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Research Article

# Reproductive Phenology of Central Amazon Pioneer Trees

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**Abstract**
This study characterizes the flowering and fruiting phenology of the 13 most common pioneer tree species in early successional forests of the Central Amazon. For each species, 30 individuals, 10 each in three secondary forests, were monitored monthly for four years at the Biological Dynamics of Forest Fragments Project, north of Manaus. Five species showed nearly continuous flowering and fruiting throughout the study, indicating that resources were available to pollinators and dispersers on a regular basis. The other eight species showed stronger seasonality in reproduction, seven of them annually, and one supra-annually. Overall, flowering was concentrated in the transition from the dry to the rainy season and fruiting was concentrated in the rainy season. There was no relationship between reproductive phenology and tree pollinator type or dispersal mode. Reproductive phenology was remarkably consistent year to year. The pioneer community showed a variety of phenological patterns but as a whole tended to be characterized by annual flowering and fruiting, either continuously or seasonally, thereby fitting generalizations of pioneer species relative to mature forest species.

**Keywords**: Phenology; flowering; fruiting; seasonality; secondary growth; succession; regeneration.

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## Introduction

Tropical pioneer species fulfill important ecosystem functions through soil development, nutrient and water cycling, forest structure development, and production of flowers and fruits for pollinators and dispersers. Despite their importance, basic life-history data on the autecology of Neotropical pioneers, especially phenological reports, are scarce [1].

It has been postulated that pioneers begin reproduction at a young age, and then reproduce annually, often continuously throughout the year [2]. However, studies of colonizers reveal significant variation among them in the timing and quantity of reproduction [3-7]. Such variation is inevitable given that pioneers naturally occupy a wide array of spatially, ephemeral clearings and light gaps and that pioneers have evolved from a wide range of plant families [6]. Still, ecologically, they seem to share certain functional traits [1, 2].

In the Central Amazon, most studies of phenology of trees in upland, unflooded (*terre firme*) sites have focused on species in mature forests, attempting to relate phenology to climatic variables [8-17]. Usually pioneers are excluded from these studies, although data on a few pioneer species in mature forest have been recorded. However, there have been no studies of pioneer species where they commonly regenerate, namely, open secondary habitats exposed to full solar radiation.

Here, our objective is to characterize the reproductive phenology of the 13 most abundant pioneer tree species in young secondary forests of the Central Amazon. All 13 occur in mixed species' associations in abandoned pastures, roadside clearings, forest clearcuts, and natural light gaps in mature forest. Disturbance and logging in Central Amazonia are often followed by attempted conversion of forest to pasture or agriculture. Low nutrient content of these ancient and weathered soils results in abandonment within a few years [18]. Subsequently, succession by native pioneer species that utilize full sunlight for growth and reproduction occurs naturally, although often irregularly as a result of differential colonization [19]. Alternative successional pathways may develop from different initial colonizations, reflecting land-use history and different life-history characteristics of the initial colonizers themselves [19]. Nevertheless, the most common pioneer species appear capable of colonizing most sites since they frequently occur together, although these same species may show some niche partitioning of light gaps in mature forests [20]. The two most prevalent genera, *Cecropia* and *Vismia*, each comprising several species, dominate initial pioneer communities throughout the central and eastern portions of Amazonia, as well as throughout much of Brazil's Atlantic Coastal Forest [20].

Despite advances in our understanding of community phenological traits for different tropical ecosystems, we still know little about the proximal cues that determine phenological events. Tropical communities are composed of diverse species, usually exhibiting diverse phenologies [21-23]. Biotic factors have been hypothesized to be the ultimate causes in the evolution of phenological patterns, whereas abiotic factors are more often the proximal stimuli for phenological events. In various tropical forests, many canopy species flower in the dry season, stimulated to flower by drought, photoperiod, temperature or leaflessness [24-29], and various hypotheses have been proposed to explain dry season flowering–i.e., reduced hydric stress, increased pollinator activity, less damage to flowers from rain [30-33]. Similarly, many studies have shown that the rainy season is associated with fruiting, seed dispersal, production of new leaves, and tree growth [25, 28, 34-38]. The effects of proximal factors in determining phenological patterns have been determined through rigorous experimentation for only a handful of tropical species [21, 34, 39].

Here, we take a necessary first step for 13 species of pioneers in the Central Amazon by monitoring flowering and fruiting of 30 trees of each species, monthly over four years.

Fig. 1. (a.) In unburned clearings, *Cecropia sciadophylla* dominates the canopy due to its rapid height growth, but (b.) the lower strata are quite diverse, here shown with the phenological observation team.

## Methods

This study was carried out at the Biological Dynamics of Forest Fragments Project (BDFFP). The BDFFP reserves are located on *terra firme* in tropical moist forest [40], about 80 km north of Manaus in the state of Amazonas, Brazil (2°30'S, 60°W) [41]. Mean annual rainfall measured in one of the reserves averaged 2,651 mm, with a distinct, but mild, dry season [42]. Mean annual temperature is 26° C [43]. The regional climate is type *Am* in the Koeppen system [44]: humid tropical with excessive rains from January to May and a moderate dry season from June to December, with an occasional month of less than 100 mm precipitation [41,45]. Soils of the region are classified as yellow latisols (Ultisol) and red-yellow podzols (Oxisol) [46].

Between 1980 and 1984, three large ranches (>10,000ha) were created by clear-cutting extensive, unfragmented forest, leaving 11 isolated forest fragments [47]. The resulting ranches were abandoned after clearcutting or converted to pasture, burned irregularly several years, and subsequently abandoned. Whereas the forest fragments formed the initial core for research, the surrounding matrix has become a second focus of long-term studies, this one on secondary succession with known land-use histories [19].

We monitored pioneer tree reproductive phenology at three sites within two of the ranches: Florestal and Cidade de Powell at the Esteio Ranch and an unnamed site in the northeastern quadrant of the Porto Alegre Ranch. The secondary growth areas utilized in this study were clearcut in 1984, followed by abandonment leading to a mixed species association which has been characterized as *Cecropia* dominant because *Cecropia* rapidly achieves height dominance [19] (Fig. 1a). Other portions of the ranches that were converted to pastures and periodically burned before abandonment are characterized by dominance of *Vismia*.

The 13 pioneer species chosen for study are the dominant early colonizers of the study area and of the *terra firme* in the Central Amazon (Table 1). They pertain to nine widely distributed families, characteristic of Neotropical secondary growth [45, 48]. Besides dominating abandoned agricultural areas, the species are found commonly in natural forest light gaps, and some of them occur in mature forest canopies at low densities [19, 45, 49].

For phenological observations over a four-year period, 30 adult individuals (≥ 5cm DBH) were selected indiscriminately along three different trails, 10 individuals per trail, each in extensive patches of secondary forest at one of the three sites. The 5-cm minimum DBH criterion was based on preliminary records of 90 individuals of each species, which showed that some species were reproductive at the 5 cm DBH (Table 1). At each monthly census, trees were inspected with binoculars for presence of four reproductive structures: flower buds, flowers, immature fruits and mature fruits, following methods of Fournier [50] (Fig. 1b).

Two phenophases were defined–flowering, which included the presence of flower buds and/or flowers, and fruiting, which included the presence of immature and/or mature fruits. Flowering and fruiting were calculated as the percentage of the number of reproductive individuals for each species. As some individuals proved too small to reproduce, calculations of monthly presence of reproductive structures were percentages of individuals that reproduced each year or in previous years. For one species, *Goupia glabra*, there were no reproductive individuals for the first seven months of the four years of observation.

Table 1. Pioneer species studied, their plant families, abbreviated species codes used in subsequent figures, minimum DBH (cm) for flowering, known pollinators, known dispersers, and sources for pollinators and dispersers. Abbreviations for pollinators and dispersers are bs=bees, bd=birds, bt=bats, mk=monkeys. Sources in the literature are [56-60, 62]. Species are listed alphabetically by family.

| Species | Family | Spp Codes | Min. DBH | Pollinator | Disperser | Sources |
|---|---|---|---|---|---|---|
| *Guatteria olivacea* R.E. Fr. | Annonaceae | GO | 12.5 | bs | bd | pers. obs. |
| *Cecropia purpurascens* C.C. Berg | Cecropiaceae | CP | 5.0 | bt | bd, bt | [56,59] |
| *Cecropia sciadophylla* Mart. | Cecropiaceae | CS | 4.8 | bt | bd, bt, mk | [56,59,62] |
| *Goupia glabra* Aubl. | Celastraceae | GG | 8.6 | bs | bd | [57,61] |
| *Vismia cayennensis* (Jacq.) Pers. | Clusiaceae | VC | 3.9 | bs, bt | bd, bt | [56,59,60] |
| *Vismia japurensis* Reich. | Clusiaceae | VJ | 4.3 | bs, bt | bd, bt | [56,59,60] |
| *Croton lanjouwensis* Jabl. | Euphorbiaceae | CL | 12.5 | bs | dehiscent | [60] |
| *Laetia procera* (Poepp.) Eichler | Flacourtiaceae | LP | 15.7 | bs | bd, mk | [57,61,62] |
| *Byrsonima chrysophylla* H.B. & K. | Malphigiaceae | BC | 15.6 | bs | mk | pers. obs. |
| *Bellucia grossularioides* (L.) Triana | Melastomataceae | BG | 7.8 | bs | bt, mk | [56,59,60,62] |
| *Bellucia imperialis* Saldanha & Cogn. | Melastomataceae | BI | 10.3 | bs | bt, mk | [56,59,60] |
| *Miconia burchellii* Triana | Melastomataceae | MB | 9.5 | bs | bd | [58] |
| *Isertia hypoleuca* Benth. | Rubiaceae | IH | 2.9 | bd | bd | pers. obs. |

We expected to place species into discrete phenological classes, based on flowering and fruiting characteristics–(1) seasonality, (2) intensity, and (3) periodicity–proposed by Newstrom [51]: The classes were continuous, sub-annual seasonal, annual seasonal, or super-annual, where continuous would indicate flowering or fruiting activity throughout the year, sub-annual flowering or fruiting would be characterized by two or more seasonal reproductive events per year, annual seasonal would represent one seasonal reproductive event per year, and supra-annual reproduction would exhibit activity in some years but not others. Classifying the species was aided by statistical analysis below.

Differences from continuous flowering or fruiting were determined with circular statistical tests of seasonality [52-53]. For each species separately, the proportion of individuals fruiting per month was averaged over the four years and used to determine the species' mean angle (µ) and vector length (r). The mean angle indicates the mean date of the phenological event. As we had monitored phenological events at the end of each month, we assigned months the following angles: Jan=30$^o$, Feb=60$^o$, .... Dec=360 $^o$. The vector length reflects the seasonality in the event and can vary from 0 for perfectly continuous to 1 for perfectly seasonal [54]. The statistical significance of each vector was determined by the Rayleigh (z) test for deviations from a circularly uniform distribution with Oriana 2.0 software [55].

To test for effects of rainfall on reproductive activities, we produced Spearman rank correlations between the proportion of individuals with a reproductive structure in a month and rainfall that month for each species. The correlations were computed for each year separately, but they were so similar among the four years that we proceeded to average monthly reproductive activity and monthly rainfall and then computed the correlation coefficients. We also computed correlations between monthly reproductive activity and monthly rainfall for one and two months later and one and two months prior to check for potential lag effects.

Finally, to investigate potential associations between phenophases and mutualists, we gathered data on pollinators and seed dispersal agents from direct observations and from the literature [56-62]. We then looked for possible interactions between seasonality and mutualist type, expecting possible associations, for example, between bee pollination and dry-season flowering.

## Results

Mean annual precipitation over the four years of study was 2,589 mm (Fig. 2). The distribution of precipitation exhibited a relatively normal annual pattern with a five-month rainy season from January through May, with mean rainfall of 330 mm a month, followed by a seven-month dry season from June through December with a mean rainfall of 134 mm a month (Fig. 2). March was the wettest month the first three years, and January the wettest in the fourth year of study. The driest month was August in 2002 (46 mm), December in 2003 (67 mm) and in 2004 (49 mm), and September in 2005 (68 mm). The 2002-2006 records at the Port of Manaus, 80km south of the BDFFP, were normal relative to the Port's long-term records. There was no unusual drought during the study as sometimes occurs in an El Niño year [63].

Minimum DBH for fruiting varied from 15.7 cm DBH in *Laetia procera* to 2.9 cm DBH for *Isertia hypoleuca* (Table 1) in our preliminary survey of 90 trees of each species across DBH sizes of 1.0-30.0 cm.

Patterns of flowering for individual species varied from continuous to supra-annual (Fig. 3, Table 2). Continuous flowering characterized five species, most uniform in *Bellucia grossularioides* (Table 2). Seven species exhibited patterns of seasonal flowering (Table 2, Fig. 3); *Laetia,* the two *Vismia* species and the two *Cecropia* species, flowered during the dry season, but two others, *Byrsonima* and *Miconia*, flowered in the rainy season (Fig. 3). Finally, one species, *C. lanjouwensis*, exhibited supra-annual reproduction, flowering in the rainy season every other year (Fig. 3).

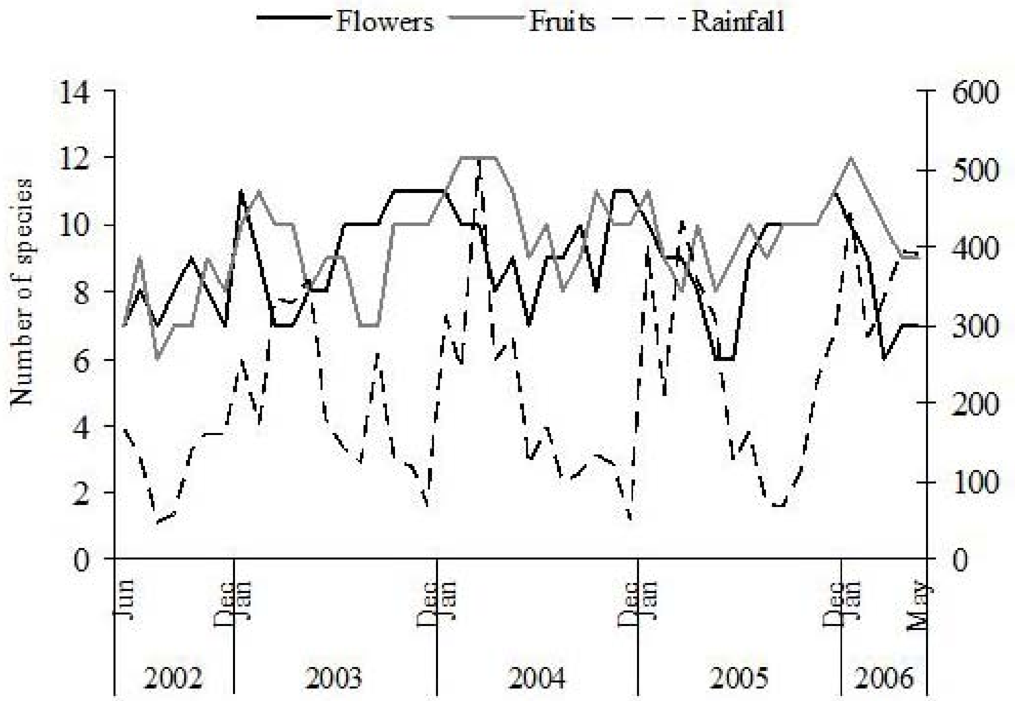

Fig. 2. Number of species producing flowers or fruits, together with annual rainfall, from June 2002 through May 2006.

Patterns of fruiting, like flowering, varied among species from continuous to supra-annual (Fig. 4, Table 2). Continuous fruiting characterized three species, *Belllucia grossularioides, Isertia hypoleuca,* and *Goupia glabra*. Nine other species exhibited annual seasonal fruiting (Fig. 4, Table 2). Only one species, *C. lanjouwensis*, showed supra-annual reproduction, fruiting once every two years.

Generally, species that were seasonal in flowering exhibited similar seasonality in flower buds, unripe fruit and ripe fruit (Table 2). While significant seasonality in "r" values was more frequent in ripe fruits (10 sp) than in flowers (8 sp), the relative size of the "r" values across all species was no different for flowering and fruiting, therein suggesting that the overall degree of seasonality between flowering and fruiting did not differ. Of course, flowering tended to occur before fruiting, but variably so, ranging from 1-6 months prior. Overall, the mean flowering date occurred most often in the dry season, whereas mean fruiting date was split between the dry season and the wet season (Table 2).

Throughout each of the 48 months of study, flowers and fruits were produced by one to many species. The number of species flowering each month varied from 6 to 11 and the number fruiting each month varied from 6 to 12 (Fig. 2). In general, the highest number of species flowered during December and January, which is the transition from the dry season to the rainy season. The fewest number of species flowered in the latter half of the rainy season, March to June. The highest number of species fruited in the first half of the rainy season, January through March. The fewest number fruited in the first half of the dry season, July and August, although fruiting ebbed earlier in 2005 (Fig. 2).

Table 2. Mean dates for reproductive structures (μ) and degree of seasonality (*r*) for flower buds, flowers, unripe fruit and ripe fruit for 13 pioneer species over four years, 2002 to 2006. Significant (P<0.05) seasonality is indicated by an asterisk. Species are ranked by degree of seasonality in flowering (r). No correction has been made for the number of tests, 52.

| **Species** | **Flower buds** | | **Flowering** | | **Unripe fruit** | | **Ripe fruit** | |
|---|---|---|---|---|---|---|---|---|
| | Mean date | *r* | Mean date | *r* | Mean date | *r* | Mean date | *r* |
| *Bellucia grossularioides* | Jan 29 | 0.14 | Mar 18 | 0.24 | Apr 5 | 0.17 | Apr 17 | 0.20 |
| *Isertia hypoleuca* | Aug 13 | 0.56* | Jul 29 | 0.35 | Jan 16 | 0.21 | Feb 4 | 0.44 |
| *Guatteria olivacea* | Set 27 | 0.52* | Nov 27 | 0.41 | Nov 5 | 0.57* | Dec 24 | 0.78* |
| *Bellucia imperialis* | Jun 25 | 0.30 | Jul 09 | 0.42 | Aug 12 | 0.34 | Sep 19 | 0.52* |
| *Goupia glabra* | Jun 10 | 0.48 | May 29 | 0.50 | Jul 11 | 0.39 | Aug 14 | 0.45 |
| *Vismia cayennensis* | Aug 24 | 0.47 | Aug 30 | 0.57* | Sep 10 | 0.44 | Oct 7 | 0.73* |
| *Cecropia purpurascens* | Sep 7 | 0.67* | Sep 12 | 0.70* | Oct 25 | 0.59* | Oct 22 | 0.63* |
| *Cecropia sciadophylla* | Oct 17 | 0.78* | Nov 8 | 0.70* | Jan 20 | 0.61* | Jan 16 | 0.75* |
| *Vismia japurensis* | Nov 22 | 0.71* | Dec 10 | 0.71* | Feb 7 | 0.56* | Feb 29 | 0.63* |
| *Laetia procera* | Sep 30 | 0.86* | Oct 27 | 0.88* | Jan 8 | 0.74* | Feb 25 | 0.88* |
| *Byrsonima chrysophylla* | Jan 7 | 0.89* | Fev 9 | 0.95* | Apr 17 | 0.69* | Jun 1 | 0.86* |
| *Miconia burchellii* | Mar 14 | 0.90* | Apr 1 | 0.95* | Jun 7 | 0.77* | Jul 2 | 0.86* |
| *Croton lanjouwensis* | Jan 23 | 0.99* | Feb 14 | 0.98* | Mar 17 | 0.93* | May 4 | 0.97* |

Although the pioneer community as a whole showed a tendency to flower in transition from the dry season to wet season and to fruit early in the wet season, the species-specific Spearman correlations of production of flowers or fruits with rainfall were rarely significant even when monthly lags were applied to the rainfall data (Table 3). At most, only three of the 13 species showed significant correlations with a given monthly precipitation or its lag.

All 13 species were pollinated by animals, mostly by bees, a few species by bats, and one species by hummingbirds (Table 1). Dispersal was spread relatively evenly among birds, bats, and primates, as well as one species by d(Table 1). There was no association of flowering season with pollinator type, nor fruiting season with dispersal agent (Table 1).

Table 3. Spearman correlation coefficients of proportion flowering or fruiting each month with monthly precipitation (0), and for precipation one and two (+1, +2) months after flowering or fruiting and for precipation one and two (-1, -2) months before flowering or fruiting. Coefficients shown in bold are statistically significant for P<0.05 when the coefficient is greater than 0.59, and for P<0.01 when the coefficient is greater than 0.78. No correction has been made for the number of tests, 130. Species are ranked as in Table 2.

| Species | Flowers | | | | | Ripe Fruit | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | (+2) | (+1) | 0 | (-1) | (-2) | (+2) | (+1) | 0 | (-1) | (-2) |
| Bellucia grossularioides | 0.16 | 0.24 | 0.06 | 0.37 | 0.23 | 0.18 | 0.16 | 0.05 | 0.12 | 0.00 |
| Isertia hypoleuca | -0.43 | -0.35 | -0.23 | -0.21 | -0.06 | 0.60 | 0.43 | 0.24 | -0.07 | -0.34 |
| Guatteria olivacea | 0.24 | -0.20 | -0.48 | **-0.68** | **-0.69** | 0.39 | 0.18 | -0.18 | -0.51 | -0.57 |
| Bellucia imperialis | -0.63 | -0.46 | -0.07 | 0.29 | **0.66** | -0.54 | **-0.63** | **-0.63** | -0.49 | -0.19 |
| Goupia glabra | 0.06 | 0.22 | 0.35 | 0.41 | 0.46 | -0.32 | -0.13 | -0.08 | 0.09 | -0.10 |
| Vismia cayennensis | -0.33 | -0.52 | -0.48 | -0.37 | 0.07 | -0.02 | -0.33 | -0.49 | -0.51 | -0.59 |
| Cecropia purpurascens | -0.53 | **-0.75** | **-0.64** | -0.47 | -0.11 | 0.11 | -0.18 | **-0.70** | -0.38 | -0.44 |
| Cecropia sciadophylla | 0.03 | -0.25 | -0.50 | -0.66 | **-0.68** | 0.57 | 0.42 | 0.07 | -0.22 | -0.54 |
| Vismia japurensis | 0.35 | 0.02 | -0.09 | -0.29 | -0.46 | 0.36 | **0.65** | 0.43 | 0.29 | 0.03 |
| Laetia procera | -0.10 | -0.25 | -0.40 | -0.42 | -0.34 | 0.56 | 0.55 | 0.51 | 0.17 | -0.19 |
| Byrsonima chrysophylla | 0.58 | 0.56 | 0.25 | -0.06 | -0.37 | -0.33 | -0.02 | 0.40 | **0.59** | **0.73** |
| Miconia burchellii | 0.31 | 0.30 | 0.50 | 0.41 | 0.16 | -0.58 | -0.36 | -0.02 | 0.31 | 0.54 |
| Croton lanjouwensis | 0.49 | 0.25 | 0.24 | 0.26 | -0.02 | 0.01 | 0.36 | **0.62** | 0.52 | 0.32 |

## Discussion

Over the course of the study, flowering was most concentrated in the transition from the dry season to the rainy season, and fruiting was most concentrated in the rainy season. Flowering in the dry season is clearly advantageous for pollination as heavy rains can inhibit pollinator activity and damage flowers. Flowering late in the dry season facilitates immediate production of fruits during the rainy season, a time when seed germination and establishment depend on available soil water. Fruiting early in the rainy season ensures a favorable period for the seedling to develop a root system capable of weathering the subsequent dry season [25], and since 12 of our 13 species are dispersed by birds and mammals, fruiting during the rainy season is unlikely to hinder dispersal. Thus, although phenological patterns varied among species, our pioneer community as a whole exhibited what might be interpreted as relatively straightforward adaptive flower and fruiting patterns in relationship to pollination, dispersal and establishment [64]. In contrast to such simple logic is one species, *Croton lanjouwensis*, which flowered and fruited in the rainy season despite being pollinated by bees and dispersed by wind (Table 1). Furthermore, species that wait to flower until the beginning of the rainy season, as did some of our pioneers, may reduce the risk of hydric stress but increase the risk of reduced pollination success [65].

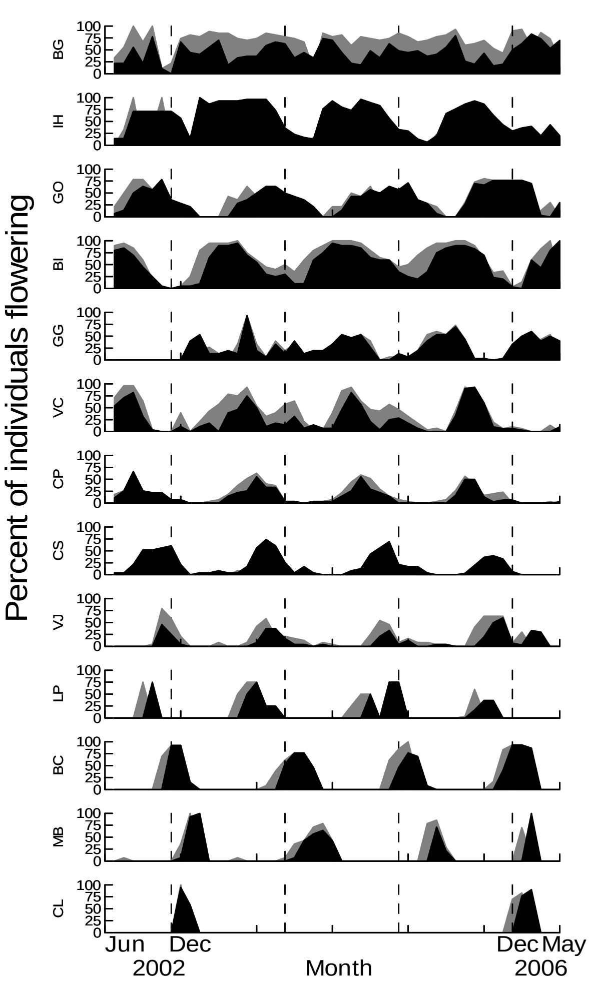

Fig. 3. Percent of individuals flowering (floral buds in gray, flowers in black) for the 13 pioneer species monitored. Species' codes conform to Table 1. Species are ranked from top to bottom by increasing degree of seasonality in flowering. Vertical dashed lines indicate January 1 of each year.

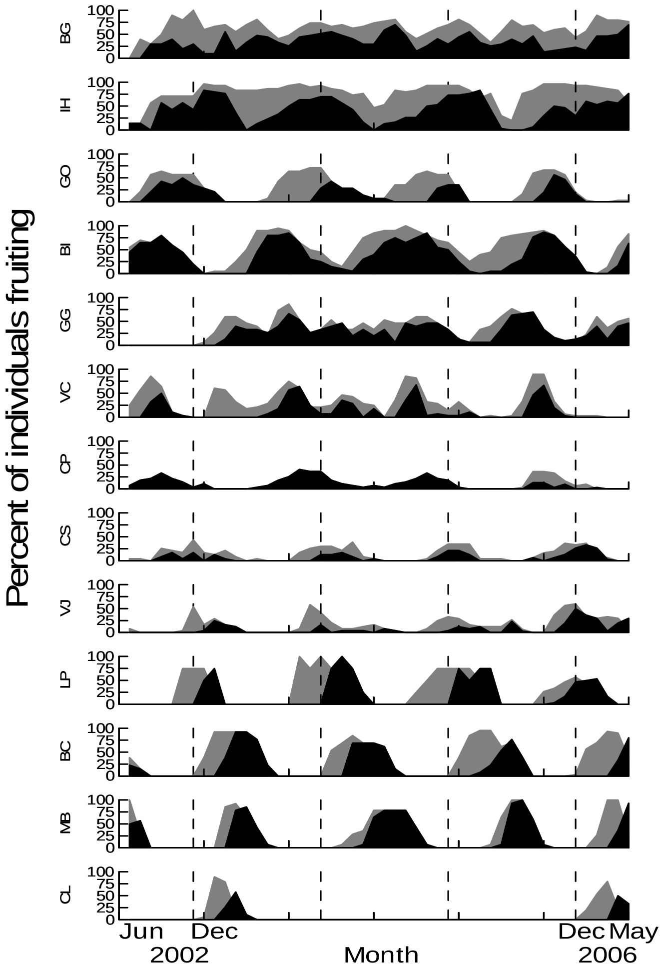

Fig. 4. Percent of individuals fruiting (immature fruits in gray, ripe fruits in black) for the 13 pioneer species monitored. Species' codes conform to Table 1. Species are ranked from top to bottom as in Figure 3. Vertical dashed lines indicate January 1 of each year.

Additionally, pioneers are intolerant of shade, so germination for many of the species in this study arises from the seed bank [66]. Therefore, fruiting in the wet season may convey little advantage from the standpoint of having water for germination because the latter is delayed by dormancy. Germinating in the rainy season may provide some other advantage, perhaps increased dispersal or improved success in the seed bank such that the potential for germination is maximized when environmental conditions are favorable [67-68]. Other studies confirm that regeneration of pioneer species is mainly from dormant seeds in the soil [6-70]. Moreover, the requirements for germination of dormant seeds [71-72] and the establishment of seedlings [73-74] vary among species, but may be triggered more by light quality and quantity than by rainfall, especially where dry seasons are moderate [75-76].

Other phenological studies in the Neotropics have similarly demonstrated a period of flowering concentrated in the dry season [8, 77-78] or during the transition from the dry to the wet season [54, 79-

80]. But outside the Neotropics, episodic reproduction occurs in most pioneer species in Diptercarpaceae forests where nearly all trees, pioneers as well as mature forest species, exhibit synchronized, supra-annual fruiting [6].

Two community trends characterized the relationship between fruiting and flowering among the 13 pioneers of the Central Amazon. First, the degree of continuity in flowering was matched closely by the degree of continuity in fruiting: continuous flowering species tended to exhibit continuous fruiting, seasonal flowering was associated with seasonal fruiting, and supra-annual flowering with supra-annual fruiting. Fruiting in a few species appeared a bit less continuous than flowering, for example*, Bellucia imperialis, Vismia cayennensis,* and *Guatteria*, but for the most part, fruiting continuity was parallel to flowering continuity. Second, the season of fruiting tended to occur shortly after the season of flowering with some overlap. This pattern was evident for individual species (Fig.3 and Fig. 4) and for the pioneer community as a whole (Fig. 2). While this pattern is intuitive from a developmental standpoint, the time from mean flowering date to mean fruiting date varied inexplicably from 1-6 months among species. A quick review of Table 2 reveals that with the exception of *Isertia*, the seven least seasonal species, *Bellucia grossularioides* through *Cecropia sciadophylla*, exhibited flowering to fruiting mean dates of 1 or 2 months, whereas the five most seasonal species posted 3 or 4 months between mean flowering and mean fruiting (Fig. 5). Perhaps greater seasonality in reproduction puts added stress on plant resources resulting in a longer delay from mean flowering to mean fruiting.

In general, pioneers in tropical wet forest have been assumed to reproduce continuously throughout their lives [81]. In our study, continuous flowering and fruiting characterized just less than half of the 13 species, and reproductive activity varied widely from continuous to supra-annual. Classifying many of the species as continuous or annual seasonal was somewhat arbitrary because the 12 species that flowered and fruited every year seemed to represent a continuum from continuous reproduction to highly seasonal, annual reproduction. Excluding our one supra-annual species, we have divided our species into continuous or annual seasonal, based solely on a statistical test. However, the "r" value of the mean vector for flowering or for fruiting clearly showed continuous variation across the twelve species, thereby suggesting that our reproductive classes are not discrete (Table 2).

In this context, each species' phenology represented a unique utilization of time for flowering and fruiting, sometimes varying from year to year, but mostly exhibiting a relatively unique species-specific pattern that repeated consistently across years for the four years of this study (Fig. 3, Fig. 4). Thus, their floral and fruit resources were available year round to support and maintain their pollinators and dispersal agents in areas of secondary vegetation regardless of seasonality in precipitation. Such phenological continuity may be adaptive for pioneer tree species that rely on birds, bats, and monkeys for effective dispersal [82].

Circular statistics have been employed in several recent tropical phenological studies [6, 83]. However, vector lengths in circular coordinates confound the incidence of flowering with the regularity of flowering [7]. Consequently, studies that have used such statistics also graphically depict their phenologies in X-Y coordinates, as we have done here.

Even without statistics, it is clear graphically that all 13 pioneer species reproduced regularly (*sensu* Newstrom et al. [51]), 12 of them annually and one biennially. This is in sharp contrast to the 48 species in the same floristic region of French Guiana where only 26 reproduced annually, 11 irregularly and 11 with a mast fruiting pattern [84]. However, there was no overlap in species studied with our study, because Norden et al. [84] specifically excluded small-seeded species. In this comparison, our pioneers, relative to larger seeded, mature forest trees, seem to fit the original hypotheses of Swaine and Whitmore [2] and Whitmore [81].

There are two disparities in our results and other studies of the same species. *G. glabra* showed continuous flowering and fruiting in the secondary growth areas of our study, but as a canopy tree in the mature forest, it flowered from April to August and fruited from June to October [9]. This latter pattern was also observed for eight adults in a nearby mature forest fragment during our study (Bentos, unpublished data). The restricted, seasonal reproduction, observed in mature forest, implies different phenologies for *G. glabra* trees of different ages or perhaps different light regimes. Trees in mature forest, as components of the canopy, receive direct light only a few hours at midday, whereas the secondary growth trees monitored in our study were in open areas with crowns exposed to full sunlight for most of the day [64, 85]. Another species, *C. lanjouwensis*, showed different phenologies in mature forest versus secondary growth. In the latter, it reproduced every other year, but larger trees in mature forest exhibited annual reproduction in the Ducke Reserve about 80 km from our BDFFP study sites [8].

Although the majority of the species in our study showed a peak of flowering in the transition from the dry to the wet season and of fruiting in the wet season, it is impossible, without experimentation, to determine the path of factors cueing reproductive events. In this context, a number of studies have shown that rainfall patterns are associated with seasonal cycles of growth, leafing, and flowering for a number of tropical species [35-38, 86-87]. Other studies have shown a correlation between changes in temperature and phenological events in tropical plants [24, 26, 53, 88-91]. However, when phenology is correlated with temperature and rainfall, there may be other causative factors that co-vary with these weather variables that provide the direct cue for phenological events. Changes in photoperiod, even in the tropics, have been shown to cue flowering in some species [24, 26, 28, 29, 91]. Also, some species appear to have endogenous rhythms of growth and reproduction; for example, *C. sciadophylla* shows a high periodicity in flowering and branching, with inflorescences at every 25 nodes, and stages of branches spaced by a multiple of 25 nodes [92].

Phyllogeny may also play a role in determining reproductive phenology. Our study included three pairs of congeners: *Bellucia imperialis* and *B. grossularioides*, *Vismia cayennensis* and *V. japurensis*, and *Cecropia sciadophylla* and *C. purpurascens*. These congeners are near each other in Table 2, indicating that they tend to share a common degree of flowering seasonality ("r" values). However, these congeners show different mean flowering dates, perhaps as a result of sharing pollinators. Related species usually have similar floral morphologies and consequently may share the same pollinators [31, 93]; through asynchrony in flowering, congeners can reduce competition for shared pollinators as well as reduce interspecific pollinations. Staggered flowering in some guilds has been attributed to competition for pollinators [31, 94-95] although not without controversy [96].

Phyllogeny may also determine to some degree the age and size of first reproduction. A quick perusal of minimum diameter for flowering (Table 1) shows that congeners start reproduction at similar diameters, more similar than unrelated taxa. Pioneers in tropical wet forests have been hypothesized to begin reproduction at an early age [2, 81]. Our data on minimum size (not age) seem to confirm this pattern for the Amazon's most common colonizing genera, *Cecropia* and *Vismia*, as they were reproductive by 5 cm DBH. Given that species in these genera generally grow quickly, it is safe to assume that the onset of reproduction occurs within several years after colonization [19]. However, eight of the other nine pioneers were not reproductive at 5 cm DBH, exhibiting a minimum DBH of 7.8-15.7 cm for flowering. Such divergences among colonizing species have been reported in other tropical forests such as the 11 species of *Macaranga* studied by Davies and Ashton [6].

Fig. 5. Reproductive structures for two continuous flowering species, (a) *Bellucia grossularioides* and (b) *Guatteria olivacea*, and two seasonally flowering species, (c) *Cecropia sciadophylla* and (d) *Laetia procera*.

## Implications for conservation

The Amazon Basin is the most extensive tropical rainforest on the globe. It presents both the greatest challenge and the greatest opportunity for biological conservation. Despite the proposal of a variety of models of development in the last century, deforestation in the Amazon is unfolding along predictable patterns that have characterized anthropogenic colonization and forest conversion in the Neotropics [97]. How much of the original forest will be conserved is unknown, but what is conserved will in the 21st century become fragments of mature forest in a matrix of anthropogenic activities and secondary vegetation, both dominated by pioneer tree species.

In this landscape, pioneer tree species will play three quintessential functions. First, as the critical first elements in the colonization of clearcuts and abandoned agriculture, they determine, together with landscape history, the rates of change and trajectories of secondary successions [19, 98]. Second, during succession, pioneer trees play critical community and ecosystem functions–

providing resources for pollinators and seed dispersers, building soil structure, recycling nutrients, and accumulating carbon stocks [99-100]. Third, the future of fragments of mature forest appears to be increasingly dependent on the quality of the matrix or surrounding secondary vegetation [101-103].

In this context, pioneer trees and their life-history traits, especially reproductive characteristics, become tools in the hands of land managers and conservationists. For example, it is now clearly established that the ability of *Vismia* species to spread vegetatively following fire in Amazon pastures changes the course of woody plant succession after ranches are abandoned [19, 20, 66]. Here, for the BDFFP reserves in the Central Amazon, we have documented the reproductive phenology of the 13 most abundant pioneer trees. Relative to tree species in mature forests of the Amazon[84], our group of pioneers tends to conform to the generalization [2, 81] that pioneers reproduce regularly throughout the year every year. However, among our pioneer species, there is considerable variability in reproductive phenology, with less than half actually showing this regular, continuous, annual reproduction presumed to characterize pioneers. Therefore, land managers and conservationists must choose carefully when developing management plans to re-forest disturbed areas with pioneer species. Those species with continuous reproduction, starting at small diameters, may produce the most rapid cover. Those dispersed by bats and birds are likely to be spread more widely than those dispersed by primates or terrestrial mammals. Finally, a mix of bird- and bat-dispersed species is likely to facilitate recruitment of mature forest species also dispersed by birds and bats and will provide a highly diverse seed rain into secondary forest.

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