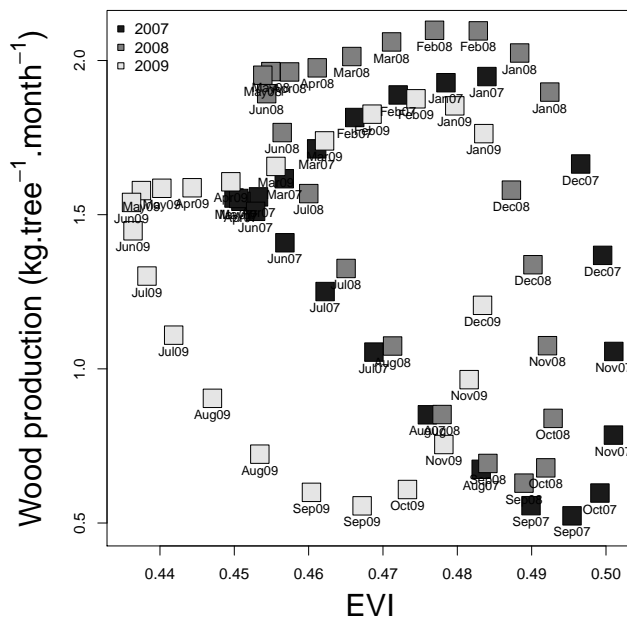


Fig. 4. Hysteresis of the correlation between wood production and EVI for the period 2007–2009.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

