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Relationship between tropical leaf phenology and ecosystem productivity using phenocameras

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Introduction: The interplay of water and light, regarded as the main driver of tropical plant dynamics, determines leaf phenology and ecosystem productivity. Leaf phenology has been discussed as a key variable to explain photosynthetic seasonality in evergreen tropical forests, but the question is still open for seasonally tropical ecosystems. In the search for implementing long-term phenology monitoring in the tropics, phenocameras have proven to be an accurate method to estimate vegetative phenology in tropical communities. Here, we investigated the temporal patterns of leaf phenology and their relation to gross primary productivity (GPP) in a comparative study across three contrasting tropical biomes: dry forest (caatinga), woodland savanna (cerrado), and rainforest (Atlantic Forest).

Methods: We monitored leaf phenology (phenocameras) and estimated gross primary productivity (eddy-covariance) continuously over time at three study sites. We investigated the main drivers controlling leaf phenology and tested the performance of abiotic (climate) and biotic (phenology) factors to explain gross primary productivity across sites.

Results: We found that camera-derived indices presented the best relationships with gross primary productivity across all sites. Gross primary productivity seasonality was controlled by a gradient of water vs. light, where caatinga dry forest was water-limited, cerrado vegetation responded to water seasonality and light, and rainforest was mainly controlled by light availability. Vegetation phenology was tightly associated with productivity in the driest ecosystem (caatinga), where productivity was limited to the wet season, and the camera-derived index (G_{cc}) was the best proxy for gross primary productivity.

Discussion: Leaf phenology increased their relative importance over gross primary productivity seasonality at less seasonal sites (cerrado and rainforest), where multiple leafing strategies influenced carbon exchanges. Our multi-site comparison, along with fine-scale temporal observations of leaf phenology and gross primary productivity patterns, uncovered the relationship between

leafing and productivity across tropical ecosystems under distinct water constraints.

KEYWORDS

leaf phenology, drivers, productivity, GPP, phenocameras, caatinga, cerrado, atlantic forest

1 Introduction

Tropical plant communities are responsible for up to 50% of all terrestrial photosynthesis and dominate precipitation recycling rates, strongly contributing to the regulation of regional and global climate (Field et al., 1998; Malhi, 2010). Leaf phenology is related to plant physiology, temporal variations of biomass, leaf area index (LAI), leaf age, deciduousness, length of the growing season (LOS) and, consequently, it is a key driver of the photosynthetic metabolism and carbon ecosystem exchange (Polgar and Primack, 2011; Restrepo-Coupe et al., 2013; Richardson et al., 2013; Wu et al., 2016). Whilst leaf phenology patterns have recently been discussed as a key variable to explain photosynthetic seasonality for temperate and some tropical plant communities (Migliavacca et al., 2011; Restrepo-Coupe et al., 2013; Toomey et al., 2015; Wu et al., 2016, 2017), the question is still opened for seasonally dry tropical ecosystems.

Leaf exchange patterns define the seasonality of tropical plant communities, which is evident in the proportion of deciduous and evergreen species (Reich, 1995; Morellato et al., 2000; Camargo et al., 2018). Light and water are key factors controlling leaf growth and primary production in the tropics (Wright and van Schaik, 1994; Huete et al., 2006; Vico et al., 2017). Water stress is considered the main limiting of dry season productivity in tropical plant communities, both globally (Guan et al., 2015; Wagner et al., 2016) and across biomes in South America (da Rocha et al., 2009; Restrepo-Coupe et al., 2013; Christoffersen et al., 2014; Vico et al., 2015). Indeed, seasonal water deficit tailored ecosystem boundaries and transition zones between humid and dry lands (e.g.: Olson et al., 2001), with mean annual precipitation of 2,000 mm yr⁻¹ proposed as a threshold of water-limited ecosystems to others responsive to day length or biotic cues (Guan et al., 2015). However, most studies have focused on evergreen Amazonian tropical forests, where an increase of leaf flush in the driest season drives the vegetation greening (Huete et al., 2006; Lopes et al., 2016; Saleska et al., 2016). The knowledge of seasonally dry tropical ecosystems remains elusive (Mendes et al., 2020; Costa et al., 2022a).

Recent studies show the seasonal dynamics of climate, vegetation indices, evapotranspiration, carbon, and energy fluxes at deciduous ecosystems in Brazil (Campos et al., 2019; Mendes et al., 2020; Costa et al., 2022a; Costa et al., 2022b). Ecosystem gross primary productivity (GPP) from satellite remotely sensed in the Amazon, Cerrado (savanna), Pantanal and Caatinga biomes, was weak related with eddy covariance (EC) GPP observed data, with different behaviour in each biome (Costa et al., 2022a). This study demonstrates the importance of investigating specific local environmental drivers and its influence on the ecosystem response captured by *in situ* and remote sensors. Studies mostly represent phenology by NDVI and/or EVI from satellite using

medium to large pixel size products, and 10–16 days of temporal resolution. Nonetheless, seasonally dry tropical forest in Brazil use to synchronize leaf flushing a few days after the first rainfall events (Alberton et al., 2019). Then, satellite-derived indices do not have the capability to track ecosystem responses so fast. It is important to use remote sensed products that combine spatial and temporal resolution to better represent the ecosystem phenology and productivity.

A comparative perspective of tropical phenology may shed light on mechanisms controlling ecosystem processes and how they respond to distinct seasonal environments. Phenological data acquisition is limited in the tropics, with scarce long-term temporal series and uncertainties regarding what triggers plant life-cycle events (Morellato et al., 2016; Abernethy et al., 2018). The use of repeated photographs taken by digital cameras (phenocameras) is an accurate method to monitor leaf phenology over time simultaneously in different plant communities (Morissette et al., 2009; Richardson et al., 2018; Alberton et al., 2017, 2019; Nezval et al., 2020). The camera-derived G_{cc} (green) index characterizes changes in canopy leaf phenology and has also been related to ecosystem gross primary productivity (GPP) temporal curves estimated from local eddy flux measurements in temperate forests and grasslands (Migliavacca et al., 2011; Toomey et al., 2015), and the drylands (Yan et al., 2019). The process of senescence, represented by the camera-derived R_{cc} (red) index, has recently demonstrated good performance in tracking canopy photosynthesis as well, especially for evergreen forests (Liu et al., 2020). Despite the successful application of phenocameras to track leafing seasonality in tropical sites (e.g.: Alberton et al., 2014, 2019; Nagai et al., 2016; Lopes et al., 2016), further evaluation is needed to ascertain if G_{cc} is a proxy of ecosystem productivity across tropical plant communities.

Here, we investigated the temporal dynamics of leaf phenology and GPP patterns, and how they affect tropical ecosystem productivity across three tropical sites under contrasting seasonality (Guan et al., 2015, Figure 1): a light-limited evergreen Atlantic Forest; a mesic seasonal woodland cerrado with a marked dry season; and the Caatinga, a xeric vegetation representing a water-limited, seasonally dry tropical forest (Supplementary Figure S1) (Morellato et al., 2000; Olson et al., 2001; Camargo et al., 2018; Alberton et al., 2019). We simultaneously monitored the top-canopy phenology using camera-derived repeated digital images, extracting the vegetation indices (G_{cc} and R_{cc}). Cameras were at the top of eddy covariance (EC) towers, providing meteorological variables and EC-derived estimates of GPP. Specifically, we asked: i) What are the main abiotic factors related to leafing community responses at each vegetation site? We expect to observe a water-light interplay along the vegetation responses where

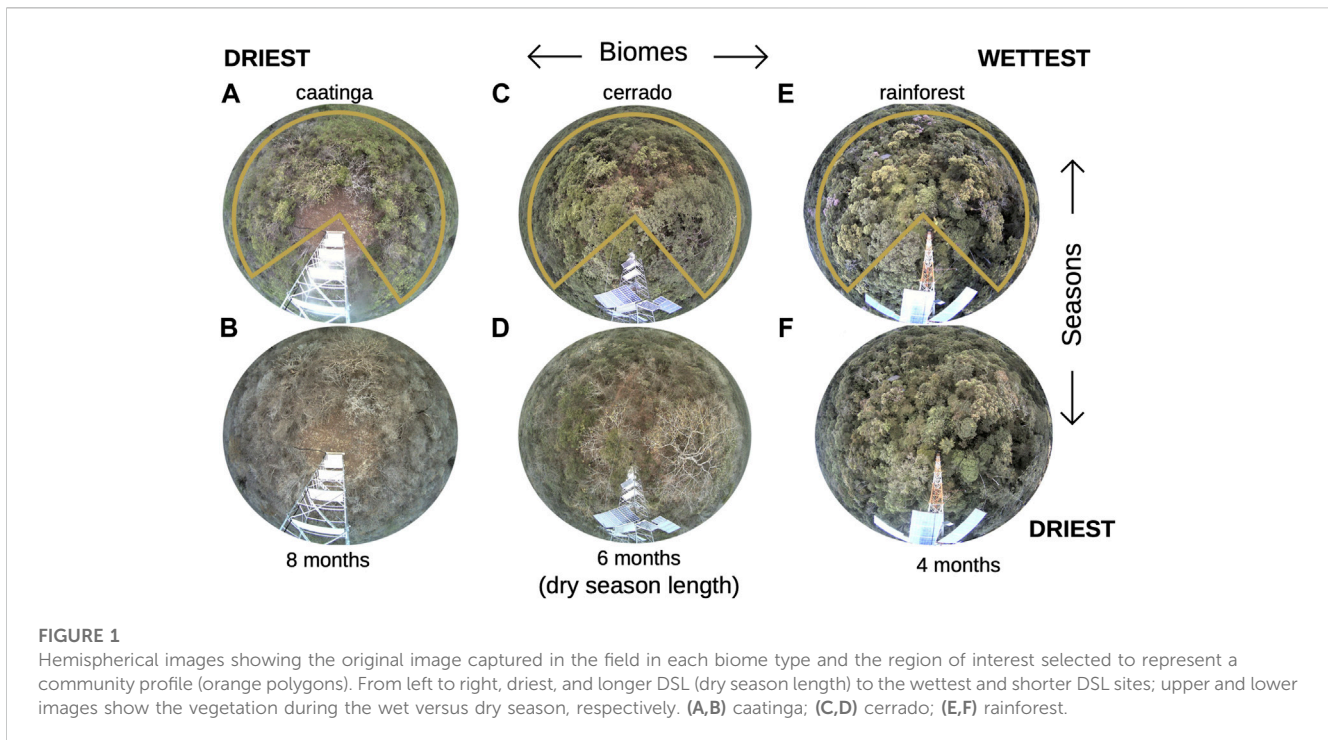


FIGURE 1
 Hemispherical images showing the original image captured in the field in each biome type and the region of interest selected to represent a community profile (orange polygons). From left to right, driest, and longer DSL (dry season length) to the wettest and shorter DSL sites; upper and lower images show the vegetation during the wet versus dry season, respectively. (A,B) caatinga; (C,D) cerrado; (E,F) rainforest.

TABLE 1 Site descriptions including: biome (according to Olson et al., 2001), vegetation type, site name and acronym, coordinates, location, canopy height, period of phenocam measurement, mean total annual precipitation (MAP, mm), dry season precipitation (DSP, mm), and length of dry season (DSL) in months. Eddy covariance measurements in all sites from 1 January 2013, to 31 December 2015.

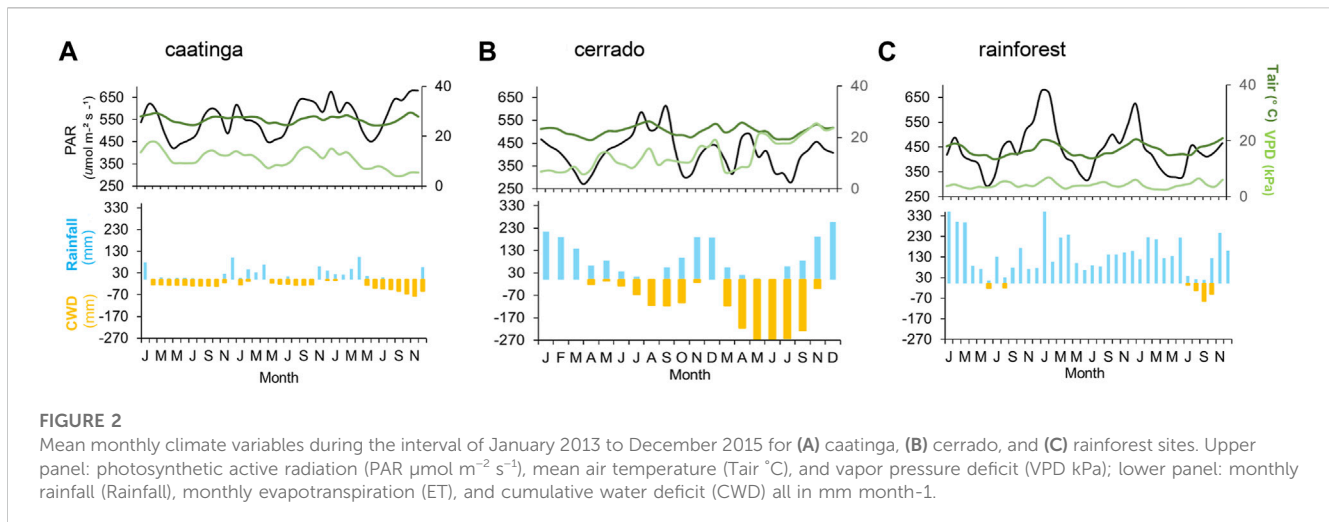
Biome	Vegetation type	Site name and acronym	Coordinates	Location	Canopy height (m)	Period of phenocam measurement	MAP (mm)	DSP (mm)	DSL (months)
desert and xeric shrubland	Caatinga	Embrapa Semi-árido, CAAT	9° 2'47.5512"S; 40° 19'16.6002"W	Petrolina, PE, Northeast Brazil	5	10/May/2013 to 31/Dec/2015	260 mm	75	8
grasslands, savannas and shrublands	Cerrado	Pé de Gigante, PEG	21° 37'9"S; 47° 37'58"W	Santa Rita do Passa Quatro, SP, Southeastern Brazil	12	26/Aug/2013 to 31/Dec/2015	1,150 mm	289	6
moist broadleaf forests	Atlantic Rainforest	Núcleo Santa Virgínia, SVG	23° 12'53.26"S; 45° 23'12.80"W	São Luiz do Paraitinga, SP	30	17/Out/2014 to 31/Dec/2015	1,800 mm	211	4

highly seasonal sites would be more constrained by water limitation towards an increase light-control on leafing patterns at less seasonal environments. ii) What is the relative importance between biotic (leaf phenology) and abiotic (climate) factors controlling ecosystem productivity? We expect that GPP would be explained by the biological process of leaf flushing and senescence, partly in combination with a light and temperature response in the rainforest and partly with an increasing water-limitation response in the cerrado and caatinga; and iii) What are the best proxies of GPP seasonality across the three tropical contrasting biomes? We expect to find more synchronicity between the camera-derived phenology and GPP curves at high seasonal sites since they would be responding to a strong common driver, while towards less seasonal sites curves asynchronies would be expected due to divergent responses between leafing and carbon phenology.

2 Materials and methods

2.1 Sites description

The study sites represent distinct vegetation types of three main tropical biomes (Velooso et al., 1991; Olson et al., 2001): the Caatinga (or the desert and xeric shrubland biome), represented by a seasonally dry tropical forest, the Cerrado (or the grasslands, savannas, and shrublands biome), represented by a woodland cerrado, and the tropical rainforest (or the moist broadleaf forests biome), represented by the Atlantic rainforest (Supplementary Figure S1), hereafter named as caatinga, cerrado, and rainforest, respectively. The sites show contrasting climate regimes reflected in their water availability throughout the year and in the length and intensity of the dry season (Table 1). The research was conducted at all three sites from January 2013 to December 2015.



2.1.1 Caatinga site

It is located at the Reserva Legal of Empresa Brasileira de Pesquisa Agropecuária (Embrapa Semiárido), Pernambuco State, Northeast Brazil. It is a typical Brazilian xeric sclerophyllous vegetation from the semi-arid (caatinga) region, in the northeastern region of Brazil, characterized as a seasonally dry tropical forest (Supplementary Figure S1, for more details, see (Alberton et al., 2019)). According to 30 years of climatic data (1960–1990) compiled from the WorldClim database v.1.0, the mean temperature is 26°C, with a minimum of 22°C and a maximum temperature of 32.9°C, and the mean annual precipitation is 566 mm. The dry season extends for 8 months (May to December), and the wet season is usually from January to April, when total monthly precipitation exceeds 100 mm (Supplementary Figure S1). The three-year monthly average of local climatic data (2013–2015) for the caatinga vegetation was hotter and drier, with 260 mm annual total mean precipitation and an annual mean temperature of 27.05°C (Figure 2A).

2.1.2 Cerrado site

The cerrado woodland is the dominant physiognomy of the study site located at the *Reserva Ecológica Pé-de-Gigante* (PEG) at 649 m a.s.l (for more details see Alberton et al., 2019), São Paulo State, southeastern Brazil (Supplementary Figure S1). According to the 30-year climatic data (1960–1990), the mean annual temperature is 21.1°C, with minimum and maximum means of 16°C and 29.0°C, respectively. The mean total annual precipitation is 1421 mm, with a wet season from October to March (precipitation above 100 mm) and a dry season from April to September (Supplementary Figure S1). During our investigation (2013–2015), the mean annual temperature was 22.5°C and the average annual precipitation of 1150 mm (Figure 2B). The year 2014 was atypical, with a dry summer: rainfall of 152 mm was registered between January to February, substantially lower than the values registered for the same period in 2013 and 2015 (374 mm and 403 mm, respectively).

2.1.3 Rainforest site

It is located at the *Núcleo Santa Virginia* (SVG) at 1,056 m a.s.l, within the *Parque Estadual da Serra do Mar*, São Paulo State, southeastern Brazil (Supplementary Figure S1). The vegetation of

the field site is characterized as a cloud forest. The 30-year climatic data (1960–1990) showed a mean annual temperature of 16°C, with a minimum of 12°C and a maximum of 23.8°C, and a mean total annual precipitation of 1,692 mm (Supplementary Figure S1). The site, despite under the proposed threshold of 2,000 mm of MAP, presents an 8-month wet season that extends from September to April and a small 4-month dry season from May to August, which is drier and colder, but a constant mist occurs daily from 9h00–10h00 in the morning and from 16h00–17h00 in the afternoon. The local climate between 2013 and 2015 showed an expected mean annual temperature of 16.7°C, and a slightly higher total annual precipitation of 1,800 mm; 2014 was the wettest year with 1,965 mm of total precipitation, but the distribution of rainfall was atypical (Figure 2C).

2.2 Measurements of atmospheric fluxes and environmental drivers

Measures with an automatic weather station and atmospheric turbulent fluxes with eddy covariance (EC) method (sensible heat flux, latent heat flux - evapotranspiration E), momentum, and CO₂ flux) were taken from January 2013 to December 2015 (Table 1). CO₂ and water vapor concentration and the three components of wind speed were measured at high frequency (10 Hz) by an open path infrared gas analyzer (LI-7500, Li-Cor, Lincoln, NE, United States of America) and by a three-dimensional sonic anemometer (CSAT3, Campbell Scientific, Logan, UT, United States of America) at all sites. Means, variances, and covariances at 30 min intervals were computed with the high-frequency raw EC data using EddyPro® software (v.6.2.1) (LI-COR Biosciences, Lincoln, Nebraska, United States of America). The anemometer tilt was compensated by double rotating method (Wilczak et al., 2001); corrections for air density fluctuations were applied according to Webb-Pearman-Leuning (Webb et al., 1980); and the spectral corrections following (Moncrieff et al., 2005).

A quality data check was performed. Spurious values due to sensor failures or field maintenance/occurrences were removed, which includes fluxes values measured during rainfall events. Values outside the physical and/or biologically plausible ranges

were also removed from the dataset (Papale et al., 2006) and the friction velocity (u^*) threshold varied seasonally for each site (caatinga— $0.16 < u^* < 0.18 \text{ m s}^{-1}$; cerrado - $0.25 < u^* < 0.35 \text{ m s}^{-1}$; rainforest - $0.17 < u^* < 0.18 \text{ m s}^{-1}$). It was used the quality control flags (“0” for best quality fluxes, “1” for fluxes suitable, and “2” for fluxes with poor quality) provided by EddyPro software, and the fluxes marked with flag 2 were discarded from the results (Foken et al., 2005). For all these reasons, we found that 35.8%, 14.5%, and 31.6% of the NEE data was unavailable on the data set, removed, and therefore filled, respectively for caatinga, cerrado, and rainforest sites.

The marginal distribution sampling (MDS) method is included in the R EddyProc R package (Wutzler et al., 2018) and was applied to fill gaps in the following variables: net ecosystem exchange (NEE), air temperature (Tair), and vapor pressure deficit (VPD). Finally, gross primary productivity (GPP) was estimated by partitioning net ecosystem exchange (NEE, in $\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) into ecosystem respiration (Reco) and GPP, where $\text{GPP} = \text{Reco} - \text{NEE}$. Reco was approximated by following the nighttime approach using the Loyd-Taylor function (Reichstein et al., 2005) implemented in the R EddyProc Package. Further information can be found at Souza et al. (2015), Carvalho et al. (2018) for caatinga; Rocha et al. (2002), da Rocha et al. (2009) for cerrado, and Freitas (2012) for the rainforest.

The following meteorological variables were monitored using a datalogger and the measured data was averaged by 30-min: photosynthetically active radiation (PAR, LI-190SA, Li-Cor, Nebraska, United States of America); air temperature and relative humidity (HMP45C, Campbell Scientific, Inc., Logan, UT, United States of America), and rainfall (CS700-L Hydrological Services Rain Gauge, Liverpool, Australia). The vapor pressure deficit (VPD) was computed by the method described in Allen et al. (1998). To evaluate dry season intensity, we calculated the cumulative water deficit (CWD) based on the cumulative difference of ET-P (Murray-Tortarolo et al., 2016; Alberton et al., 2019). Day length was used to represent the photoperiod seasonality and was calculated based on the latitude of each location (geosphere package in R, (Hijmans et al., 2022)). Environmental variables were summarized into weekly values of mean air temperature (Tair), rainfall, photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and photoperiod.

2.3 Temporal patterns of leaf phenology

At each site, a digital hemispherical lens camera Mobotix Q 24 (Mobotix AG—Germany) was set up at the top of the tower using settings as (Alberton et al., 2017, 2019) and at different dates (see Table 1). At the rainforest site, we used the images in the interval October 2014—December 2015 to minimize gaps. We filled sequence gaps (more than 7 days with no images recorded) using the StructTS algorithm with a structure model fitted by maximum likelihood (see Hyndman and Khandakar, 2008) with the package imputeTS in R (R Core Team 2017).

Regions of interest (ROI) were defined for each camera image as described by (Richardson et al., 2009; Alberton et al., 2014). We defined a community-level image ROI from the original image to extract the relative brightness of the green, red, and blue color

channels (RGB), and then calculate the vegetation indices of leaf color changes: green-up (G_{cc}) and green-down (R_{cc}), which represent flushing and senescence events (Woebbecke et al., 1995; Richardson et al., 2009; Alberton et al., 2017). We calculated the normalized indexes of the green and red color channels according to the formulas:

$$Total_avg = (Red_{avg} + Green_{avg} + Blue_{avg}) \tag{1}$$

$$G_{cc} = \left(\frac{Green_{avg}}{Total_avg} \right) \tag{2}$$

$$R_{cc} = \left(\frac{Red_{avg}}{Total_avg} \right) \tag{3}$$

G_{cc} and R_{cc} were calculated separately for each of the five hourly images taken each day. Daily G_{cc} and R_{cc} time series were taken as the 90th percentile of all daytime data (adapted from (Sonnentag et al., 2012) and eventually aggregated as a weekly moving average to the analyses.

2.4 Data analysis

To answer questions i) and ii), we started investigating the variables with the highest correlations related to leaf phenology and GPP. A set of climatic variables (rainfall, Tair, CWD, VPD, and photoperiod) were correlated to the temporal patterns of leaf flushing and senescence, represented by the camera-derived indices of G_{cc} and R_{cc} , respectively. Equally, the same analysis was conducted with GPP, testing the highest correlated variables using the same set of climatic factors in addition to the phenology variables of G_{cc} and R_{cc} . To do so, we applied a canonical correspondence analysis (CCA). Canonical Correspondence Analysis (CCA) is a statistical tool to find linear combinations in a lower-dimensional space that maximizes the correlation between two multivariate datasets (Härdle and Simar 2007). It was used to encounter the relative importance of multivariate features to predict leaf phenology and GPP values, while simultaneously identifying the temporal lag at which maximum correlation occurs.

The vectors projected in the lower-dimensional space are called canonical vectors (CVs, or component scores) and are linear combinations of the original dataset variables and canonical weights (or component loadings):

$$CV_x = aTX \tag{4}$$

$$CV_y = bTY \tag{5}$$

where a and b are the canonical weight of the original datasets X (length n) and Y (length m), respectively, and k is the covariate number on the lower-dimensional space ($k \leq$ the smallest dimensionality of the two datasets). Here Dataset X is either composed solely of climatic variables or climatic and biotic variables, while Dataset Y is composed of the G_{cc} , R_{cc} , or GPP time series. Initially, the algorithm finds the canonical weight for $k = 1$ that maximizes the correlation between CV_{x1} and CV_{y1} , then the step is repeated to create k CV couples. The weight magnitude indicates the combined strength of the original variables in the pattern captured by the CV. Before the CCA, both datasets were normalized to values between 0 and 1.

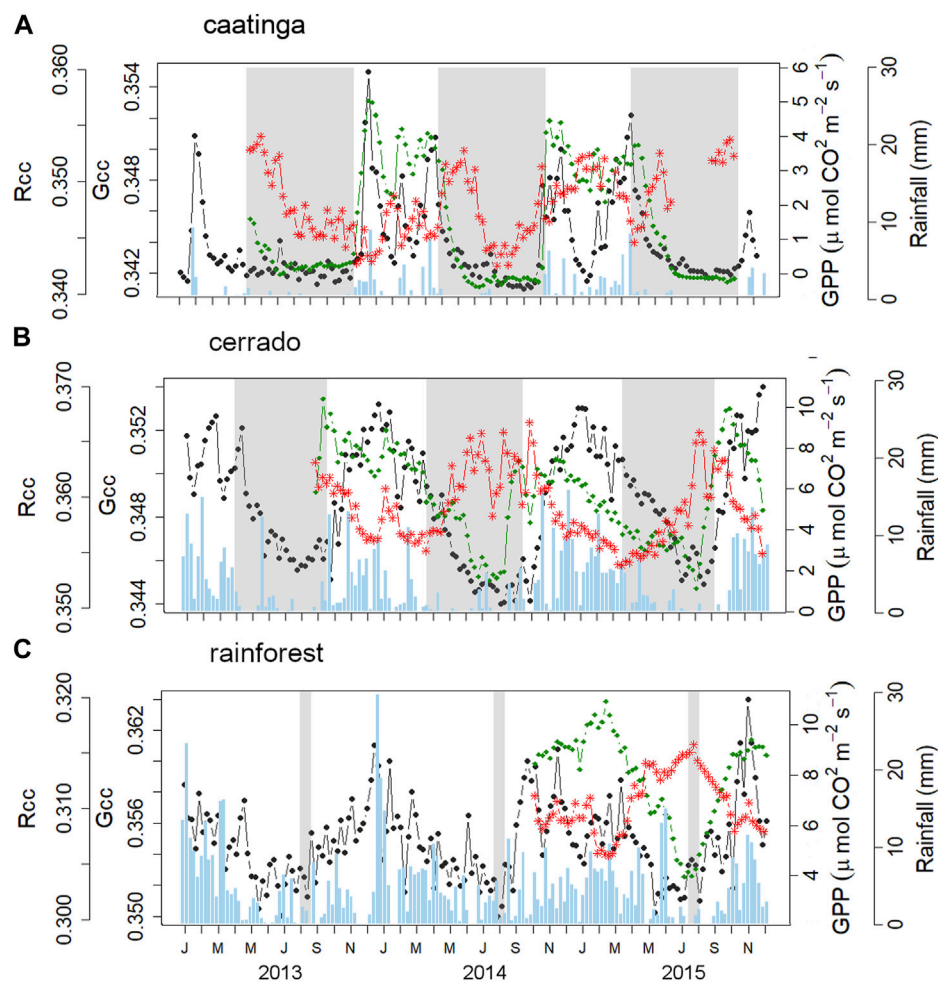


FIGURE 3

Time series (7 days composite) of the camera-derived color indices: G_{cc} (green dotted line), and R_{cc} (red dotted line); and EC estimates of gross primary productivity (GPP, black dotted line), for each vegetation type—(A) caatinga; (B) cerrado; and (C) rainforest. Blue bars refer to the weekly cumulative precipitation time series (mm); gray shaded areas indicate the dry season.

Then, to answer question iii), we evaluated GPP best predictors by performing Generalized Additive Mixed Models (GAMM), using as dependent variable Y the temporal patterns of GPP, and as explanatory variables X the CVx canonical weights with the highest correlation. We used GAMMs as they can capture nonlinear relationships, handle with time series structural in ecological studies, and have been previously used in phenology analyses (Polansky and Robbins, 2013; Alberton et al., 2019). To find the subset of variables that resulted in the best-performing models (i.e., the one that lowers predictive errors), we applied an automatic term selection (Marra and Wood, 2011; Alberton et al., 2019) to identify terms that are not statistically significant (significance with p values < 0.001) and remove them altogether from the model (Marra and Wood, 2011). The variable selection was carried using the double penalty approach, described in (Marra and Wood, 2011) and available in the mgcv R package as *null space penalization* (Wood, 2017). The method constructs an additional penalty for each smooth term, penalizing only functions of the null space of the original penalty. If all the smoothing parameters for a term tend to infinity, the term will be selected out of the model.

Finally, to understand how each term is interacting with GPP, we plotted the partial fits of each smoother parameter and evaluated F-tests of model outcomes.

3 Results

3.1 Temporal patterns of leaf phenology and GPP

Leaf flushing and senescence patterns were seasonal for all sites regardless of the intensity of the drought period. The flush of new leaves was restricted to the rainy months for the caatinga, while for cerrado and rainforest, leaf onset began earlier, still during the dry season (Figure 3). In general, leaf senescence was higher in the dry season (Figure 3). Similarly, GPP time series were seasonal for all sites. For the caatinga and cerrado, there was a marked increase and peaking within the wet season (Figure 3 a-b). Growing season in the caatinga was restricted to the rainy season, with GPP following an intermittent pattern according to the pulses of precipitation.

Cerrado growing season presented a more subtle decay entering the dry season. The rainforest site demonstrated a smoother pattern of increase and decrease of GPP (Figure 3C).

Green up for the caatinga was very sharp (within 2–4 weeks), starting at the very early rainy season and quickly declining with suppression of rainfall (Figure 3A). The measures of G_{cc} were concurrent to GPP year around and especially in the intra-seasonal variability during the growing season. There was a degree of greenness during the caatinga dry season (Figure 3A), related to the Cactaceae *Pilosocereus pachycladus* F. Ritter (Facheiro). This species is dark green year around and likely one of the species responsible for keeping G_{cc} steady during the dry season. R_{cc} peaked at the beginning of the dry season, when the senescence process is intense for the entire plant community, followed by a decrease towards the mid-to-end of the driest months (May to November), when almost all plants are already leafless (Figure 3A). GPP and G_{cc} curves were highly synchronic with correspondent peaks and troughs, although there were observational dates where G_{cc} did not follow GPP decreases to zero values.

The cerrado green-up was notably marked at the late dry season, peaking after 4–7 weeks, through the early-middle wet season, that thereafter declined smoothly until the next year's flushing (Figure 3B). GPP start recovering around the peaking of G_{cc} , although the GPP peak was 4 weeks later than G_{cc} peak. Cerrado green-down and R_{cc} increasing began at the late wet season and extended continuously until the late dry season (August) (Figure 3B), with R_{cc} and G_{cc} peaking nearly together in August. R_{cc} demonstrated an opposite pattern in relation to GPP, while G_{cc} and GPP curves presented an evident temporal lag at the beginning of the growing season. GPP and G_{cc} asynchronies were also noticed during the GPP decay at the second growing season cycle (Figure 3B).

The rainforest green-up started during August, at the end of the coolest and driest season, thereafter G_{cc} increased through the early wet season, peaking at about 4–6 weeks later (Figure 3C). Green-down started in the middle of the wet season and declining smoothly towards the dry season. GPP and G_{cc} increased and decreased together, although G_{cc} presented a slighter more seasonal dynamic compared to GPP, which demonstrated a day-to-day oscillation (Figure 3C). The R_{cc} pattern peaked in August, the driest month when G_{cc} scores started to increase (Figure 3C).

3.2 Factors controlling leaf phenology and GPP

The relative importance of factors related to leaf phenology and GPP were evaluated based on the canonical loading values (Figure 4; 5, respectively). Regarding leaf phenology, in the Caatinga site, Rainfall and Tair presented the highest loading values related to the leaf flushing index G_{cc} (Figure 4A), while Rainfall and VPD were related to R_{cc} (Figure 4B). In the Cerrado, photoperiod was the highest factor, followed by Tair controlling G_{cc} patterns (Figure 4C). Rainfall exhibited the highest importance related to the cerrado senescence process (R_{cc}), followed by photoperiod (Figure 4D). In the Rainforest site, photoperiod followed by Tair demonstrated

similar relative importance controlling G_{cc} and R_{cc} patterns (Figures 4E, F).

By integrating both climatic and phenological variables, we tested the canonical loadings to evaluate the highest correlated variables with the temporal patterns of GPP (Figure 5). In the caatinga, G_{cc} index demonstrated the highest correlation with GPP followed by the Rainfall and VPD (Figure 5A). In the Cerrado site, R_{cc} and Rainfall presented the highest loading values, followed by the G_{cc} index (Figure 5B). G_{cc} and R_{cc} were the main variables correlated to GPP, followed by Tair, in the rainforest site (Figure 5C).

3.3 GPP model predictions

Predictor variables were selected as smooth terms in most of the models. Only R_{cc} presented linear relationship when modeled against GPP in the Cerrado vegetation site. In general, the GAMMs produced models with medium to high explanation power (R^2 from 0.46 to 0.79). Camera-derived phenology (G_{cc} and R_{cc}) were recurrent predictors in all sites, although other variables were significant in explaining GPP (Table 2).

For caatinga, G_{cc} and VPD were the variables that best explained GPP. The partial fit between predictors and the response variable demonstrated that GPP started to be sensitive within an interval of values between 0.345 and 0.350 of G_{cc} (Figure 6A), while presented a negative relationship with VPD, tending to reach zero values above a VPD of 10 (Figure 6B).

In the cerrado site, R_{cc} index demonstrated to be highly significant in model predictions, with a negative relationship controlling GPP decay and the end of the growing season (Figure 6C). Rainfall and G_{cc} index were also significant variables showing a similar relationship with GPP increase according to their partial fits (Figure 6D-E). The rainforest GPP estimates were significantly related solely to the G_{cc} index, demonstrating a logistic function relationship (Figure 6F).

4 Discussion

Our study disentangled the factors driving phenology and GPP across contrasting tropical biomes and the influence of water availability. Leaf flushing drivers differed among biomes from Rainfall and Tair (caatinga), photoperiod and Tair (cerrado) to daylength and Tair (rainforest), reflecting as expected, reduced water constraints affecting leafing temporal patterns towards humid vegetation (Figure 1). On the other hand, leaf senescence drivers tended to be primarily constrained by water availability as demonstrated in the caatinga and cerrado sites. Our analysis partitioned the relative importance of biotic (phenology) and abiotic (environmental) factors, demonstrating that leaf phenology increased its relative importance over GPP towards less seasonal sites. We argue that biotic factors increase control of carbon-water interactions from driest to wettest vegetation sites, although camera-derived time series performed as a reliable proxy of GPP especially in harsh seasonal ecosystems, as the caatinga dry forest, when both leafing and GPP respond quickly to the common driver of rainfall.

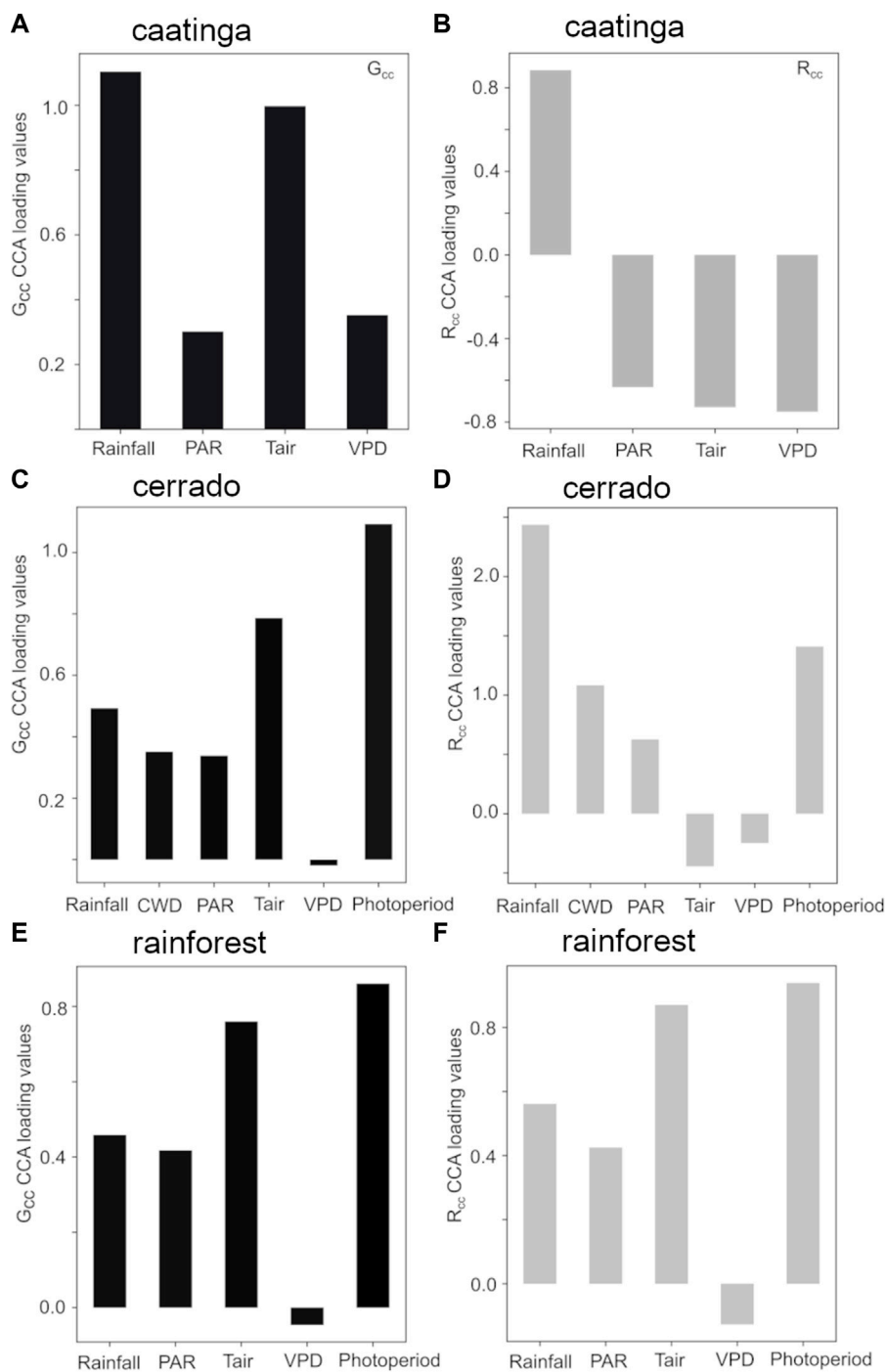


FIGURE 4 Canonical weights (or component loadings) representing the relative importance of each abiotic variable correlated with the camera-derived phenological indices of G_{cc} (black bars) and R_{cc} (gray bars) at each study site: (A,B) caatinga; (C,D) cerrado; and (E,F) rainforest.

4.1 Leaf phenology in tropical ecosystems

The harsh seasonal condition of the caatinga explains the observed dominance of species with a deciduous leaf strategy (Murphy and Lugo, 1986; Machado et al., 1997; Singh and Kushwaha, 2005; Alberton et al., 2019). In fact, rainfall was the main parameter affecting our caatinga G_{cc} and R_{cc} predictions. We

argue that the high interannual variability of precipitation rates and the long, severe drought, selected species that are drought-avoiders, losing all leaves, and with leafing constrained to the short periods of water availability (Vico et al., 2015; Alberton et al., 2019). In fact, the interannual variation in annual rainfall distribution influenced the length of the growing season and its amplitude in a satellite-derived monitoring in the Caatinga (Medeiros et al., 2022). This scenario

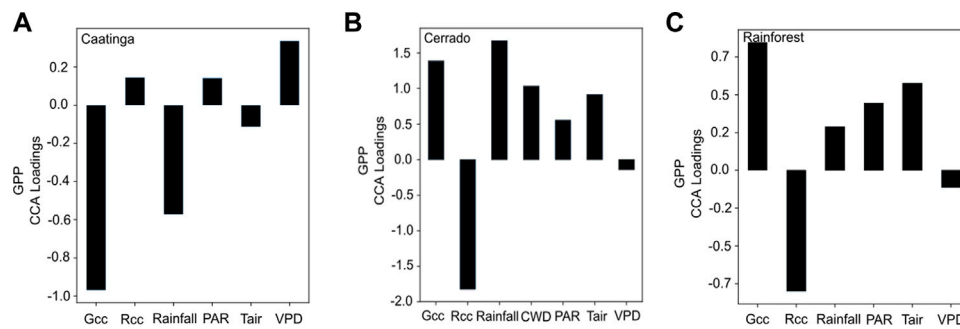


FIGURE 5 Canonical weights (or component loadings) representing the relative importance of each variable correlated with GPP (black bars) at each study site: (A) caatinga; (B) cerrado; and (C) rainforest.

also explained the fast response to rainfall, usually within a few days to a couple of weeks after the first rain events, as detectable by the phenocamera daily monitoring (Alberton et al., 2019; Paloschi et al., 2021).

Leaf onset in the cerrado was concentrated in the late-dry season, with old leaves and leafless crowns concentrated in the dry season. Even though the Cerrado is below the proposed annual 2000 mm threshold (Guan et al., 2015), our cerrado woody species produced new leaves still in the dry season, indicating no water-limitation to leaf onset (Rossatto, Hoffmann, and Franco, 2009; Rossatto et al., 2012; Camargo et al., 2018). Cerrado woody plants, like other wood savanna species, present adaptations to maximize their carbon gains, such as water storage and deep root systems that access belowground water sources (Borchert, 1998; Eamus, 1999; Fabian G. Scholz et al., 2002; F. G. Scholz et al., 2008; Rossatto et al., 2012; Camargo et al., 2018), allowing start leaf production yet in the dry season. As suggested by (Dalmolin et al., 2015) leaf emergence associated with branching during the dry season may maximize carbon gain by increasing rates of C assimilation by plants at the onset of the rainy season. For those species flushing at the start of the wet period, water availability may play a key role as a driver of leaf expansion (Lenza and Klink, 2006; Silvério and Lenza, 2010; Camargo et al., 2018; Alberton et al., 2019). Also, cerrado plants responded to a consistent cue, the day length, for the beginning and synchronization of leaf flushing (Camargo et al., 2018). Synchronous, anticipated leaf flushing may also be an adaptation mechanism to avoid herbivory (Aide, 1988; Camargo et al., 2018), a matter that needs further study associating phenology and leaf defense traits (da Silva and Batalha, 2011).

The low range of variation in the rainforest G_{cc} index suggests the dominant presence of evergreen species. Studies reporting camera-derived phenology from high diverse tropical rainforest have also demonstrated low variation in the G_{cc} index when considering the whole community ROI (Nagai et al., 2016). Leaf green up and brown down (G_{cc} and R_{cc}) were mainly driven by photoperiod in the rainforest plant community, as suggested in a previous phenology study across Atlantic rainforest sites (Morellato et al., 2000) and

further demonstrated by Borchert et al. (2005). Older tropical rainforest formations, as the Monsoon forests from South-East Asia, subject to the heterogeneity of climate variability in the rainfall distribution, may demonstrate intriguing patterns of phenological activity (Suepa et al., 2016). Rainforest evergreen species may show asynchronous activity throughout the year, which is likely related to the environmental conditions allowing growth and reproduction year-round (Fenner, 1998; Morellato et al., 2000).

4.2 The role of plant phenology and environment in determining GPP patterns across tropical ecosystems

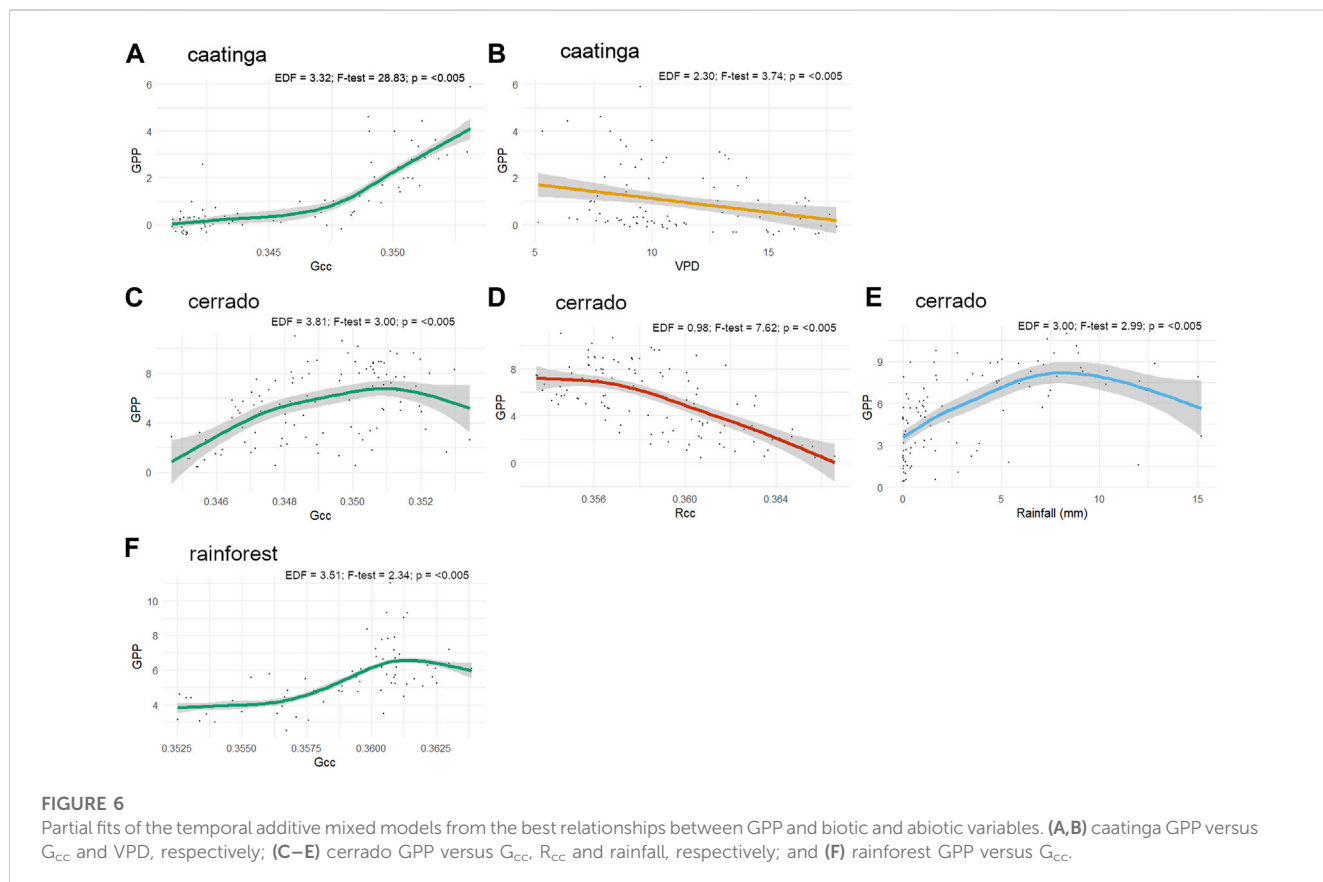
Our models demonstrated a partitioned effect of biotic (phenology) and abiotic (environment) variables on GPP, with biotic and abiotic covariables contributing to the caatinga and cerrado, and a dominant contribution of the biotic factors in the rainforest. Then, GPP was controlled by a gradient of water vs. light, where caatinga dry forest was water-limited, cerrado responded to water and light seasonality, and less seasonal rainforest was mainly controlled by light availability, corroborating our initial predictions of a hydroclimate control of tropical ecosystem productivity (Guan et al., 2015).

The caatinga showed the strongest, fast-leaving response to the first rains, with GPP peaking early in the wet season with more than 90% decline during the dry season. The caatinga corroborated the prediction that under an annual rainfall threshold of 2,000 mm, seasonal plant communities might not be able to surpass the water stress imposed by the dry season, reducing productivity (Guan et al., 2015; Wagner et al., 2016; Vico et al., 2017). There are still few records of productivity rates from the caatinga derived from MODIS (da Silva et al., 2013; Brito Morais et al., 2017), but recent studies (Mendes et al., 2020; Paloschi et al., 2021) showed similar patterns, characterizing the caatinga fast-leaving response to water pulses.

The highest synchronicity of caatinga trees reinforced the length and intensity of the dry season as a major control of GPP, with precipitation triggering and synchronizing leaf onset, enabling

TABLE 2 Approximate significance of the smooth terms used in the GAMMs. Effective degrees of freedom (edf), F-test and *p* values are given for each of the following variables: green chromatic coordinate (Gcc), red chromatic coordinate (Rcc), Rainfall (mm), vapor pressure deficit (VPD), Air temperature (Tair), and cumulative water deficit (CWD). The coefficient of determination (*R*²) of each model is also shown. All variables were significant, with *p* values < 0.001.

Site location	Response variable	Explanatory variables	edf	F-test	<i>p</i>	<i>R</i> ²
Caatinga	GPP	Gcc	3.322716	28.835	2.00E-16	0.797
		VPD	2.304155	3.744	3.79E-07	
		Rainfall	0.898921	0.331	N.S	
		Tair	0.001674	0	N.S	
Cerrado	GPP	Gcc	3.814181	3.00	1.10E-05	0.768
		Rcc	0.986036	7.628	2.00E-16	
		Rainfall	3.0017226	2.993	3.26E-06	
		Tair	0.0005444	0	N.S	
		CWD	0.8453574	0.607	N.S	
		VPD	3.420685	1.717	N.S	
Rainforest	GPP	Gcc	3.5100	2.347	7.66E-05	0.463
		Rcc	0.2579	0.035	N.S	
		Rainfall	1.1881	0.275	N.S	
		Tair	0.5130	0.117	N.S	
		PAR	1.1734	0.296	N.S	



species to recover their water status at the beginning of the wet season (Machado, Barros, and Sampaio, 1997; Alberton et al., 2019), a pattern similar found for other tropical dry forest (Christian et al., 2015). High interannual variability in precipitation rates contributes to the variability and intensity of leaf flushing onset in the community at a given year (Machado, Barros, and Sampaio, 1997; Gutiérrez et al., 2014; Medeiros et al., 2022). Thus, climatic constraints and leaf phenology were tightly coupled in the caatinga, explaining the high correlation between phenology and GPP. The camera-derived G_{cc} index demonstrated to be a reliable proxy of GPP for harsh seasonal environments, where the highly synchronized leafing responds quickly to rainfall.

In the cerrado, leaf senescence (R_{cc}) was the best parameter predicting GPP, along with G_{cc} and precipitation. Based on the rainfall contribution in our models, the senescence process in the cerrado, although not pervasive as in the dominant deciduous caatinga, could be a response to water stress. Our findings agree with the general suggestion that mild seasonal savanna ecosystems would present a complex interaction of climatic and phenological factors (Devi Kanniah, Beringer, and Hutley, 2010; Whitley et al., 2011; Ma et al., 2014; Moore et al., 2017) and that the overall semideciduous vegetation, incorporates complex and multiple leaf-exchange strategies (Rossatto, Hoffmann, and Franco, 2009; Alberton et al., 2014; Camargo et al., 2018). Hence, the strategy of trees to produce new leaves in the dry season is especially important for cerrado carbon-water interactions (Vico et al., 2015) since early leaf flushing may contribute to major carbon gains. Species anticipating leaf emergence, increase carbon assimilation rates when the rainy season begins, thus extending the growing season (Dalmolin et al., 2015). Based on that, different drives may control the onset of leaf flushing and productivity in the cerrado, explaining the observed asynchrony between G_{cc} and GPP curves.

We suggest that incorporating leaf senescence, rather than only greenness indices, will improve predictions of productivity in the tropics. The effects of foliage senescence on ecosystem processes and their main drivers are still neglected in productivity models (Cueva et al., 2021). However, recent studies are incorporating leaf senescence as a parameter explaining dryland productivity (Cueva et al., 2021) and plant response to climate change in temperate zones (Zani et al., 2020). Based on our visual imagery analysis, the R_{cc} index is mainly related to leaf senescence and the decrease of green biomass. However, it also may be linked to the many colorful, reddish, new leaves produced at the beginning of the cerrado leaf flushing.

Different from the two seasonally dry sites, as expected, rainforest productivity was the least affected by water throughout the year. Rainforest GPP was mainly controlled by phenology, with the G_{cc} as the dominant selected variable in the GPP model, despite presenting the lowest explanation power among all sites. The low mean air temperature, although not selected in the GPP model, may be limiting GPP by reducing photosynthetic activity (Vieira et al., 2011; Marchiori et al., 2016; Malhi et al., 2017), most likely due to the elevated altitude of the study site (1056 m a.s.l.). Other factors, such as the mechanisms of leaf demography associated with leaf ontogeny are also relevant to control photosynthesis seasonality

as suggested for a slightly seasonal evergreen Amazon Forest that is not water-limited (Wu et al., 2016, 2017). Also, G_{cc} index is sensitive to the onset of new leaves production (Lopes et al., 2016), which may be responsible to cause curves asynchronies between G_{cc} and GPP towards less seasonal vegetation sites. That is a subject deserving further study combining species synchronicity analysis within and among biomes in a comparative approach.

Our study demonstrated how temporal dynamics of leaf phenology swings according to the dryness intensity imposed in the environment. There was an interplay of water and light triggering plant community responses, indicated by the decrease of water constraining on community leaf flushing and senescence. The multi-site comparison, along with fine-scale temporal observations of leaf phenology and GPP patterns, uncovered the relationship between leafing and productivity across tropical ecosystems under distinct water constraints. Camera-derived indices showed to be reliable in predicting GPP seasonality for high seasonal constraint environments.

Leaf phenology interannual variations were yet detected in our results, but with the use of longer time series, we can further investigate the consequences that extreme climate events may have on ecosystem metabolism. We highlight the likely impacts that future changes on water regimes, mostly related to climate change, may have on plant phenology and productivity of tropical ecosystems (Vico et al., 2015; Morellato et al., 2016; Restrepo-Coupe et al., 2017) especially considering the drying trends presented in the last IPCC report (IPCC, 2021). Integrated methods are expected to significantly improve our understanding of patterns and drivers of tropical phenology and ecosystem metabolism across scales (Miura et al., 2023; Shin et al., 2023; Wang et al., 2023). Cross-scale monitoring phenology, linking phenocameras with high resolution orbital sensors, is promising to effectively track large-scale phenology with a fine individual tree resolution and the response of tropical vegetation to climate change (Wang et al., 2023).

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

BA, AR, RT, and LM conceived and designed the study; BA processed and analyzed imagery, climatic and fluxes data; TM performed CCA models; BA, MM, HR, and LM analyzed and discussed the results; BA led the manuscript writing with significant input from all authors. All authors contributed to the article and approved the submitted version.

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Supplementary material

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