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FENOLOGIA FOLIAR DA FLORESTA AMAZÔNICA DE TERRA FIRME POR IMAGENS DIGITAIS RGB

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Sinopse

Acompanhou-se com sucesso a fenologia foliar do dossel de uma área de Floresta Amazônica de Terra Firme em um ano de imagens diárias tiradas a partir de uma câmera RGB instalada em uma torre. Duzentas e sessenta e sete copas individuais foram monitoradas digitalmente através da construção da linha temporal do seu verdor, na forma da métrica *green coordinate*. Oitenta e dois por cento das copas do dossel superior mostrou um claro episódio de rápido e massivo *flush foliar* e 30% mostrou uma perda rápida e massiva de folhas. O *flush foliar* foi fortemente concentrado nos cinco meses mais secos (50% de todas as copas) comparado com os cinco meses mais chuvosos (10% de todas as copas). Árvores com abrupta perda e emissão de folhas atingiram o seu verdor mínimo 26 +/- 16 dias antes do verdor máximo. Assim, a perda de folhas foi um rápido preâmbulo para o *flush foliar* na estação seca e não foi determinada pelo aumento do fotoperíodo.

Palavras-chave: fenologia, *flush foliar*, *phenocam*; estação seca, sazonalidade, Amazônia Central

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RESUMO

A fenologia foliar tem sido apontada como vetor da sazonalidade da capacidade fotossintética do dossel florestal e do fluxo de carbono na Amazônia Central. O monitoramento visual a partir do chão é demorado e difícil, sobretudo, contra um céu nublado. Mudanças sazonais nos índices de vegetação obtidos por sensores orbitais têm sido questionados devido a tendências sazonais no ângulo de iluminação solar. Câmeras RGB montadas em torres são uma atrativa opção. A coordenada cromática verde (GC = brilho no canal verde dividido pela soma do brilho dos três canais RGB) tem sido empregada para este propósito. Entretanto, sutis mudanças sazonais no GC das florestas tropicais em escala de paisagem podem ter menor amplitude do que os artefatos relacionados com o balanço de cores, tamanho da sombra das copas, ângulo de iluminação, velocidade de exposição e deriva do sensor. Além disso, mudanças graduais no GC são afetadas tanto pela idade das folhas quanto pela quantidade de folhas. Mesmo assim, mudanças abruptas e de grande amplitude no GC ocorrem em escala de copas individuais e podem ser atribuídas com confiança a eventos de massiva emissão ou perda foliar. Nós analisamos um ano de imagens diárias obtidas por uma câmera RGB instalada a 50 metros acima do dossel florestal no sítio Observatório de Torre Alta da Amazônia (59.00ºW, 2.14ºS), em um platô bem drenado. Nós minimizamos os artefatos mantendo o sol atrás da câmera, aceitando apenas imagens de iluminação difusa, dando peso igual a cada uma das copas e procedendo a intercalibração radiométrica de todas as imagens selecionadas contra uma imagem padrão. Para cada uma das 267 áreas de copas individuais, nós então preparamos uma linha temporal do verdor com valores diários de GC. Oitenta e dois por cento destas copas do dossel superior mostrou um claro episódio de rápido e massivo *flush foliar* (inclinação suavizada do GC > 0,01/mês, sustentada por pelo menos 15 dias, culminando acima do 75º percentil dos valores diários do GC) e 30% mostrou uma perda rápida e massiva de folhas (inclinação suavizada do GC < -0,01/mês, sustentada por pelo menos 15 dias, atingindo valores abaixo do 25º percentil dos valores diários do GC). O *flush foliar* foi fortemente concentrado nos cinco meses mais secos (50% de todas as copas) comparado com os cinco meses mais chuvosos (10% de todas as copas). Isto contradiz o recentemente proposto controle por fotoperíodo na fenologia foliar das árvores na região equatorial úmida. Árvores com abrupta perda e emissão de folhas atingiram o seu verdor mínimo 26 +/- 16 dias antes do verdor máximo, indicando que a perda de folhas foi um rápido preâmbulo para o *flush foliar* na estação seca.

ABSTRACT

Leaf phenology may drive seasonal variation in canopy-scale photosynthetic capacity and carbon flux in the Central Amazon. Visual monitoring of leaf flush from the forest floor is time consuming and difficult against an overcast sky. Seasonal trends of vegetation indices from orbital sensors have been challenged due to artifacts from seasonal trends in solar illumination angle. Tower-mounted RGB cameras are an attractive alternative. The Green Chromatic Coordinate (GC = green brightness divided by summed brightness of the three RGB channels) has been employed for this purpose. However, subtle seasonal change of tropical forest GC at landscape-scale may be of smaller amplitude than artifacts related to color balance, crown shadow size, illumination angle, exposure speed and sensor drift. Furthermore, gradual change in GC is affected by both leaf age and leaf amount. Nonetheless, abrupt GC change of large amplitude occurs at the individual crown scale and can be reliably attributed to massive leaf flush or leaf loss events. We analyzed a full year of daily images from an RGB camera mounted 50 m above the forest canopy at the Amazon Tall Tower site (59.0ºW, 2.1ºS), on a well-drained plateau. We minimized artifacts by maintaining the sun behind the camera, accepting only images with diffuse illumination, by giving equal weight to each tree crown and by radiometric inter-calibration of all selected images against a standard. For each of 267 individual crown areas we then prepared a greenness timeline of daily GC values. Eighty-two percent of these upper canopy crowns showed a clear episode of rapid and massive leaf flush (smoothed GC slope >0.01/month, sustained for at least 0.5 month and peaking above 75th percentile of daily GC values) and 30% showed massive rapid leaf drop (smoothed GC slope <-0.01/month, sustained for at least 0.5 month, ending below 25th percentile of daily GC values). Flushing was strongly concentrated in the five driest months (50% of all crowns) compared to the five wettest months (10% of all crowns). This contradicts the recently proposed photo-period control over humid equatorial tree phenology. Trees with both abrupt leaf drop and abrupt leaf flush reached minimum greenness 26 +/- 16 days prior to maximum greenness, indicating that leaf drop was a brief preamble to dry season leaf flush.

SUMÁRIO

INTRODUÇÃO

A fenologia foliar, definida como o estudo da sazonalidade do desenvolvimento, senescência e abscisão foliar em relação às condições ambientais, constitui um potencial indicador das mudanças climáticas (Badeck *et al*., 2004; Chuine *et al*., 2004; Parmesan, 2007). As informações sobre a fenologia do dossel das florestas tropicais são importantes *inputs* para os atuais modelos do sistema terrestre. Alguns destes modelos sugerem que o aumento da temperatura global ocasionará aumento no número de eventos de seca extrema na Amazônia, mudanças no porte da vegetação, redução da extensão do bioma e/ou perdas nos estoques de carbono (Cox *et al.,* 2004; Salazar *et al*., 2007; Huntingford *et al*., 2007; Malhi *et al*., 2008). Outros estudos apontam uma intensificação do ciclo hidrológico nesta região (Gloor *et al*., 2013; Durack *et al*., 2012). Em vários destes modelos, as maiores incertezas estão associadas com as respostas fisiológicas das plantas, enquanto as incertezas sobre as projeções climáticas são significantemente inferiores (Huntingford *et al.,* 2013).

Em geral, os modelos genericamente assumem que a capacidade fotossintética é constante com o aumento da idade da folha (Weirdt *et al*., 2012). Entretanto, estudos mostram que a eficiência de assimilação da energia incidente fotossinteticamente ativa incidente em uma folha aumenta rapidamente após a expansão foliar, declinando após alguns meses idade (Kitajima *et al*., 1997). Epifilos podem contribuir com este declínio causado pela idade da folha. Cerca de dois meses após a expansão foliar, hifas de fungos já estavam visíveis em folhas de uma árvore emergente em uma floreta de terra firme na Amazônia (Roberts *et al.,* 1998). Líquens, briófitas e outros epifilos cobriram 15 a 18% da área superficial de folhas de um ano de idade no sub-bosque de uma floresta úmida no Panamá (Coley *et al*., 1993). Assim, a idade das folhas, mais do que a quantidade de folhas, pode ser o principal direcionador da variação sazonal da capacidade fotossintética em escala de dossel e do balanço de carbono na Amazônia Central (Hutyra *et al*., 2007; Brando *et al*., 2010; Restrepo-Coupe *et al*., 2013). A incorporação de padrões sazonais de mudanças na fisiologia foliar e na idade foliar do dossel irão melhorar o desempenho dos modelos do sistema terrestre (Weirdt *et al*., 2012; Wu *et al*., 2014).

Dois platôs de floresta de terra firme na Amazônia Central, próximos a Santarém e Manaus, atingiram seus picos de abscisão foliar (medida com coletores de serapilheira) nos meses mais secos do ano (Restrepo-Coupe *et al*., 2013). Outros estudos de campo também mostram que a produção de folhas novas, evento chamado *flush foliar*, é mais frequente na estação seca, mesmo período em que a irradiância solar atinge o seu pico (Alencar, 1991; Wright e Schaik, 1994; Doughty e Goulden, 2008; Brando *et al.*, 2010). Entretanto, os métodos de amostragem fenológica não são padronizados (Eça-Neves e Morellato, 2004) e as áreas amostradas em geral são muito pequenas.

Estudos de sensoriamento remoto têm examinado a sazonalidade da fenologia foliar da floresta amazônica através do índice de vegetação EVI (*Enhanced Vegetation Index*) do sensor orbital MODIS. Huete *et al*. (2006) reportaram um padrão de *green-up* na estação seca, representado por valores de EVI maiores do que a média durante esta estação. Padrão semelhante também foi identificados nos anos mais secos (Saleska *et al.*, 2007), sugerindo uma certa resiliência da floresta frente às secas. Entretanto, o aumento no EVI do começo até o final da estação seca para a maior parte da Amazônia (Junho a Outubro) tem sido questionado como sendo um artefato causado pelo decrescimento sazonal da fração de sombra em escala sub-pixel, ocasionado por uma tendência sazonal entre a geometria do sensor em relação à iluminação solar (Galvão *et al*., 2011; Moura *et al*., 2012; Morton *et al*., 2014). Além disso, a maior ocorrência de nuvens durante a estação chuvosa e a maior ocorrência de fumaça durante a estação seca também podem criar artefatos sazonais no EVI (Samanta *et al*., 2010). Após correções da geometria do sensor e da iluminação solar, nenhuma variável climática explicou a variação interanual do EVI em grande escala na Amazônia (Brando *et al*., 2010). Entretanto, este EVI melhorado foi localmente correlacionado com o *flush foliar* na estação seca em uma área próxima a Santarém.

Restrepo-Coupe e colaboradores (2013), integrando mensurações de um rede de torres de fluxo turbulento distribuídas pela Amazônia equatorial (5^{o}N, 5^{o}S), corroboram com a hipótese do *green-up* na estação seca. Os autores concluíram que a produtividade primária bruta (GEP) nesta região não é limitada pela disponibilidade de água e que os fluxos mensurados exibiram altos ou crescentes níveis de atividade fotossintética ao longo da estação seca, o que foi sugerido como uma consequência da alocação de esforços para o crescimento de folhas novas.

Perante este contínuo debate sobre a confiabilidade do EVI do sensor MODIS para a detecção da sazonalidade do verdor da floresta, uma atrativa opção consiste em monitorar o dossel superior da floresta com o uso de câmeras montadas em torres, chamadas *phenocams*. Estas abordam o verdor em uma escala intermediária entre organismos individuais e pixels de imagens de satélites (Richardson *et al.*, 2013) e proporcionam uma alta frequência de amostragem temporal, sendo também muito útil para estudar e controlar os artefatos de iluminação.

O estudo da fenologia das florestas temperadas com o uso das *phenocams* está muito avançado (Richardson *et al*., 2007; Richardson *et al*., 2009; Hufkens *et al*., 2012; Sonnentag *et al*., 2012; Yang *et al*., 2014). Entretanto, o sinal fenológico em escala de paisagem em uma floresta tropical de terra firme é mais sutil do que o sinal em uma floresta temperada decídua, tanto que os artefatos de iluminação compreendem uma grande fração das mudanças detectáveis. Folhas de diferentes espécies e diferentes idades, considerando uma mesma espécie, exibem diferentes colorações no espectro da luz visível (Toomey *et al*., 2010). A idade das folhas pode ser confundida com a quantidade de folhas ao usar "indicadores de verdor" derivados de câmeras RGB, seja para espécies arbóreas de florestas tropicais ou para espécies decíduas de florestas temperadas durante a estação de crescimento (Yang *et al*., 2014). Por estes motivos, o estudo da fenologia das florestas tropicais com o uso das *phenocams* ainda está em desenvolvimento. Até o presente momento, na Amazônia, as *phenocams* estão restritas a dois sítios na sua porção central, sendo áreas de florestas primárias de terra firme em platôs bem drenados com solos argilosos inférteis.

Uma câmera Tetracam, modelo ADC (*Agricultural Digital Camera*), com três bandas similares às bandas 2, 3 e 4 do *Landsat Thematic Mapper* (verde, vermelho e infravermelho próximo, respectivamente) foi mantida por dois anos a 64 m de altura em uma torre na Florestal Nacional do Tapajós, em Santarém (2.897°S, 54.952°W). Esta torre se localiza muito próxima ao local do estudo de Brando e colaboradores (2010). Um padrão similar de *flush foliar* foi encontrado na estação seca, precedido por uma rápida e preparatória abscisão foliar em parte das árvores que emitiram folhas novas (Wu *et al*., 2014). Valores mensais do Índice de Área Foliar (LAI) e da eficiência no uso da luz em escala de dossel (LUE), extraída de medições de fluxo turbulento, foram usados para modelar a abundância de folhas por classe de idade. A idade das folhas, e não o LAI, melhor explicou a produtividade primária do ecossistema (GEP).

Uma câmera Stardot, modelo Netcam XL 3MP, com três bandas na região do espectro visível (RGB) tem sido mantida desde setembro de 2010 a 54 m de altura em uma torre na Reserva Biológica do Cuieiras, em Manaus (2.609°S, 60.209°W). Para 65 copas monitoradas durante 24 meses, Nelson e colaboradores (2014) com o uso do método de análise visual expandiu o trabalho de Tavares (2013) e reportou que 60% das copas emitiram massivamente folhas novas a cada ano, com uma razão quatro vezes maior para o *flush foliar* nos cinco meses mais secos do que nos cinco meses mais chuvosos. Os casos de massiva abscisão foliar foram um preâmbulo para o *flush foliar*. Nelson e colaboradores (2014) e Tavares (2013) encontraram que cerca de 25% das copas ficaram completamente decíduas, principalmente nos cinco meses mais secos.

Menos que uma centena de copas de dossel foi monitorada em cada um destes sítios, de modo que generalizações ainda não podem ser baseadas apenas nestes dois sítios. Mais sítios monitorados com *phenocams* são necessários, preferencialmente usando torres mais altas para prover campos de visadas mais amplos.

Assim, neste estudo, nós descrevemos as mudanças sazonais na fenologia foliar em um terceiro sítio na Amazônia Central, usando um ano inteiro de imagens diárias registradas a partir de uma câmera RGB acoplada a uma torre a 80 m de altura (aproximadamente 50 m acima do dossel superior). Os resultados permitem abordar as seguintes questões para as áreas de Floresta de Terra Firme na Amazônia Central:

(1) Quais são os padrões sazonais de perda e renovação foliar?

(2) Qual é o tamanho amostral requerido para detectar o padrão sazonal de *flush foliar*?

(3) Mudanças no fotoperíodo direcionam os eventos de *flush foliar*?

(4) Os eventos de abscisão foliar massiva em direção a um estado de deciduosidade são estratégia para a conservação de água?

Para responder à primeira questão, nós aplicamos métodos de análise digital que maximizam a detecção do sinal sazonal de fenologia enquanto minimizam os artefatos relacionados às mudanças na coloração das folhas com a idade, às mudanças na qualidade da iluminação e a possíveis erros do instrumento. Uma análise da sensitividade do tamanho amostral, juntamente com um teste da correlação entre detecções feitas pelos métodos visual e digital, é considerada como uma validação da contagem dos eventos de *flush foliar* feitas visualmente com uma menor amostra de árvores, monitorada por câmeras em torres mais baixas na Amazônia Central. A terceira questão aborda o modelo de fotoperíodo, recentemente proposto por Borchert e colaboradores (2014) para as áreas de Floresta Amazônica na região equatorial. Estes autores predizem que as comunidades arbóreas nesta região são direcionadas a produzir dois episódios de florescimento e *flush foliar* por ano, coincidentes com os dois períodos do ano em que o comprimento do dia aumenta. A quarta questão fornece indicações sobre a sensitividade da floresta ao aumento das secas e ao aumento da evapotranspiração com as mudanças climáticas. A floresta que não sofre forte estresse hídrico sob o clima atual possivelmente será mais resiliente às futuras secas do que uma floresta que já esteja experimentando estresse hídrico sazonal.

OBJETIVOS

Objetivo geral

Caracterizar o comportamento fenológico intra-anual do dossel de uma de Floresta de Terra Firme na Amazônia Central, a partir de uma câmera RGB acoplada em uma torre de observação.

Objetivos específicos

Os objetivos específicos são apresentados a seguir na forma de perguntas:

a) Quais são os padrões sazonais de perda e renovação foliar?

b) Qual é o tamanho amostral requerido para detectar o padrão sazonal de *flush foliar*?

c) Mudanças no fotoperíodo direcionam os eventos de *flush foliar*?

d) Os eventos de abscisão foliar massiva são uma estratégia para a conservação de água?

Capítulo único

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Central Amazon leaf phenology: from individuals to landscape

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ABSTRACT

Understanding how land surface seasonality emerges from individual tree crown phenology is a key challenge of tropical ecology. Here we used a tower-mounted camera to quantify the annual phenology of 267 individual tree crowns in an evergreen Central Amazon forest (59.00ºW, 2.14ºS). We detected rapid large-amplitude positive (leaf flushing) and negative (leaf dropping) changes in crown greenness. Abscission toward a deciduous state occurred in 30% of all crowns, but lasted only briefly (~1 month) before massive leaf flush replenished crown foliage. An additional 52% of crowns flushed new leaves without rapid prior leaf loss. Individual crown abscission and flushing events were distributed across the year, but heavily concentrated in the five driest months, causing a strong emergent dry season “green up”, consistent with patterns seen at larger scales from satellites. Crowns were not synchronized to the twice-annual cycle of equatorial photoperiod.

INTRODUCTION

For a fixed level of incident photosynthetically active radiation, leaf-level assimilation efficiency in the humid tropics increases rapidly after leaf expansion but declines as early as seven months after expansion (Kitajima et al. 1997). Epiphylls may contribute to the loss of efficiency with age. Black fungal hyphae were visible on leaves of an Amazonian canopy tree by two months after expansion (Roberts et al 1998). By one year of age, lichens, bryophytes and other ephiphylls covered 15-18% of leaf area in Panamanian moist forest understory (Coley et al. 1993). Leaf age, more than leaf amount, may be the key driver of seasonal variation in canopy-scale photosynthetic capacity and carbon balance in the Central Amazon (Hutyra et al. 2007; Brando et al. 2010; Restrepo-Coupe et al. 2013). Earth System models generally assume that photosynthetic capacity is constant with leaf age (Weirdt et al. 2012). Incorporating seasonal patterns of changing leaf physiology and canopy level leaf-age structure will improve their performance (Weirdt et al. 2012; Wu et al. 2014).

On Central Amazon upland plateaus near Santarém and near Manaus, leaf abscission measured by litter traps reached a peak in the dry months of August, September and October (Restrepo-Coupe et al. 2013, Sup Fig 4). The few existing field studies also show that new leaf production is more frequent in the dry season when solar irradiance is at its peak (Alencar 1991; Wright & Schaik 1994; Doughty & Goulden 2008; Brando et al. 2010). Phenological sampling methods are not standardized across these studies (Eça-Neves & Morellato 2004) and sample areas were in some cases very small.

More recently, remote sensing studies have examined seasonality of the Enhanced Vegetation Index (EVI) from the MODIS sensor across the entire Amazon forest. Dry season "green-up" was reported by Huete et al. (2006). Higher-than-average dry season EVI values were found in drier years (Saleska et al. 2007), suggesting resilience in the face of drought. Increasing EVI from start to end of the dry season for most of Amazonia (June to October) has, however, been challenged as an artifact caused by the seasonal decrease in sub-pixel shadow fraction, related to sun-sensor geometry (Galvão et al. 2011; Moura et al. 2012, Morton et al. 2014). Cloud contamination during the rainy season and smoke contamination during the dry season can also create seasonal artifacts in EVI (Samanta et al. 2010). After corrections for sun-sensor geometry, no climate variable explained interannual variation of EVI over large areas of intact forest (Brando et al. 2010). This improved EVI was, however, locally correlated with a dry season peak in new leaf flush near Santarém.

Given the continuing debate on the reliability of MODIS EVI for detection of seasonal patterns of Amazon forest greenness, an attractive alternative is to monitor the upper canopy with tower-mounted cameras, or phenocams. These provide very high temporal frequency, useful for controlling lighting artifacts. They address greenness at a scale intermediate between individual organisms and satellite pixels (Richardson et al. 2013).

The study of temperate forest phenology using phenocams is well advanced (Richardson et al. 2007; Richardson et al. 2009; Hufkens et al. 2012; Sonnentag et al. 2012), though still improving (Yang et al. 2014). The landscape-scale annual phenological signal of a tropical evergreen forest is much more subtle than that of a deciduous temperate forest, so that lighting artifacts comprise a larger fraction of detected change. Leaves of different species and of different ages for the same species exhibit different colors in the visible spectrum (Toomey et al. 2010). Leaf age can be confused with leaf amount when using “greenness” indicators derived from RGB cameras, whether applied to an evergreen tropical tree species or to temperate deciduous species during the growing season (Yang et al. 2014).

Phenocam studies in Amazonia have so far been restricted to two tower sites in the Central Amazon. A Tetracam Agricultural Digital Camera (ADC) with three bands similar to Landsat Thematic Mapper bands 2, 3 and 4 (green, red and near infrared, respectively) was maintained for two years at 64m height on a tower near Santarém (2.897°S, 54.952°W). A Stardot Netcam model XL 3MP with three bands in the visible spectrum (RGB) has been maintained since September of 2010 at 54m height on a tower near Manaus (2.609°S, 60.209°W). Both sites are upland primary forest on well drained plateaus with infertile clay-rich soil, within large protected areas. Corroborating earlier field observations, unpublished camera based data from both sites (Marostica 2011, Tavares 2013, Nelson et al. 2014, Wu et al. 2014) describe a concentration of both leaf flush and pre-flush leaf abscission in the drier months. Fewer than one hundred canopies were monitored at each of these sites, and generalizations cannot yet be made based on just two sites. More phenocam sites are required. Until adequate sample size has been determined, these should preferably use high towers that provide large image footprints.

To this end, we describe the seasonal changes in leaf phenology at a third Central Amazon site, using a full year of daily images from an RGB camera mounted ~50 m above the upper canopy. The results allow us to address the following questions for equatorial upland Amazon rainforest:

(1) What are the seasonal patterns of leaf drop and leaf flush?
(2) What sample size is required to detect the seasonal pattern of leaf flush?
(3) Does photoperiod cue leaf flush?
(4) Is massive leaf abscission toward a deciduous state a water-conservation strategy?

To answer our first question we develop and apply digital methods that maximize detection of changes in leaf amount while minimizing artifacts related to leaf color change with age, seasonal variation in light quality and instrument errors. Our sample size sensitivity analysis, together with a test of the correlation between visual and digital detections, is intended as a validation of leaf flush counts made visually with smaller samples of trees monitored with cameras on shorter towers in the Central Amazon. Our third question addresses the photoperiod model of Borchert et al. (2014) for near-equatorial Amazon forest. They predict that tree communities are cued to produce two episodes of flush and of flowering per year, coincident with the two times per year that day length increases. Our fourth question provides insight into the sensitivity of Central Amazon forests to increased drought and/or increased evapotranspiration with climate change. A forest that does not suffer strong seasonal water stress under present climate will be more resilient to future drought than a forest that is already experiencing seasonal water stress.

MATERIAL AND METHODS

Study area and camera details

We studied the upper canopy of an upland forest on a well-drained clay-soil plateau 150 km northeast of Manaus, Brazil at the Amazon Tall Tower site (59.00ºW and 2.14ºS). About 600 trees and more than 140 trees species occur per hectare (Andreae et al. 2015). The most abundant genera are in the families Sapotaceae, Lecythidaceae, Burseraceae, Lauraceae and Chrysobalanaceae.

We mounted a Stardot Netcam model XL 3MP (2048 x 1536 pixels) 81 m above the ground and ~50 m above the forest canopy. The camera was controlled by a microcomputer model Fit-PC2i with heat-resistant solid-state drive. All components were installed inside weather- and insect-resistant boxes with thermal shielding and passive ventilation. The camera box was fitted with a new acrylic window and cleaned every four months. The camera view was west (270º), always monitoring the same crowns and excluding the sky (Fig. 1a). A 96^{o} wide-angle lens and variable distances to trees caused scale to vary, so that two crowns of the same size can have very different areas in the image. Automatic exposure was turned on and automatic color balance turned off. The camera and the computer automatically rebooted and reestablished communication and control settings after power losses.

Greenness, leaf amount and abrupt phenological change

Greenness as used here is the Green Chromatic Coordinate of a pixel, or GC (Woebbecke et al. 1995, Richardson et al. 2007), defined as the fractional contribution of the green channel's digital brightness value to the summed brightness values of all three RGB channels. While the GC of pixels in a leafless crown is lower than the GC of a fully leafy crown, "greenness" as measured by GC is not a perfect metric of leaf amount, because GC also changes with leaf color. Recently flushed, fully expanded leaves have high GC values. As a leaf or a cohort of leaves matures, this peak is followed by a gradual drop in GC. In crowns of the temperate broadleaf species *Quercus alba*, Yang et al. (2014) found a gradual decrease of 0.05 GC units (from 0.45 to 0.40) during the summer growing period in New England, between 09 June and 28 August. At the individual leaf scale and over approximately the same period, GC derived from convolved laboratory spectra of fresh *Q. alba* leaves also decreased by 0.05. This agreement between crown level and leaf level change in GC as leaves aged during the growing season indicates that substantial decrease in crown level GC can be caused by pre-autumn change in leaf color alone, with no change in leaf amount. This "greendown" during the summer growing season is associated with darkening of leaves and of tree crowns. Laboratory spectra of *Q. alba* leaves collected from mid-June to mid-August showed that this darkening was caused almost entirely by a drop in green reflectance of the leaf, with little change in blue or red reflectance.

Changing leaf color with age therefore prevents reliable measurement of seasonal change in landscape scale leaf amount using GC alone, whether during the growing season of a temperature broadleaf forest (Yang et al. 2014) or year-round in an evergreen tropical forest. However, a large and abrupt decrease in GC within a *single crown* can be safely attributed to rapid leaf loss toward a deciduous or semi-deciduous crown state. Similarly, a large abrupt increase in the GC of a single crown can only indicate rapid production of a new light-green leaf cohort in that crown. One can reliably measure these two leaf phenology events in the GC timeline of individual crowns in a tropical forest. Seasonal patterns over the larger forest area can then be inferred from monthly counts of crowns showing these two types of change.

Removal of lighting and sensor artifacts

We minimized artifacts related to changing color balance of incident light, changes in shadow area and position, forward-scattered versus back-scattered illumination, diverging channel responses with different exposure speeds, sensor drift and changes of scale within the image. We did this by maintaining the sun behind the camera, by using only photos from a two-hour window (1030-1230h local), by accepting only images under overcast sky (to minimize differences in crown shadow position or size), by radiometric intercalibration of all images and by giving equal weight to each tree crown. We selected one image per day that met our criteria. In the dry season, images with densely overcast sky are not available every day and direct light leaks through the thinner clouds. This causes some variation in the incident light color balance that has a seasonal bias. Densely overcast sky in the rainy season causes longer shutter speeds and a consequent bias toward the blue channel, lowering the GC. These two image-wide seasonal biases were removed by radiometric intercalibration of all selected images against a single standard image that was obtained under an overcast sky. Intercalibration was by matching of the mean and the variance of each channel of each daily image to the corresponding channel of the reference image (Leonardi et al. 2003). For this intercalibration we selected a region of interest that excluded large tree crowns close to the camera, because phenological changes in any one of these crowns would bias the correction (Fig. 1a). Images were also geometrically adjusted so that each crown's position is stable in the daily time series.

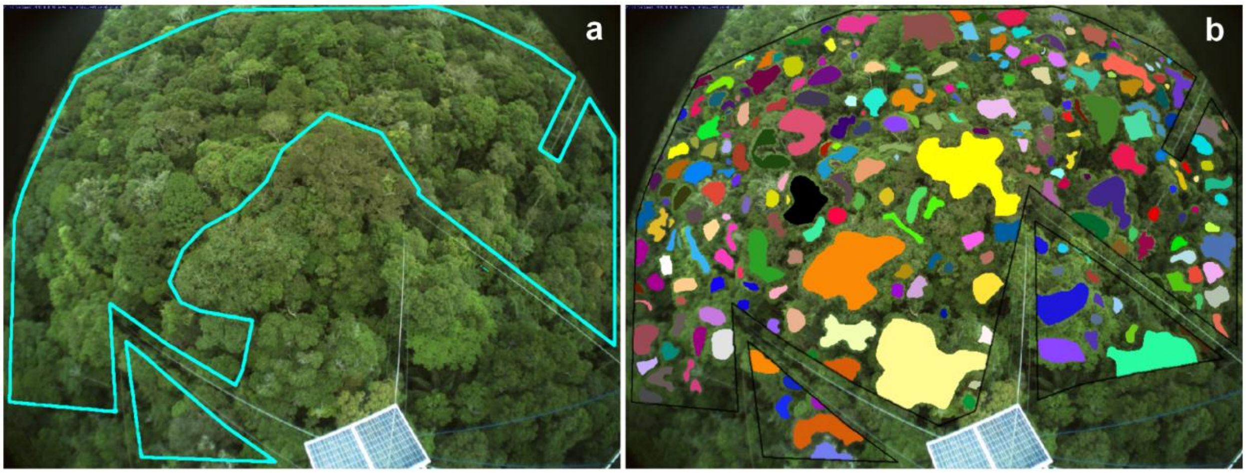

Figure 1. Regions of interest used in digital analysis. The image area covers approximately four hectares. Radiometric intercalibration to a single reference date used the large forest area outlined in (a); corrected daily values of Chromatic Green Coordinate were then obtained for each of 267 individual crowns shown in (b).

Pre-calibration landscape-scale seasonal change in GC is of very low amplitude (Figure 2a). This may be partly a consequence of seasonal change in incident color balance and in detector response at lower light levels described above, so was removed by the radiometric intercalibration (Figure 2b). But this also removed any true seasonal change in average greenness across the larger forest canopy area. For this reason, and because GC changes gradually with leaf age even when leaf amount is constant (Yang et al. 2014), we do not attempt to quantify changes in leaf amount within the landscape-scale region of interest, using the Chromatic Green Coordinate. We instead make a monthly census of the number of trees experiencing abrupt increase in greenness (leaf flush) or abrupt decrease (leaf abscission). Abrupt events were detected separately for each crown (Fig 1b). For each crown we prepared an X-Y plot of daily GC values, where Y = Chromatic Green Coordinate, X = months, and defined these two events as:

"Abrupt abscission = TRUE", if "[slope <-0.01, sustained for at least 0.5 mo] AND [endpoint of negative slope < percentile 0.25 of all daily observations over one year]"

"Abrupt leaf flush = TRUE", if "[slope >0.01, sustained for at least 0.5 mo] AND [endpoint of positive slope > percentile 0.75 of all daily observations over one year]"

These thresholds never occurred in the larger forest landscape, in either pre- or post-radiometric correction images (Fig. 2a, 2b).

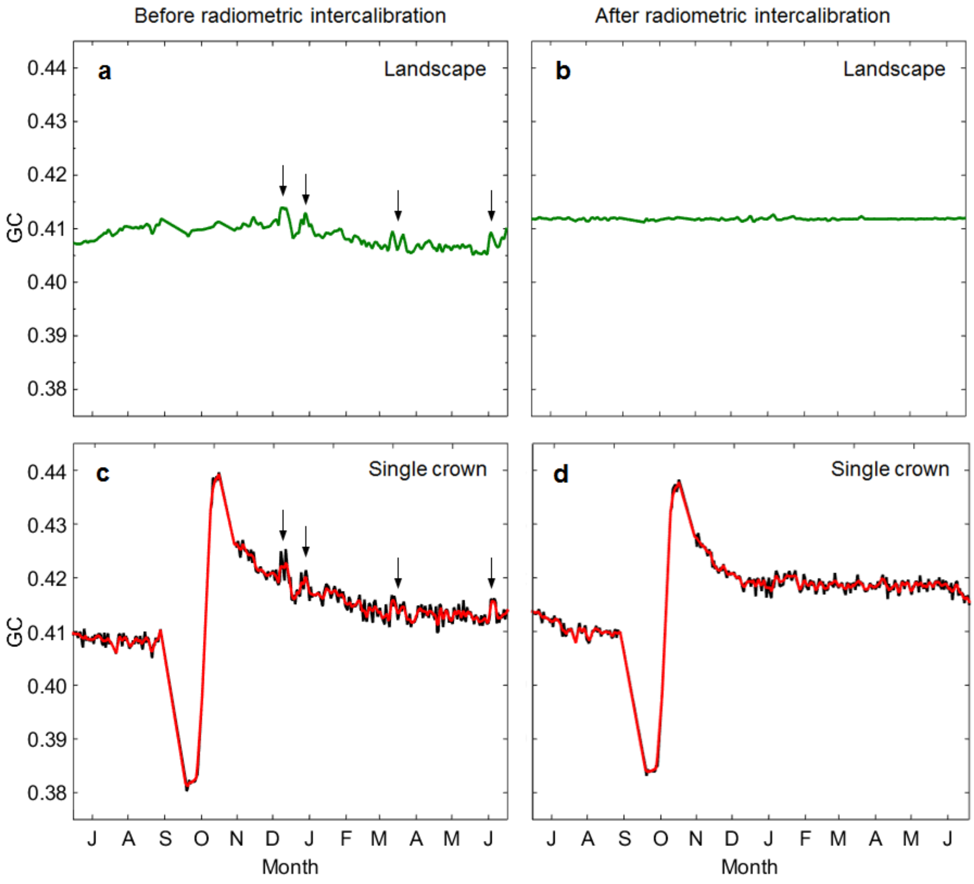

Figure 2. Daily values of Chromatic Green Coordinate before (left) and after (right) radiometric intercalibration. Small gradual change in greenness of the overall forest landscape is evident in (a), but this includes any seasonal trend in incident color balance and leaf color change with age, so was removed by radiometric intercalibration (b). Arrows in a and b point to the same brief artifacts caused by differences in illumination; these and the long-term gradual change of greenness in (a) are smaller than the signals of rapid leaf loss and rapid leaf flush seen in the timeline of a single tree crown (large dip and large peak in c & d).

Data analysis

We monitored the Chromatic Green Coordinate (GC) of 267 upper canopy tree crowns spread across four hectares of forest (Figure 1b). (Our time series of daily photos had three gaps that exceeded three days in length: 13 September to 02 October, 18-22 October and 1-11 November.) Abrupt leaf flush and leaf drop events of each crown were identified by the slope and percentile criteria, then pegged to the date when GC of that crown reached its peak or its minimum, respectively. The number of trees at their maximum GC (leaf flush) and the number at their minimum GC (maximum deciduousness) were aggregated by month. If photoperiod controls leaf phenology at the community level (Borchert et al. 2014) the aggregated flushing curve should have two peaks per year. If flushing is cued by photoperiod within each individual, many crowns will show two flushing events per year in their greenness timelines.

Though we examine phenology on a crown by crown basis to understand the overall tree community, we do not examine phenology on a species by species basis. In a forest of such high diversity, only a very few species – and therefore only a few individuals, representing a very small portion of the tree community – would have sufficient replicates for meaningful interpretation.

To determine the minimum sample size required to detect seasonal flush patterns in the Central Amazon, we correlated the 12 monthly flush counts obtained with a smaller random sample and the 12 monthly counts observed in the full set of all flushing trees. We repeated this with increasing sample sizes until reaching the size that passed a threshold of strong correlation with the full set ($R > 0.9$). As a check on our digital detection of flush events we visually counted the number of flushing crowns per month using a time series of images in six day intervals and the same set of 267 crowns. We report the correlation between the monthly counts of flushing events obtained by the two methods.

We compared the fraction of all trees abscising in the five driest and the five wettest months of the year and did the same for flushing trees. We used chi-square to determine if these two events were significantly seasonal. The total fraction of all 267 trees that exhibited abrupt flushing was also obtained to see if this behavior was present in the majority of upper canopy crowns. We also compared monthly flush and abscission counts to monthly precipitation, photosynthetically active radiation (PAR) and soil humidity.

To determine if massive leaf abscission toward a deciduous state is a strategy related to strong water stress, we first identified the day of lowest soil water content during the year of monitoring (October 30, 2013). We then identified all trees that abscised their leaves and reached their minimum greenness 30-90 days prior to this driest soil day. If these trees became deciduous or semi-deciduous to conserve water, they would wait to flush out new leaves until after October 30, when soil water increased. If, on the other hand, they are not experiencing strong water stress, staying leafless for 30-90 days would be dis-advantageous and they would flush out new leaves even as soil humidity continued to drop toward its annual minimum.

Soil water was measured at five depths between 10 and 60 cm at ten minute increments, using time-domain reflectometers (CS 615 Volumetric Water Content TDR, Campbell Scientific). We used the data from 60 cm, but all other depths showed the same seasonal pattern. Monthly precipitation was from the TRMM satellite and was averaged over the years 2001-2013. PAR was recorded by a quantum sensor (PAR LITE, Kipp & Zonen) mounted at 75m height.

RESULTS

The full annual amplitude of the Chromatic Green Coordinate for the forest landscape as a whole was only 0.008 units (Figure 1a). At the individual crown scale and after radiometric intercalibration, the average GC amplitude was about four times larger, 0.030 +/- 0.012. Given this higher signal to noise ratio (or signal to seasonal illumination bias), patterns of leaf phenology of the evergreen tropical forest canopy should be based on counts of events detected in individual crowns.

Eighty-two percent of the 267 upper canopy crowns experienced abrupt leaf flush. As conservatively defined here, massive rapid leaf drop was seen in 30% of crowns. Flush timing – the date of Green Coordinate maximum for flushing trees – was concentrated in the five driest months (50% of all crowns) compared to the five wettest months (10% of all crowns) a highly significant difference ($\text{Chi-square}_{df1} = 64.3$, $p<0.001$). Leaf abscission was also concentrated more in the five driest months (17% of all crowns) versus the five wettest months (4%) ($\text{Chi-square}_{df1} = 30.2$, $p<0.001$) (Figure 3).

When peak flush dates were aggregated by month, there was only one annual peak at the community level. This is inconsistent with the bimodal prediction of the photoperiod control model (Borchert et al. 2014). Multiple flushes over the year did occur within the same crown but were uncommon (4.5% of all crowns) and may be the result of lianas flushing new leaves at a time different from their host tree.

A sample size of just 50 trees would be sufficient to detect the strong monthly pattern in flushing seen in the full set of 267 trees (Figure 4). Monthly aggregated flushes using digital criteria were corroborated by monthly flush counts from visual analysis (R = 0.95). Therefore visual counting of monthly flushes using much smaller samples will provide data of similar quality. This can be accomplished with smaller image footprints from shorter towers.

Massive leaf abscission toward a deciduous state was not a strategy to conserve water. Of the 27 trees that reached their maximum leaf abscission in the 30-90 days prior to the driest soil day of the year, only one tree waited for the rains to begin before flushing out new leaves (Figure 5).

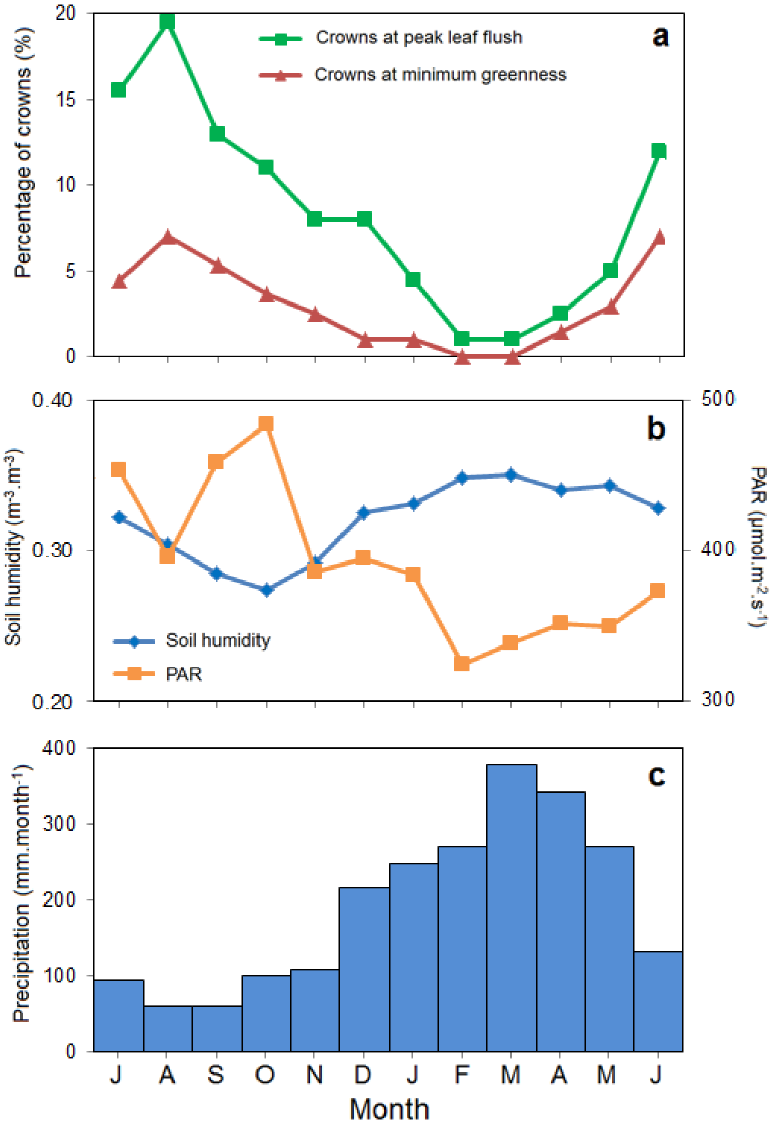

Figure 3. Percent of all 267 crowns with abrupt leaf flush or abrupt leaf loss, reaching their peak or their minimum greenness, by month, from July 2013 to June 2014 at the Amazon Tall Tower (a); soil humidity and daytime PAR by month (b); mean monthly precipitation from 12 years of TRMM data (c).

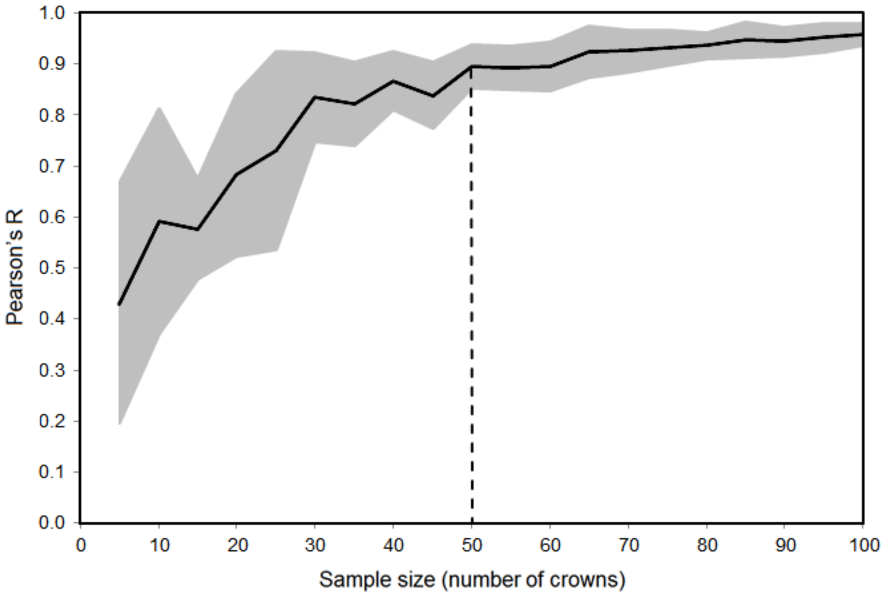

Figure 4. Correlation between the 12 monthly flush counts obtained with a smaller random sample and the 12 monthly flush counts observed in the full set of all flushing trees. Shaded area is one standard deviation. A sample size of 50 trees is sufficient to accurately measure the observed flush seasonality.

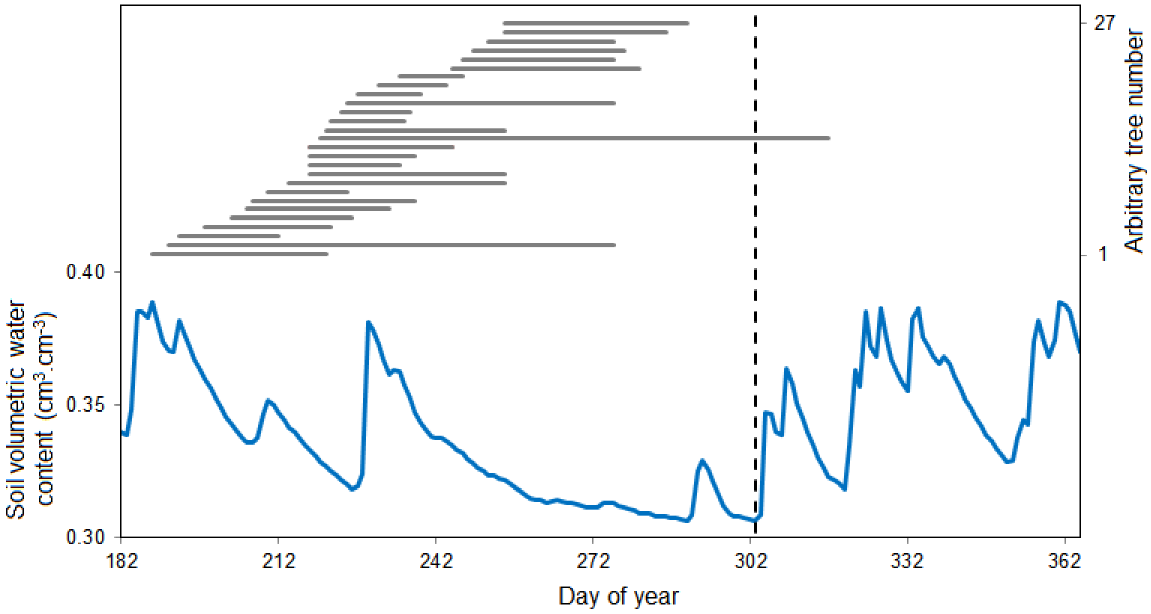

Figure 5. Deciduous trees flushed new leaves prior to driest soil day of the year (dashed vertical line). Each grey line is a single tree that reached its most-deciduous state 30-90 days prior to the driest soil day of the year. Each grey line starts at a tree's most-deciduous date and ends at its peak flush date.

DISCUSSION

Central Amazon leaf phenology

Though only covering one year, ours is the second largest sample of trees among published Amazon forest leaf phenology studies. Similar results were found by four other published and unpublished studies at three different Central Amazon sites having upland forest on clay soil (Alencar 1991; Brando et al. 2010; Nelson et al. 2014; Wu et al. 2014). All studies were located 2^{o}-3^{o}S with dry months (monthly evapotranspiration > monthly rainfall) lasting 2-5 months. Consistently across these sites, leaf flushing occurred as a single annual peak during the dry season. Alencar et al. (1979) and Alencar (1991) describe leaf phenology patterns for 27 species (81 trees) monitored from the ground every month for 12 years in the upland forest of the Ducke Forest Reserve (2.98°S, 59.96°W). They found that 70% (19 of 27 species) had their highest production of new leaves in the dry months, 30% (8 of 27 species) were semi-deciduous and 10% (3 of 27) were fully deciduous. Leaf drop was greatest in the dry season. On a plateau at the Tapajós National Forest (2.897°S, 54.952°W), Brando et al. (2010) monitored from the ground two crown categories – having or not having new leaves – for 480 trees (> 10 cm diameter at breast height) at 15 day intervals during five years. They found that ~60% of all trees had new leaves at any one time during an annual flush peak in the dry season. The precise timing of the tree community flushing peak varied, but always occurred within the six driest months of July to December. In the wet season the percent of trees with new leaves consistently dropped to ~20%. The peak and the dip were both monomodal per year.

The other two studies used tower-mounted cameras. For 65 crowns monitored from a tower near Manaus during 24 months, using the same camera model of our study, Nelson et al. (2014), expanding on work by Tavares (2013), report that 60% of trees flushed each year, with a 4:1 ratio for flushing in the driest:wettest periods of five months. Nelson et al. (2014) and Tavares (2013) found about 25% of all upper canopy crowns become fully deciduous, mainly in the five driest months. As at our site, they found that massive leaf drop was a preamble to leaf flush. The leafless stage was brief, lasting 36 +/- 25 days. Their analyses were based on visual detection of flushing events, of leaf drop events and duration of the leafless stage, using images obtained under overcast sky at six day intervals. Nelson et al. (2014) also estimated the monthly age mix of canopy leaves, considering only those leaves that appear as a new cohort when a crown flushes. Though trees flushed in the dry season, this causes the leaf age class with highest photosynthetic efficiency to be most abundant in the early wet season (Figure S6).

The other camera-based study (Wu et al. 2014) used a Tetracam ADC on a tower very near to the ground-based study of Brando et al. (2010). They found a similar pattern of dry season leaf flush, preceded by a brief preparatory leaf-drop in a subset of these flushing trees. They also used 24 monthly values of Leaf Area Index (LAI), and canopy scale Light Use Efficiency from a flux tower to model leaf abundance by age class. They found that leaf age, not LAI, explained most of the seasonal change in canopy level Gross Ecosystem Productivity.

Tower mounted cameras see only the upper canopy. The high percentage of flushing trees reported here may not be representative of mid-canopy and lower canopy leaves. Turning over leaves every dry season would have a high cost in these low light environments, so one would expect longer-lived leaves and therefore less seasonal variation of the community-wide leaf age in the understory.

Drivers of Central Amazon leaf phenology patterns – new directions of study

What drives seasonal leaf phenology in the central Amazon? Four hypotheses are considered below. The first is rejected by our study. The others point to new directions of research.

1. Photoperiod. The monomodal leaf flush reported here and by others (Alencar et al. 1991, Brando et al. 2010, Tavares 2013, Nelson et al. 2014, Wu et al. 2014) does not support the idea of leaf flush driven by two periods per year of increasing day length near the equator, as recently proposed by Borchert et al. (2014). Furthermore, for upland forest on well-drained clay soil near Manaus, their own data shows nine species flushing in the dry season versus only two in the wet season.

2. Water stress. Based on flux tower data, Restrepo-Coupe et al. (2013) found that strong dry season water stress drives seasonality of photosynthesis south of 10^{o}S, but at Central Amazon sites, with their more moderate dry seasons, photosynthesis and photosynthetic capacity both increase during the dry months. They attributed this to dry season leaf flush. Dry season leaf phenology at the ATTO site was consistent with their Central Amazon pattern. Trees with both abrupt leaf drop and abrupt leaf flush did not delay flushing until the end of the dry season (Fig. 5). Moderate water stress cannot be precluded, however, because exchanging old leaves for new ones during the dry season may lead to improved stomatal control of water loss (Reich & Borchert 1988). Indeed, the presence of annual rings in all upland forest trees examined (Fichtler et al. 2003) indicates a season less favorable for wood growth, consistent with moderate water stress. Restrepo-Coupe et al. (2013), however, pointed out that wood growth remains low during the entire dry season in the Central Amazon despite photosynthesis increasing in the mid to late dry season. Slower dry season wood growth even as photosynthesis increases suggests that leaf phenology, and not water stress, drives seasonality of wood increment. Massive flush of young leaves diverts energy from wood tissue to leaf tissue formation (Restrepo-Coupe et al. 2013).

3. Diffuse x direct incident PAR. Because cloud cover is lower in the dry season, leaf flush is positively correlated with total irradiance (Figure 3). At first glance, this suggests that new leaf production in the dry season is taking advantage of higher total PAR as inferred by Wright & Schaik (1994; see also Huete et al. 2006). At the community level, however, monthly changes in leaf age structure maximize photosynthetic capacity in the early wet season, when total incident PAR is low (Figure S6; also see Restrepo-Coupe et al. 2013; Wu et al. 2014; Albert et al. 2014). Positive correlation between GEP and cloudiness at two eddy flux towers in the Amazon has been interpreted as showing that diffuse PAR is used more efficiently than direct PAR by the forest canopy as a whole (Oliveira et al. 2007; Cirino et al. 2014). Leaf age structure at the community level therefore appears to be calibrated to maximize photosynthetic efficiency when light quality is at its best. However, many trees flush in the early months of the dry season. Their leaf cohorts attain maximum photosynthetic efficiency (Albert et al. 2014) when direct light fraction of PAR is still high. They remain in this physiologically efficient age bracket when the diffuse fraction of PAR is high in the early rainy season. These trees therefore appear to be indifferent to light quality.

4. Escape from herbivores and pathogens. Young unexpanded leaves are more palatable to herbivores, which are more abundant in the rainy season (Wright & Schaik 1994; Coley & Barrone 1996; Murali & Sukumar 1993). Trees which self-prune old infected leaves prior to flushing new leaves (30% of trees in our study) reduce nearby sources of inoculation by microbial pathogens. Disease control by pruning of infected tissues is common in tropical and temperate orchards (Marini & Burden 1987; Azevedo et al. 2013). Similarly, leaf flush concentrated in the dry season may be a consequence of avoiding the production of new leaves in the wet season. Young unhardened leaves are more vulnerable to fungal pathogens which are in turn favored by stable high humidity under cloudy sky and frequent rain. Two commercially important native Amazon tree species and the pathogenic microorganisms with which they have evolved provide an apt illustration. Only young unexpanded leaves of the rubber tree *Hevea brasiliensis* are susceptible to infection by the South American leaf blight fungus *Microcyclus ulei*. Infection is strongly impeded under drier climate at the southern fringe of Amazonia (Lieberei 2007). Basidiospores of witches' broom (*Moniliophthora perniciosa*) only germinate on wet surfaces of the cocoa plant, *Theobroma cacao.* Though mature leaves can be infected, directional hyphal growth towards stomata is seen only on unhardened leaf flushes (Frias et al. 1991).

Detecting these evolutionary pressures in native Amazon forest may be difficult. For the two commercial species described above, natural pathogen pressures are more easily seen when amplified by the high host densities of plantations. Seasonality of insect herbivores has not been studied in the Central Amazon but they are more abundant in the rainy season of drier tropical forests (Coley & Barrone 1996; Murali & Sukumar 1993). Litter traps in the Central Amazon collect many aborted unexpanded young leaves during the flushing season (Giordane Martins *pers. com.*). Expressed as a percent of new bud breaks, this is a net-effect metric of whatever agents damage young leaves. It would be difficult, however, to devise an experiment in native forest to compare abortion rates of new leaves in wet versus dry seasons. The tree species most sensitive to wet-season damage to their new leaves are presumably those that produce new leaves exclusively in the dry season.

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SUPPORTING INFORMATION

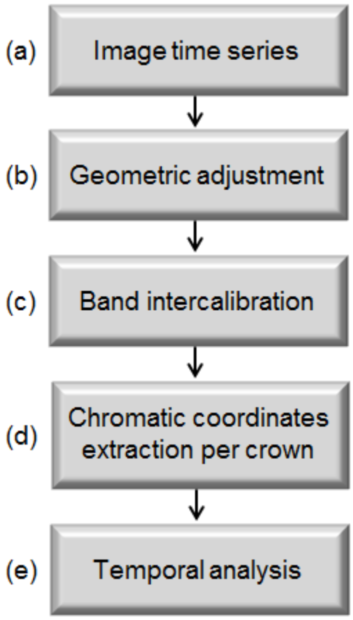


Figure S1. Workflow: select a daily time series of images with stable crowns (no wind) under overcast sky (a); spatially match all images to a single reference image using control points (b); radiometric calibration to this same reference produces a fixed average and fixed variance for each band over the year, for the overall forest area, excluding all large crowns in foreground of image (c); for the pixels within each crown, for each day of the year query the mean brightness of each of the three bands to calculate the daily Green Chromatic Coordinate (GC) of the crown (d); the GC timeline of each crown is plotted, allowing detection of abrupt leaf flush, abrupt leaf abscission, maximum GC at peak flush and minimum GC value at the "most deciduous" stage (e).

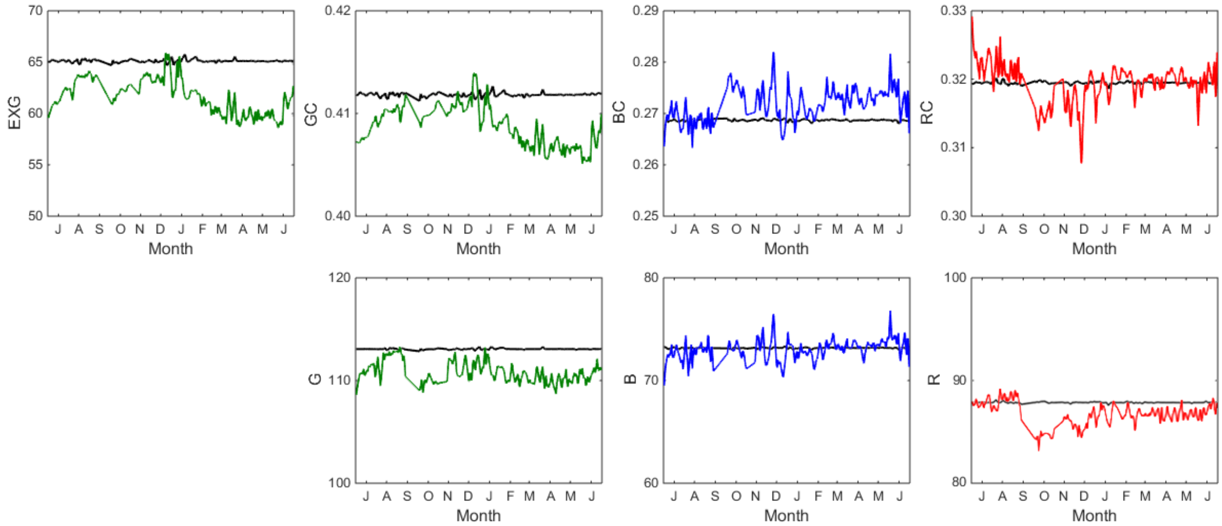


Figure S2. Grey lines are post-radiometric correction, colored lines pre-correction for annual timeline of the overall forest area, which excludes large crowns in foreground. Bottom row shows red, green and blue image bands. Top row shows the Excess Green Coordinate (EXG), the Green Chromatic Coordinate (GC), the Blue Chromatic Coordinate (BC) and the Red Chromatic Coordinate (RC). See Sonnentag (2012) for formulas.

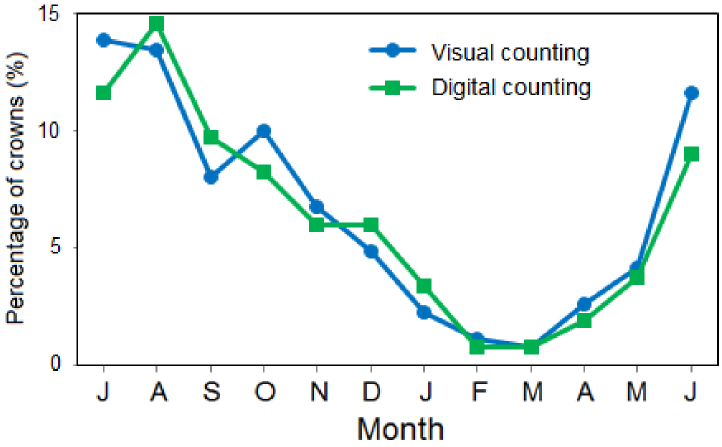
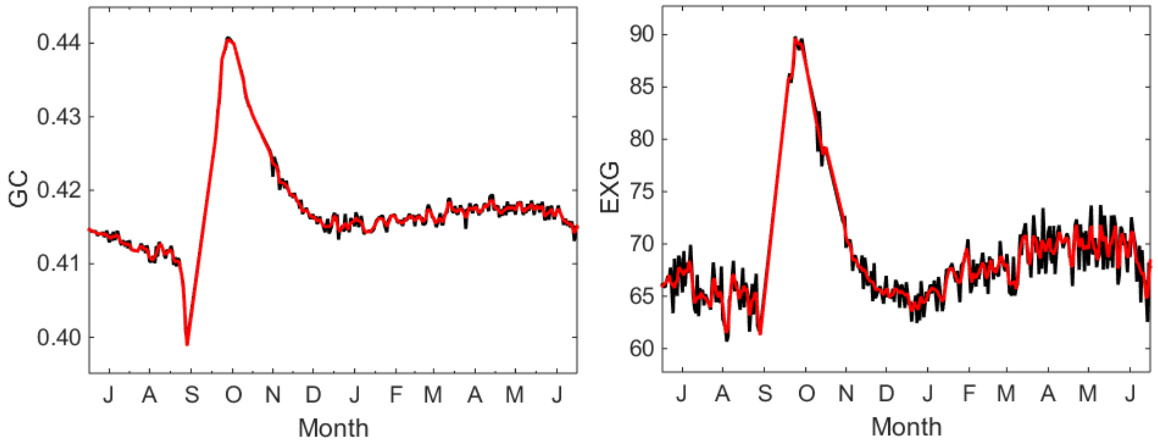


Figure S3. Comparison of visual and digital detections of abrupt leaf flush events by month (Pearson’s R = 0.95).



Appendix S4. One year timeline for the same crown using the Green Coordinate (GC) and the Excess Green coordinate (EXG) With EXG, abscission is not detected and data is noisy. Red lines are smoothed data.

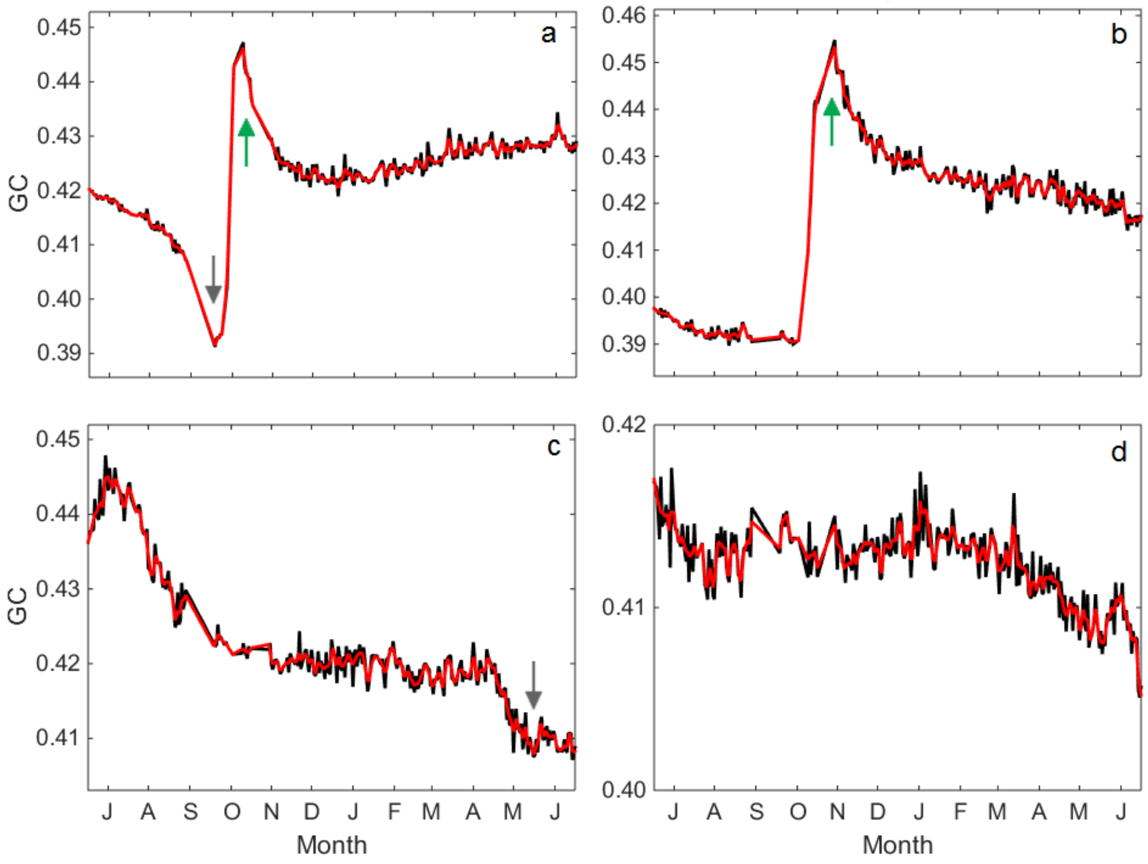


Figure S5. Green Chromatic Coordinate timelines of four crowns selected to show detection of both abscission and flush (a), flush only (b), abscission only (c) and no abrupt change in leaf phenology. Types a + b comprise 82% of all 267 monitored tree crowns. Y axes have different scales. Red lines are smoothed data.

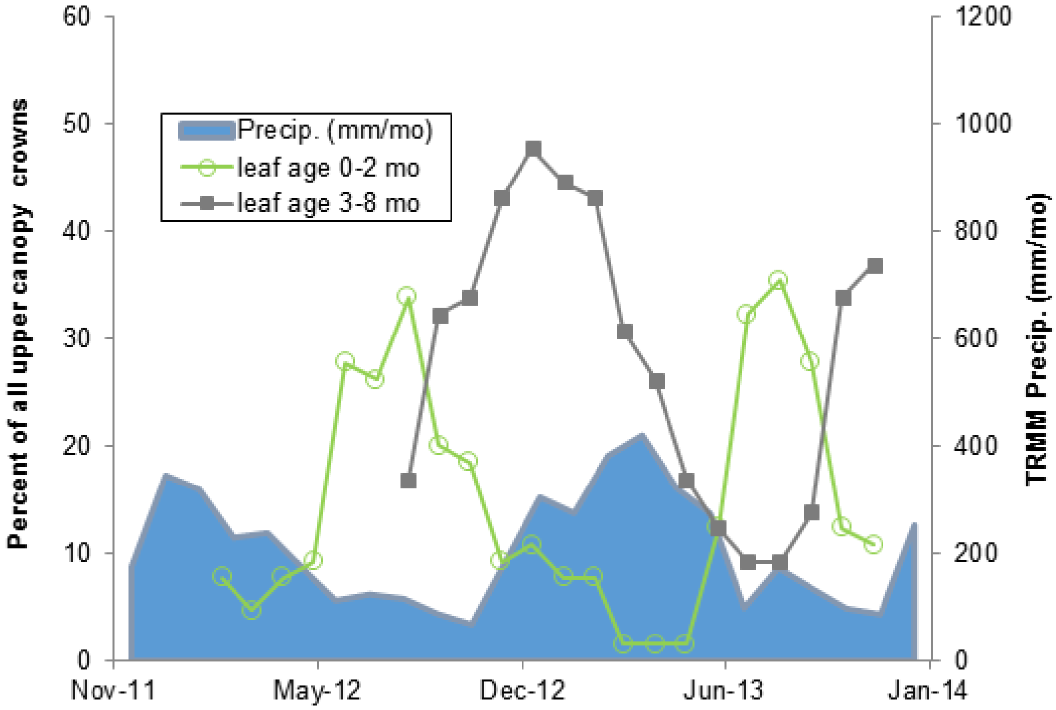


Figure S6. Canopy-level fraction of photosynthetically efficient leaves (3-8 mo old) peaks in the early wet season in the Central Amazon at the 54m tall LBA tower. Leaf age based on time since flushing of each new leaf cohort, observing 65 crowns over 24 months with images selected at six-day intervals under overcast sky (from Nelson et al. 2014).

CONCLUSÕES

As câmeras de monitoramento com bandas RGB podem ser podem ser usadas para estudar a fenologia foliar do dossel em florestas de terra firme na Amazônia Central. Para isto, é necessário: 1) o ajuste geométrico da série temporal, 2) a intercalibração de bandas e 3) a extração das métricas do verdor (*greenness*) por ROIs de copas individuais, nesta ordem.

Existe uma grande concentração do *flush foliar* no dossel superior na época seca, corroborando com os estudos anteriores, com os estudos de observação direta em campo e com os estudos de sensoriamento remoto que utilizam o EVI. O *flush foliar* tipicamente monomodal, concentrado nos meses mais secos, contradiz a hipótese de controle pelo aumento do fotoperíodo. A queda de folhas pode ser entendida como um preâmbulo para um *flush foliar* massivo na época seca, não determinado por forte estresse hídrico.

Trabalhos futuros devem englobar o estudo de longas séries temporais, para captar todo o ciclo fenológico das árvores, sobretudo, das que renovam sua cobertura foliar não anualmente, e o acompanhamento em campo em nível de copas individuais para melhor entender o real significado das mudanças na linha temporal do verdor de cada copa.

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Principais recomendações feitas pelos revisores

Recomendações	Recomendação acatada?	Ação tomada / Justificativa
Apresentar informações sobre a composição florística da área de estudo	Sim	Dados sobre a composição florística da área foram gentilmente cedidos pelo Dr. Florian Wittman e pelo Dr. Jochen Schongart. Tais informações foram adicionadas na página 12.
Reformatar as hipóteses	Sim	As hipóteses foram reformatadas na forma de perguntas, conforme disposto nas páginas 6 e 12.
Rever a interpretação dos dados Foi recomendado considerar também a formação sazonal de anéis de crescimento, a teoria da conservação de nicho e informações sobre a fenologia foliar de outras fisionomias florestais da Amazônia, como áreas alagáveis e campinas.	Sim	Buscamos atender a esta recomendação nas páginas 22 e 23, trecho do texto no qual discutimos a hipótese do estresse hídrico.