Patterns of Plant Phenology in Amazonian Seasonally Flooded and Unflooded Forests

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Abstract

Few studies have successfully monitored community-wide phenological patterns in seasonally flooded Amazonian várzea forests, where a prolonged annual flood pulse arguably generates the greatest degree of seasonality of any low-latitude ecosystem on Earth. We monitored the vegetative and reproductive plant phenology of várzea (VZ) floodplain and adjacent terra firme (TF) forests within two contiguous protected areas in western Brazilian Amazonia, using three complementary methods: monthly canopy observations of 1,056 individuals (TF: 556, VZ: 500), twice monthly collections from 0.5-m² litterfall traps within two 100-ha plots (1 TF, 1 VZ; 96 traps per plot), and monthly ground surveys of residual fruit-fall along transect-grids within each 100-ha plot (12 km per plot). Surveys encompassed the entire annual flood cycle, and employed a floating trap design to cope with fluctuating water-levels. Phenology patterns were generally similar in both forest types. Leaf fall peaked during the aquatic phase in várzea forest, and the dry-season in terra firme. Flowering typically followed leaf fall and leaf flush, extending into the onset of the terrestrial phase and rainy season in várzea and terra firme, respectively. Abiotic seed dispersal modes were relatively more prevalent in várzea than terra firme; the main contrast in fruiting seasonality was more likely a result of differences in community composition and relative abundance of seed dispersal modes than differences within individual genera. We emphasize the difficulty in distinguishing the role of the flood pulse from other seasonal environmental variables without multi-annual data or spatially replicated studies across the spectrum of Amazonian forest types.

Key words: Dispersal modes; Floodplain forest; Fruit traps; Litterfall; Phenophase; Seasonality; Terra firme; Várzea.
Resumo

Poucos estudos monitoraram com sucesso a fenologia de toda a comunidade de plantas em florestas de várzea na Amazônia, onde um pulso anual de inundação bastante prolongado gera um dos padrões de sazonalidade mais intensos em quaisquer ecossistemas terrestres de baixa latitude. Nós monitoramos a fenologia vegetativa e reprodutiva de plantas lenhosas em florestas de várzea (VZ) e terra firme (TF) em duas áreas protegidas contíguas na Amazônia brasileira ocidental, através de três métodos complementares: observações mensais das copas de 1,056 árvores e cipós lenhosos (TF: 556, VZ: 500), coletas quinzenais através de armadilhas de serapilheira (0,5 m²) inseridas em duas parcelas de 100-ha (1 TF, 1 VZ, 96 armadilhas por parcela), e levantamentos mensais da queda residual de frutos no solo ao longo de uma grade de transectos dentro de cada parcela de 100-ha (12 km por parcela). Estas abordagens abrangeram todo o ciclo anual de inundação, empregando um desenho inovador de armadilhas flutuantes para lidar com as flutuações no nível da água. Os padrões fenológicos destes tipos de florestas geralmente se semelham. A queda de folhas atingiu um pico durante a fase aquática na floresta de várzea, enquanto que na terra firme isto ocorreu na época seca. As florações tipicamente seguiram a queda de folhas maduras e o rebrotamento de folhas novas, estendendo-se até o início da fase terrestre e a estação chuvosa na várzea e terra firme, respectivamente. Modos abióticos de dispersão de sementes foram mais predominantes na várzea do que na terra firme; o principal contraste na sazonalidade de frutos entre os dois tipos florestais provavelmente resulta de diferenças na composição florística do que diferenças entre populações no mesmo gênero. Destacamos a dificuldade em distinguir o papel do pulso anual de inundação de outras variáveis ambientais sazonais na ausência de dados supra-anuais ou estudos replicados espacialmente em todo o espectro de tipos de floresta na Amazônia.
PLANT PHENOLOGY, THE TIMING OF PLANT VEGETATIVE AND REPRODUCTIVE CYCLES, TYPICALLY DISPLAYS STRONG PERIODICITY IN BOTH TROPICAL AND TEMPERATE ZONES (van Schaik et al. 1993, Newstrom et al. 1994, Ting et al. 2008), and is increasingly relevant to a wide range of applied issues (Morisette et al. 2009). However, we still lack information on local variation within tropical forest macromosaics consisting of different forest types. A case in point is the variation between flooded and unflooded forests across lowland Amazonia, which are subjected to strikingly distinct environmental gradients despite often occurring side-by-side and experiencing similar climatic conditions.

Phenological patterns in unflooded *terra firme* forests, where dry-season water stress is more demarcated, are primarily understood to be driven by radiation, photoperiod and precipitation (Borchert et al. 2005, Zimmerman et al. 2007, Bradley et al. 2011). Extensive lowland floodplain forests (e.g. in the Amazon, Congo, and Mekong river basins), however, are subjected to an additional annual force, in the form of a predictable ‘flood pulse’ (Junk et al. 1989). For example, white-water Amazonian floodplain forests, known as *várzea* forests (Prance 1979), are typically inundated to a depth of up to 7.5 m for up to 230 days per year (Junk et al. 2011). This extended period of submersion and waterlogging has severe consequences for plant physiology, notably oxygen deficiency (Parolin 2009), reduced photosynthesis due to low light penetration through water and silt deposition on leaves, and low water conductance which paradoxically results in water deficits in the tree crown (Parolin et al. 2004a).

The regularity of this powerful flood pulse is expected to influence many ecological processes within *várzea* forests, including phenological strategies (Schöngart et al. 2002, Parolin et al. 2004b, Ferreira et al. 2010). In addition to the timing of fruiting, further adaptations to seasonal inundation are expected to include other plant life-history traits (Parolin et al. 2004b), including seed dispersal modes that take advantage of the prolonged
flood pulse. Animal-dispersed plants bearing fleshy fruits are well represented in Amazonian forests, and tropical humid forests in general (Fleming & Kress 2011), while abiotically dispersed plants are typically more common in dry forests (Griz & Machado 2001). In seasonally-inundated forests such as várzea, a higher proportion of plants is also expected to bear seeds dispersed by abiotic agents, in particular water, which is expected to be one of the main dispersal vectors (Kubitzki & Ziburski 1994, Oliveira & Piedade 2002, Parolin et al. 2010b, 2013). However, this is likely to be tempered to some extent by the importance of fish in seed dispersal in flooded forests (Horn et al. 2011). Examining the relative importance of different seed dispersal modes between terra firme and várzea forests may help interpret the communities of vertebrate frugivores found in these two adjacent forest types (Hawes & Peres 2014).

Despite accounting for >400,000 km² (Junk et al. 2011, Melack & Hess 2010), várzea forests are one of the most poorly studied Amazonian forest types (Parolin et al. 2010a). In particular, few quantitative assessments of community-wide plant phenology are available, with most studies located in close proximity to Manaus and focusing on a select few tree species (Table S1). With the exception of one study (Haugaasen & Peres 2005), which also compares várzea to igapó (black-water flooded forests), there is a distinct lack of direct comparisons between várzea (VZ) and terra firme (TF) forests.

We redress this regional imbalance using a landscape-scale approach to explicitly compare adjacent terra firme and várzea forests of the Juruá floodplain in a remote part of western Brazilian Amazonia. Here, we present community-wide phenology patterns from terra firme and várzea forests, including both reproductive and vegetative characters, recorded using three complementary field methods (canopy observations, litterfall traps, and residual fruit-fall surveys). We tested the hypotheses that the additional influence of the flood pulse in várzea forest will induce (i) vegetative and reproductive phenological patterns,
including the timing of peak fruiting, to differ between the two forest types; and (ii) abiotic dispersal modes (including anemochory and hydrochory) to be relatively more important than in adjacent *terra firme* forests. In addition to community-wide patterns we also include a comparison of dominant plant genera present in both forest types.

**METHODS**

**STUDY SITE.** — This study was conducted within two contiguous sustainable use forest reserves in the state of Amazonas, Brazil, encompassing nearly 0.9 Mha: the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha) (Fig. S1). These two reserves border the Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large expanses of upland unflooded *terra firme* forest (80.6% of combined reserve area) and seasonally-flooded *várzea* forest (17.9%) closer to the main river channel (Hawes *et al.* 2012).

The Médio Juruá region has a wet, tropical climate with marked seasonal variation in rainfall, temperature, humidity and floodwaters (Fig. 1). There is a mean annual temperature of 27.1°C and annual rainfall, based on daily records over three consecutive years (2008-2010) at the Bauana Ecological Field Station (BEFS; 5°26′19″ S, 67°17′12″ W), averaging 3,679 mm/yr. Additional rainfall data were obtained from Eirunepé meteorological station (315 km from the study area, 2000-2010, source: INMET). Water-level data were recorded locally at BEFS (Oct 2009 – April 2010) and also obtained from the Juruá river at Porto Gavião, Carauari (90 km from the study area, 1972-1994 and 2008-2010, source: Petrobrás S.A.). Although hot and humid throughout the year, the hottest months are August-November, and humidity peaks in January-April. The precipitation pattern (rainy season: November-April, dry season: May-October) is asynchronous with the flood pulse, so that the river and floodplain water-level lags approximately 6 weeks behind rainfall (aquatic phase: January-
June, terrestrial phase: July-December) (Fig. 1). Climatic variables during the study period relate closely to records from the previous decade, while the flood-pulse displays a slightly delayed fall in water-level compared to long-term trends (Fig. 1).

The elevation range within the study area is 65-170 m asl and all sites surveyed consisted of undisturbed primary forest. *Terra firme* soils are typically heavily leached and nutrient poor in comparison to the eutrophic soils of *várzea* forests (Furch 1997), which are renewed with a fresh layer of pre-Andean alluvial sediments every year. Fabaceae, Lecythidaceae, and Sapotaceae were the most abundant tree families in both *terra firme* and *várzea*. Chrysobalanaceae and Moraceae were particularly abundant in *terra firme* compared to *várzea*, whereas Annonaceae and Malvaceae were comparatively more abundant in *várzea*.

**CANOPY OBSERVATIONS.** — We conducted monthly crown inspections from the ground for twelve consecutive months (April 2009 – March 2010) along eight 1-km transects (April: 2 TF, 2 VZ; May-June: 3 TF, 3VZ; 4 TF, 4 VZ July-March), divided equally across *terra firme* and *várzea* forests on either bank of the Juruá river (Fig. S1). We utilized a selection of available pre-existing transects, either along the opposite edges of two 100-ha plots or near the starts of longer 5-km transects, which were distributed evenly across the wider landscape avoiding large streams and lakes (see Hawes & Peres 2014 for details). Mean elevation (SRTM; Jarvis et al. 2008) was 100-106 m and 86-92 m in *terra firme* and *várzea* transects, respectively, with mean flood depths measured directly along *várzea* transects from high-water level marks visible on tree trunks of 192-304 cm (Hawes et al. 2012, Hawes unpubl. data).

All live trees ≥30 cm in diameter at breast height (DBH), and all live woody lianas or hemi-epiphytes ≥10 cm, within 5 m either side of each transect were measured (above buttress roots where required), aluminium tagged, and identified. Palms (Arecaceae) are not
best assessed by DBH but only understory palms were present along our transects, which
were not included in our sample. Within a total survey area of 8 ha (eight 1000-m x 10-m
transects; 4 ha per forest type), we examined a total of 1,056 live stems (TF: 556, VZ: 500;
874 trees, 182 lianas) comprised of 120 genera from 45 families (Table S2).

The phenophase of each stem was recorded for each plant part at monthly intervals,
using a pair of 10x40 binoculars: leaves (new, mature, shedding), flowers, and fruits
(immature, mature). Dehiscent fruits were defined as mature when they visibly opened.
During the aquatic phase, transects in várzea forest were surveyed using dugout canoes.
Phenophase activity was estimated as the proportion of individual stems (and genera) bearing
a given phenophase in each forest type. For vegetative phenology we used observations of
leaf condition to classify each stem as displaying leaf fall, leaf flush or leaflessness. For fruit
availability we calculated the Fruit Availability Index (FAI), multiplying a monthly fruit
production score of 0-5 for each stem (Fournier 1974) by its basal area (Develey & Peres
2000), which is a strong predictor of fruit crop size in trees (Chapman et al. 1992). This value
was summated for all trees per transect to derive a density estimate of fruit production (FAI/ha).
Basal area is not a strong predictor of fruit crop size in high-climbing lianas (Chapman et al.
1994) so we excluded all lianas and hemi-epiphytes (representing only 17.2% of stems) from
this measure.

LITTERFALL TRAPS. — We used square traps constructed of polyester mesh with PVC tubing
support (Stevenson & Vargas 2008). Each trap had a collection area of 0.5 m² (0.71 x 0.71 m)
and was supported 1 m above the ground. To cope with the seasonal fluctuation of
floodwaters in várzea forest, we added buoyancy to this basic design using four empty,
water-tight 2-litre plastic bottles at each corner of the trap, to maintain the polyester mesh
above water. Traps were also tied loosely to the upper branches of surrounding vegetation to
stabilize the trap position within a vertical column, as they rose above their supports with the
floodwater (Fig. S2).

Litterfall traps were employed for twelve consecutive months (May 2009 – April
2010) within two 100-ha plots (1 TF, 1 VZ), each plot consisting of a grid of 1-km transects
at 200-m intervals (Fig. S1). Traps were located along all transects at 100-m intervals,
resulting in a total of 96 traps per plot (total collection area = 48 m²). All material was
collected from traps twice monthly (by canoe during the aquatic phase in várzea), dried in
direct sunlight during the hottest time of day (09.00h – 15.00h) to a constant weight over at
least 72 h, and separated by plant part into fruits and seeds, flowers, leaves, and
twigs/branches (maximum diameter not defined). Each fraction was then dry-weighed
separately (using a 0.01 g resolution electronic scale) and all fruits and seeds were retained
for collection and identification. Mean monthly litterfall collections were estimated as Mg/ha
and trap collections were summed to provide annual estimates, standardizing for any
variation in number of days per collection period and the occasional omission of individual
damaged traps.

RESIDUAL GROUND SURVEYS. — We conducted monthly ground surveys for residual fruit-fall
within three 100-ha plots (2 TF, 1 VZ), as described above. Surveys were completed
between April 2008 and July 2010 (TF: total 18 months, 15 consecutive; VZ: total 26 months,
13 consecutive). All transects were surveyed slowly over four days (3 transects per day) each
month, recording all patches of fallen fruit detected along a 1-m wide strip (total transect
length and survey area per plot = 12 km and 1.2 ha). For each fruit patch encountered we
recorded its position along the transect, and sampled a specimen for our reference fruit
collection. In each case we also located the source fruiting stem, and measured its DBH and
perpendicular distance from the transect. During the aquatic phase in várzea forest, floating
fruits/seeds were also recorded, but unless their source crowns could be located overhead, these were assumed to have originated outside the transect and were therefore excluded from analyses.

TREE AND FRUIT IDENTIFICATION. — Number-tagged phenology trees were identified to the highest possible level of taxonomic resolution (species 10.6%, genus 82.3%, family 15.0%) by a trained herbarium technician from the Botany Department of the Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus). Additional tree and fruit identification was aided by van Roosmalen (1985), Gentry (1993), Ribeiro et al. (1999), Cornejo & Janovec (2010), and Wittmann et al. (2010a), which also assigned each species/genus recorded to the appropriate seed dispersal mode: anemochory, hydrochory, barochory/boleochory, synzoochory or endozoochory. All fruit/seed specimens were deposited at the Herbarium of the Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM, Manaus).

DATA ANALYSES. — Phenophase activity was calculated for each of the three methods employed: (1) canopy observations were quantified as the percentage of stems or genera observed in a given phenophase (further partitioned by seed dispersal mode for unripe and ripe fruit), and as the FAI index of fruit production; (2) trap collections were used to derive the monthly mean dry weight (Mg/ha) across all traps and the overall mean per trap across all months; (3) fruit/seed collections from ground surveys were used to estimate the monthly basal area density of all fruiting stems (m²/ha). Our general focus compared community-wide phenology patterns between terra firme and várzea forest, including the relationship with seed dispersal modes, but also included an examination of fruiting phenology in individual plant genera present in both forest types (>2 individuals in each) using circular statistics with January being 15° (Morellato et al. 2010). All analyses were conducted in R (R
Development Core Team 2010); circular statistics were conducted using the CircStats package (Lund & Agostinelli 2012), graphics were produced using the ggplot2 package (Wickham 2009).

RESULTS

VEGETATIVE PHENOLOGY. — Both terra firme and várzea forests displayed high seasonality, although canopy observations of leaf fall and leaf flush were recorded at low levels continuously throughout the year; leaf fall peaked in both forest types in March-April, while leaf flush peaked in March in várzea and was more steady in terra firme (Fig. 2). Deciduous species occurred in both forest types, but peaks in leaflessness occurred towards the end of the aquatic phase (June) in várzea forest, compared to the end of the dry season (September) in terra firme (Fig. 2).

Mean total fine litterfall in várzea forest was not significantly different from that in terra firme (Table 1). Although leaf fall was significantly lower, the amount of twigs/branches, bark and trash was higher. The proportion of total fine litterfall comprising leaves was 80.4% and 74.7% in terra firme and várzea forest, respectively, with litterfall fractions consisting of fertile material making the smallest contributions (Table 1, Fig. S3). Leaf-fall collections were highest during the middle of the aquatic phase (March-May) in várzea forest, compared to the dry season (August) in terra firme (Fig. 3).

REPRODUCTIVE PHENOLOGY. — Canopy observations of flowering reached maximum levels shortly after peaks in leaflessness and leaf flush in both forest types, with peaks in várzea and terra firme in July-September and October-November, respectively. Flowering in both forest types persisted until December, with subsequent fruit development and maturation appearing much more synchronous between the two forest types than other phenophases (Fig. 2).
Production of immature fruits peaked in November-January, whereas that of mature fruits peaked in March-April.

Data from litterfall traps correspond closely with canopy observations. Peak flower fall in várzea and terra firme forest was recorded in June and September-November, respectively but they were not significantly different. Peak fruit-fall was recorded in January for both várzea and terra firme forest (Fig. 3). There was no significant difference in fruit biomass density between the two forest types. Surveys for residual fruit-fall showed considerable inter-annual variation but suggest a unimodal pattern in terra firme forest with a peak associated with maximum rainfall (Fig. 4). In contrast, temporal fruit availability in várzea was more complex with the strongest peaks during the aquatic phase, but also secondary peaks during the terrestrial phase (Fig. 4).

FRUITING SEASONALITY AND SEED DISPERSAL MODES. — The timing of fruiting was relatively consistent within most individual genera occurring in both forest types (Fig. 5) and while the community-wide pattern in fruit production also appeared similar in both terra firme and várzea forest, there were noticeable differences across seed dispersal modes (Fig. S4). The proportion of plant genera exhibiting abiotic dispersal modes (wind, water and ballistic) was relatively higher in várzea forest (TF: 19 genera, 21.1% of genera; VZ: 17 genera, 26.2 % of genera), whereas terra firme forest was more dominated by animal-dispersed plants (TF: 71 genera, 78.9% of genera; VZ: 48 genera, 73.8 % of genera). Fruiting peaked in terra firme forest during the mid-rainy season almost exclusively due to animal-dispersed plants, with wind-dispersed and ballistic genera bearing fruit at a more steady low level. In várzea forest, both wind- and water-dispersed genera bore fruits most frequently during the aquatic phase (Fig. S4).
DISCUSSION

Our study reports two important observations: (1) vegetative and reproductive phenological cycles show strong seasonality in várzea and terra firme forests although patterns are broadly similar, including peak fruiting within plant genera occurring in both forest types; and (2) abiotic seed dispersal modes are relatively more prevalent in várzea forest than in terra firme forest, where plants are more heavily dependent upon animal seed-dispersal vectors. Note that litterfall material could not be oven-desiccated during this study and, in addition to the definition of branch size categories, may represent a potential source of error to be considered in the following comparisons with other studies.

Vegetative phenology. — Phenological studies often focus on flowers and fruits although leaf production and abscission are potentially key stages in the timing of other phenophases. Fine litterfall is strongly seasonal in Amazonian floodplains (Chave et al. 2009) but the proportions of individual fractions are not always reported, since this is typically quantified as a measure of primary productivity. In the várzea forests of the Médio Juruá, leaves comprised 74.7% of total fine litterfall, in close agreement with records for central Amazonia (Schöngart et al. 2010) but higher than in Peruvian várzea forests (Nebel et al. 2001). Absolute values for várzea total fine litterfall in our study were intermediate between a successional stage várzea (Schöngart et al. 2010) and a 60-year-old stand (Worbes 1997) in Central Amazonia and, in contrast to regional analyses (Chave et al. 2009), we found no significant differences in total fine litterfall between flooded and unflooded forests.

Leaf fall, recorded as a fraction of fine litterfall in traps, showed a peak during the aquatic phase in várzea (February-May), but during the dry season (August) in terra firme. This supports evidence from previous studies (Ayres 1986, Worbes 1997, Schöngart et al. 2002, Haugaasen & Peres 2005, Schöngart et al. 2010) that leaf fall in várzea is related to
cambial dormancy induced by the onset of the aquatic phase, with peak leaflessness
coinciding with the maximum flood pulse. In contrast, leaflessness in terra firme peaked
during the height of the dry season, although we failed to find evidence for varying degrees
of deciduousness between these forest types (but see Parolin 2001, Haugaasen & Peres 2005).

REPRODUCTIVE PHENOLOGY. — The timing of flowering we recorded concurs with previous
findings that peak levels in várzea forest occur towards the end of the aquatic phase, but can
extend into the terrestrial phase once floodwaters recede (Ayres 1986, Schöngart et al. 2002,
Haugaasen & Peres 2005). However, while Haugaasen & Peres (2005) report no difference
between peak flowering in terra firme and várzea, we found flowering in terra firme to peak
two months later than in várzea, and continue beyond the dry season into the onset of the
rainy season. Small differences in flowering between forest types could reflect an influence
of seasonal flooding on the availability of pollinators (van Dulman 2001). Canopy
observations also showed community-wide flowering to extend for almost six months,
reflecting a wide range of reproductive strategies for individual species.

Fruiting in humid tropical forests typically occurs during the early- to mid-rainy
season (van Schaik et al. 1993, Zhang & Wang 1995). Our data were consistent with this
pattern and fruit availability was similar in both várzea and terra firme, despite small
differences in the phenology of leaves and flowers. Likewise, fruiting peaks at Lago Uauaçú
were observed in December-March (early-mid rainy season) and January (start of the aquatic
phase) in terra firme and várzea forest, respectively (Haugaasen & Peres 2005). However, on
closer inspection, this pattern seems more complex in várzea forest than a simple lag behind
terra firme. While our trap collections indicate a várzea peak in December-January (early-
rainy season) as in terra firme, the amplitude is lower and a more pronounced peak occurs
during maximum flood levels in April-May. This is supported by ground surveys for residual
fruit-fall, which suggest a bimodal distribution in fruit production in várzea forest in contrast to a unimodal pattern in terra firme. This is similar to the várzea forest at Lago Teiú, Mamirauá (Ayres 1986), where a first fruit peak follows peak rainfall but precedes peak water-levels, and a secondary peak precedes the onset of the rainy season, coinciding with the submergence of low-lying várzea (chavascal). In our study the secondary peak occurred during the terrestrial phase (onset of the rainy season), and was notably comprised of fleshy fruits such as Byrsonima spp. and Manilkara spp.

The lack of a difference in fruit biomass between the two forest types is surprising considering the much higher nutrient availability in várzea forests (Furch 1997). This may imply that flooding and nutrient availability in the floodplain forest does not affect fruit production. However, this finding fails to take in to account the lower stature and less continuous nature of the várzea forest canopy, which suggests that relative fruit production (per stem or per unit of aboveground forest biomass) is actually higher in this forest type, where overall basal area is greater despite similar stem density (Hawes et al. 2012). That fruit biomass recorded in litterfall traps was similar despite these differences in forest structure is testament to the high productivity of várzea forests.

FRUITING SEASONALITY AND SEED DISPERSAL MODES. — Our results suggest that any contrast in fruiting seasonality between várzea and terra firme is more likely a result of differences in community composition and the relative prevalence of various seed dispersal modes than differences within single genera. Our results from terra firme were consistent with previous studies, in terms of the maturation of fleshy fruits consumed by vertebrate frugivores during the humid early wet season (Lieberman 1982) and, conversely, the dry-season maturation of fruits and seeds dispersed by abiotic agents (van Schaik et al. 1993). The greater prevalence of wind-dispersed trees and lianas within várzea forest is likely related to the lower stature
and less continuous nature of the canopy, as well as the history of plant colonization of the floodplains from adjacent terra firme forest communities (Wittmann et al. 2010b). That we failed to detect any hydrochorous plants bearing mature fruits during the várzea terrestrial phase is unsurprising, but mature fruits in anemochorous plants in this forest type appear more tightly aligned to the dry season *per se* than to the terrestrial phase.

While we documented a surprisingly low proportion of hydrochorous plant genera in várzea forest, seed dispersal in several plants classified as anemochorous or zoochorous may in fact also be assisted by the floodwaters. Buoyancy represents just one of many strategies employed by plants with fruits or seeds falling during flood conditions (Ferreira et al. 2010). Others alternatively sink, remaining dormant on the forest floor until water-levels recede (Kubitzki & Ziburski 1994) where they provide a food resource for terrestrial frugivores returning to floodplain forests. During the aquatic phase moreover, many zoochorous fruits are consumed and potentially dispersed by fish, rather than mammals or birds (Goulding 1980, Kubitzki & Ziburski 1994, Correa et al. 2007, Horn et al. 2011). As a result, the proportion of tree species in floodplain forests that benefit from floodwaters, either directly or indirectly and even without obvious hydrochoric characteristics, may be underestimated by current classifications of seed dispersal modes.

PHENOLOGICAL TRIGGERS. — Varying levels of precipitation have often been considered the principal environmental trigger for plant phenology in the tropics (van Schaik et al. 1993), with the key proximate cue usually assumed to be the period of water stress (but see Wright & Cornejo 1990). In terra firme forest, the period of most intense water stress is the dry season, while within várzea, paradoxically, the greatest degree of water stress is a result of anoxia from the extended period of water-logging and deep submersion (Parolin 2009). Other environmental variables, however, may also potentially contribute as proximate triggers.
Indeed, the role of water stress may not be as important as the seasonality of daily insolation, with this mechanism of photoperiod control now recognized as a factor triggering leaf flush and flowering, even in tropical forests near the equator (Borchert et al. 2015). Given the wide variety of plant strategies, different triggers may be relevant for different species in both terra firme and várzea forests (Wright & Cornejo 1990, Schöngart et al. 2002, Parolin et al. 2010a). This is shown by the variation in phenological schedules between plants with different seed dispersal syndromes, where fruiting events in wind-dispersed species in várzea forest appears more closely related to the dry season than to the flood pulse.

Phenological triggers are best identified by examining long-term datasets; the importance of multi-year studies is highlighted by the supra-annual reproductive cycles in many species (Newstrom et al. 1994, Haugaasen & Peres 2005, Norden et al. 2007) and the inter-annual variation in climatic conditions resulting in substantial oscillations in flood pulses. However, apart from residual fruit-fall, we lacked such multi-year datasets. Further caution in defining the environmental triggers of plant phenology is necessary due to the difference between proximate triggers (environmental events correlated with phenology) and the ultimate factors driving evolutionary scale selection pressures (Hamann 2004). Because of these issues we resist the temptation to over-analyze possible phenological triggers in this study.

CONCLUSIONS. — Our year-round community-wide assessment along the Rio Juruá represents one of the most extensive efforts conducted to date in Amazonian várzea forest, including a large sample area for canopy observations, litterfall traps and ground surveys, making a substantial contribution to understanding phenological patterns and processes within this forest type. Our successful use of three complementary methods, including a
novel floating trap designed to cope with the fluctuating flood levels in várzea forest, enabled us to quantify litterfall and fruit production throughout the year and illustrates the possibilities for long-term studies in várzea and other flooded forests.

The increasingly threatened várzea forests remain vastly understudied, in terms of both sampling effort and the distribution of study sites across Amazonia, partly as a result of the practical difficulties associated with fieldwork in such a dramatically seasonal habitat.

While recent large-scale advances have been made in digital and remote phenology monitoring (Pennec et al. 2011, Zhao et al. 2012), there remains no substitute for field surveys, especially for reproductive phenophases.

Within any single short-term study, it is difficult to disentangle the relationships between phenology and environmental variables and, despite the general consistency between forest types, it remains possible that the annual flood pulse still has an important contributory role to play in plant phenology in várzea forests. Clarification of the relative roles of environmental triggers in the phenology of flooded forests would be aided, not just by multi-year studies, but by a systematic effort to increase the geographic distribution of phenology studies.

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TABLE 1. Annual fine litterfall fractions (Mean ± SD, Mg/ha/yr) sampled by 96 traps in each forest type from April 2009 to March 2010. *P*-values are represented by * P < 0.05, ** P < 0.005, *** P < 0.001.

<table>
<thead>
<tr>
<th></th>
<th>Terra firme</th>
<th>Várzea</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td>8.27 ± 0.96</td>
<td>7.43 ± 1.04</td>
<td>-5.76</td>
<td>&lt;0.001 ***</td>
</tr>
<tr>
<td>Twigs/branches, bark and trash</td>
<td>1.69 ± 0.39</td>
<td>2.36 ± 0.51</td>
<td>10.16</td>
<td>&lt;0.001 ***</td>
</tr>
<tr>
<td>Flowers</td>
<td>0.15 ± 0.24</td>
<td>0.05 ± 0.07</td>
<td>-4.09</td>
<td>&lt;0.001 ***</td>
</tr>
<tr>
<td>Fruits</td>
<td>0.18 ± 0.20</td>
<td>0.12 ± 0.24</td>
<td>-1.94</td>
<td>0.054</td>
</tr>
<tr>
<td>Total</td>
<td>10.29 ± 1.18</td>
<td>9.95 ± 1.33</td>
<td>-1.84</td>
<td>0.068</td>
</tr>
</tbody>
</table>
SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Médio Juruá region of western Brazilian Amazonia, showing locations of eight 1-km phenology transects (stars) and two 100-ha plots (squares) in terra firme (no shading) and várzea forest (gray shading). Black circles represent local communities (BAU=Bauana, NUN=Nova União); gray lines represent perennial streams; dashed lines represent the spatial extent of the várzea floodplain according to high-resolution ALOS ScanSAR imagery (Hawes et al. 2012).

FIGURE S2 Floating fruit/seed trap design used in várzea forest, supported at a height of 1m during the terrestrial phase, but free to float within a vertical water column with fluctuating floodwaters during the aquatic phase.

FIGURE S3. Annual fine litterfall (Mg/ha/yr) recorded from 24 twice monthly collections of 96 traps in both terra firme and várzea forest, showing total fine litterfall and values for individual vegetative and reproductive fractions.

FIGURE S4. Percentage of genera with either unripe or ripe fruit, recorded during canopy observations in terra firme (A) and várzea forest (B) and partitioned according to seed dispersal modes.
FIGURE LEGENDS

FIGURE 1. Seasonal variation in climate and river water-level in the Médio Juruá region of western Brazilian Amazonia. Mean monthly records for (A) temperature, (B) humidity, and (C) rainfall from Eirunepé meteorological station: gray shading represents 95% confidence intervals, solid circles represent study months April 2009 – April 2010 (source: INMET 2000-10); mean daily records for (D) water-level of the Juruá river at Porto Gavião, Carauari: gray fill represents long-term records 1972-94, solid circles represent daily measurements during the study period: April 2009 – April 2010 (source: Petrobrás S.A., 1972-94 and 2009-10).

FIGURE 2. Percentage of stems for each phenophase recorded by monthly canopy observations in terra firme (open circles, dashed line) and várzea forest (shaded circles, solid line).

FIGURE 3. Mean monthly values for (A) total fine litterfall (Mg/ha), recorded from twice monthly collections of 96 traps per 100-ha plot in both terra firme (open circles, dashed line) and várzea forest (shaded circles, solid line), and for individual vegetative and reproductive fractions: (B) leaves, (C) fine woody litter (twigs/branches, bark, trash), (D) flowers, and (E) fruits.

FIGURE 4. Fruit production estimates in terra firme (open circles, dashed line) and várzea forest (shaded circles, solid line) using three complementary sampling methods: canopy observations of (A) unripe and (B) ripe fruit, (C) trap collections of the fruit fraction in litterfall, and (D) ground surveys of residual fruit patches (stem basal area: m²/ha). Seasonal variation in (E) rainfall: black points represent total monthly values from daily records at the Bauana field station; dotted line represents records from the Eirunepé meteorological station (source: INMET), and (F) water-level: solid circles represent daily measurements at the Bauana field station; gray fill represents daily records obtained at Porto Gavião, Carauari (source: Petrobrás, S.A.).
FIGURE 5. Correlation of peak fruiting (mean angle ± circular standard deviation) from canopy observations of 20 plant genera occurring in both *terra firme* and *várzea* forest. Point shading represents seed dispersal modes; dashed lines represent equal angle in both forest types; number codes refer to plant genera listed in Table S3.