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Annual cycles are the most common reproductive strategy in African tropical tree communities

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ABSTRACT

We present the first cross-continental comparison of the flowering and fruiting phenology of tropical forests across Africa. Flowering events of 5446 trees from 196 species across 12 sites and fruiting events of 4595 trees from 191 species across 11 sites were monitored over periods of 6 to 29 years and analyzed to describe phenology at the continental level. To study phenology, we used Fourier analysis to identify the dominant cycles of flowering and fruiting for each individual tree and we identified the time of year African trees bloom and bear fruit and their relationship to local seasonality. Reproductive strategies were diverse, and no single regular cycle was found in >50% of individuals across all 12 sites. Additionally, we found annual flowering and fruiting cycles to be the most common. Sub-annual cycles were the next most common for flowering, whereas supra-annual patterns were the next most common for fruiting. We also identify variation in different subsets of species, with species exhibiting mainly annual cycles most common in West and West Central African tropical forests, while more species at sites in East Central and East African forests showed cycles ranging from sub-annual to supra-annual. Despite many trees showing strong seasonality, at most sites some flowering and fruiting occurred all year round. Environmental factors with annual cycles are likely to be important drivers of seasonal periodicity in trees across Africa, but proximate triggers are unlikely to be constant across the continent.

Key words: Africa; annual cycles; flowers; fruits; phenology; seasonality; tropical forest.

Plant phenology, the timing of cyclical biological events (phenophases) such as leafing, flowering, and fruiting, is essential for the reproductive success of plants and equally important for animals that rely on plant resources to survive and reproduce (van Schaik *et al.* 1993, Sakai 2001). Phenology is well studied in northern, temperate systems (Visser & Both 2005), and changes in phenology associated with climate warming are widespread (Parmesan & Yohe 2003). However, the phenology of tropical plants is poorly understood, due to both the paucity of long-term datasets and the complexity of individual patterns (Gentry 1974, Hudson & Keatley 2010). Ultimately, if we are to understand how phenology is changing in the tropics, it is vitally important to establish how canopy-level patterns emerge from variation at the levels of species and communities.

Globally, tropical forests are characterized by an exceptionally high diversity of plant species, which can flower or fruit at any time of the year, often with very different patterns to other species within the same forest, including closely related taxa (Bawa *et al.* 2003, Zhou *et al.* 2014). Flowering and fruiting events in tropical forests vary from complete intraspecific synchrony to extreme asynchrony and from constant activity to recurrent short pulses (van Schaik *et al.* 1993). Depending on the environmental conditions, species, individual tree characteristics, location, and sometimes year, different phenophases occur at different times of the year, in different seasons, and vary in their frequencies and duration (Sakai *et al.* 1999, Pau *et al.* 2013, Bush *et al.* 2017).

To produce leaves, flowers, or fruits, an adult tree needs to accumulate sufficient nutritional resource before a phenophase onset can be triggered (Opler *et al.* 1976). Consequently, weather conditions that could trigger phenophase onset cannot do so if the tree has not first acquired sufficient resources to enable it to respond (Bullock & Solis-Magallanes 1990). Fruiting events also do not necessarily always follow flowering, as flowers may not be pollinated, flowers may be damaged by weather and herbivores, or trees may abort unripe fruits (Stephenson 1981). These factors make the study of phenological responses in relation to climate extremely challenging. Large and long-term datasets are therefore required to study general phenological patterns, and this is especially needed to offset the high heterogeneity of individual tree responses.

Regular patterns in phenophase expression can be a first indicator of the factors that drive and mediate plant responses. Analysis of both cycle length and timing of regular patterns in phenology at annual (including supra-annual and sub-annual variants) and seasonal scales is a first step to elucidating potential environmental triggers for various phenophases. In tropical forests, climate is not as seasonally restrictive for plant growth as in temperate areas, with the exceptions of dry forests, which have little or no rainfall for months. Seasonality in the tropics is dominated by the inter-tropical convergence zone (ITCZ), a band of warm air, which carries precipitation north and south over the equator in annual cycles (National Weather Service 2010), but regular seasonal differences in rainfall and temperature are relatively small for the majority of forests (van Schaik *et al.* 1993).

Asian and South American studies dominate our current knowledge of tropical phenology (Sakai 2001, Chambers *et al.* 2013, Morellato *et al.* 2013, Mendoza *et al.* 2017). In these regions, phenology has been described in terms of timing, duration, synchronicity, and dominant cycles (McEwan & McCarthy 2005). In Southeast Asia and South America, the highly variable phenological patterns of trees can be triggered by various cues, including sudden drops in solar radiation, plant moisture availability, heavy rain, or increased temperatures (Corlett & Lafrankie 1998, Sakai *et al.* 1999, Butt *et al.* 2015,). Compared to Asian and Neotropical forests, tropical forests in Africa have been little studied in terms of phenology, and this is mainly because of the relative lack of long-term datasets. As a stark comparison, a recent review of Neotropical phenological studies compiled data from 218 phenological study sites, with 10 sites yielding information from more than a decade (Mendoza *et al.* 2017). In contrast, our efforts to analyze phenological patterns across tropical Africa produced data from just 17 sites, of which only nine have data from more than a decade (Plumptre 2012, this study).

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Despite the shortcomings of scant long-term phenological datasets from tropical Africa, what we do know from the few African forests (East and West Africa) that have been previously studied in detail is that (1) flowering and fruiting frequencies vary from sub-annual to supra-annual (Chapman *et al.* 1999, Polansky & Boesch 2013, Janmaat *et al.* 2016, Bush *et al.* 2017) and (2) annual flowering cycles were found to be the most common. These important findings from less than a handful of studies representing a narrow range of tropical Africa beckoned for a more in-depth analysis across the continent. In an effort to undertake initial steps toward describing continental patterns in phenological responses and defining likely environmental cues for phenological behavior in African forests, we here (1) analyze cycles observed in phenophases at different sites and (2) examine the site-based relationships between phenophases and seasonal weather cycles that can reliably be extracted from global datasets.

Understanding phenology in African forests has become a fundamental issue in tropical forest ecology and conservation of trees and inter-dependent fauna whose survival is threatened by climate change and other anthropogenic pressures such as logging and hunting (Butt *et al.* 2015). We therefore consider this continental-wide analysis as a vital step toward understanding and elucidating phenological patterns of African forest tree species. As such, this study provides a first overview of variability in cycle profiles within and between African sites. It allows initial comparisons between the general characteristics of phenological profiles from African forests with those observed on other continents or outside the tropics. Furthermore, this study lays the foundation for future analyses of the climatic conditions that may be driving phenological responses in flowering and fruiting across different African sites. We use a Fourier analysis of trees from 12 long-term studies in tropical forests to examine the dominant pattern of flowering and fruiting cycles at each site and compare cycle profiles across the African continent. We also explore the seasonal phase of flowering and fruiting events of individual trees at each site.

METHODS

DATA COLLECTION.—We assembled data from 12 long-term research sites across East, Central, and West Africa (Fig. 1), including montane, sub-montane, semi-deciduous, evergreen, and swamp forests (Table 1). With the exception of M'Baïki, which was in a conservation area within a logging concession, all forest

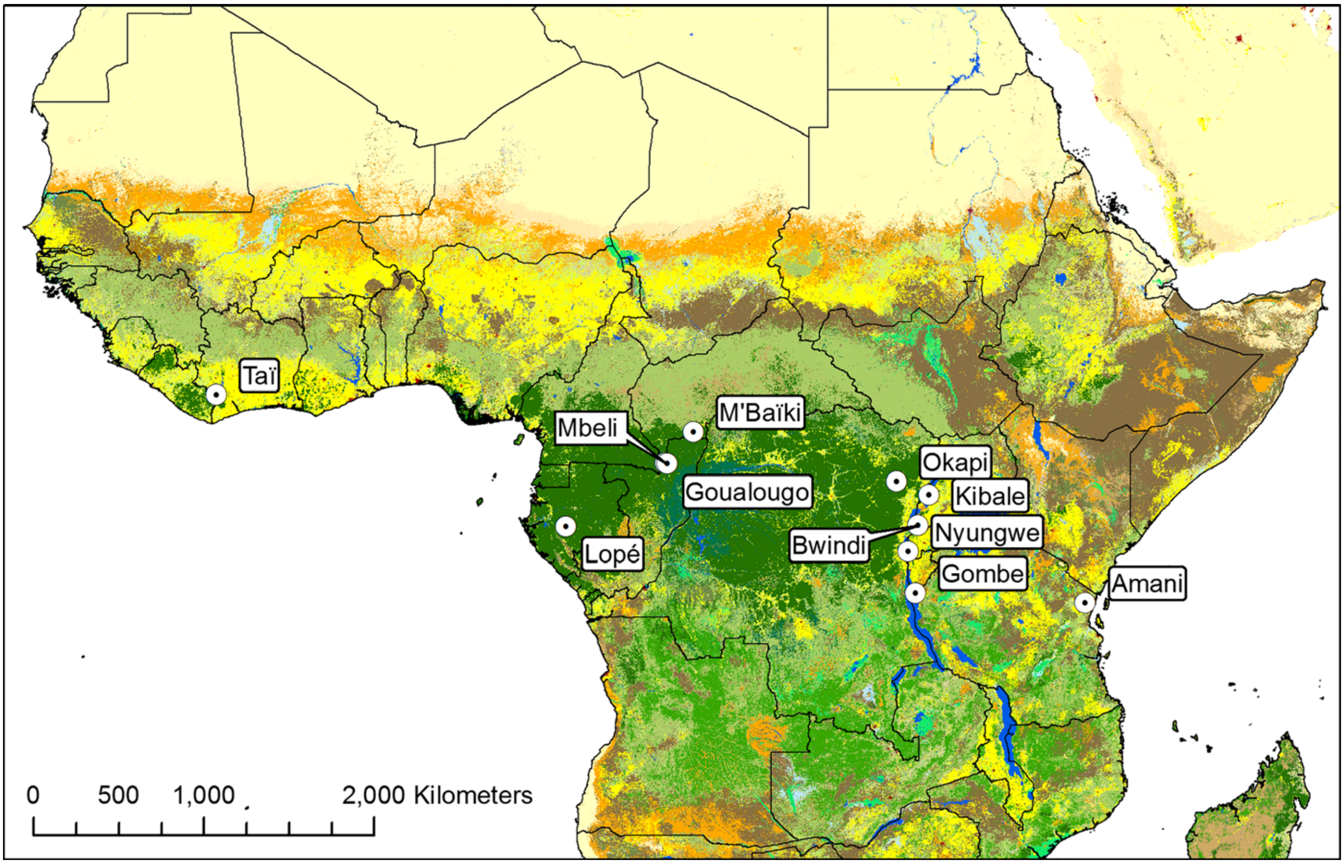

FIGURE 1. Geographic position of the 12 long-term, cross-continental phenological studies in Africa. Okapi Wildlife Reserve is represented by two sites: Okapi Lenda and Edoro. Due to the scale of the map, dots for Goualougo and Mbeli overlap, as do the dots for Bwindi and Nyungwe. Colors indicate spatial variation in land cover on a spectrum of high (green)-to-low (orange) cover (data downloaded from ESA at 5° × 5° resolution; Arino *et al.* 2009).

TABLE 1. *Characteristics of the 12 African study sites, including country, geographic coordinates, and monitoring period for flowering and fruiting phenology of tropical trees. Sites are organized from east to west. Latitude and longitude are expressed in decimal degrees.*

	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean altitude	Mean time series length for flower	Mean time series length for fruit
1	Amani Nature Reserve	Tanzania	−5.13	38.62	7 (2006–2012)	Moist sub-montane forest	950 m	78 (SD = 0)	78 (SD = 0)
2	Kibale Forest National Park	Uganda	0.56	30.36	15 (1998–2012)	Moist sub-montane forest	1500 m	148 (SD = 23.7)	142 (SD = 27.9)
3	Okapi Wildlife Reserve Lenda site	Democratic Republic of Congo	1.26	28.64	20 (1993–2012)	Humid mixed evergreen forest	750 m	OL: 200 (SD = 53.3)	OL: 200.9 (SD = 53.1)
4	Okapi Wildlife ReserveEdoro sites	Democratic Republic of Congo	1.26	28.64	20 (1993–2012)	Humid mixed evergreen forest	750 m	152 (SD = 57.9)	No data
5	Bwindi Impenetrable National Park	Uganda	−1.05	29.77	8 (2005–2012)	Montane forests	2240 m	93 (SD = 5.9)	93 (SD = 7.4)
6	Nyungwe Forest National Park	Rwanda	−2.43	29.26	14 (1996–2009)	Montane forest	2260 m	150 (SD = 15.3)	184 (SD = 21.6)
7	Gombe National Park	Tanzania	−4.61	29.64	14 (1998–2006)	Evergreen riverine forest, deciduous woodland, and grassland	1000 m	98 (SD = 5.4)	97 (SD = 5.5)
8	M'Baïki forest	Central African Republic	3.90	17.90	8 (2005–2012)	Semi-deciduous tropical forest	560 m	82 (SD = 0.9)	81 (SD = 0.4)
9	Goualougo Triangle Nouabalé-Ndoki National Park	Republic of Congo	2.21	16.52	6 (2007–2012)	Semi-deciduous rain forest	300 m	69 (SD = 2.7)	70 (SD = 2.1)
10	Mbeli Bai Nouabalé-Ndoki National Park	Republic of Congo	2.26	16.41	13 (2004–2016)	Semi-deciduous rain forest	300 m	134 (SD = 22.8)	140 (SD = 13.2)
11	Lopé National Park	Gabon	−1.09	11.16	20 (1986–2014)	Semi-evergreen, tropical lowland rain forest	300 m	237 (SD = 91.1)	236 (SD = 90.5)
12	Taï National Park	Côte d'Ivoire	5.84	−7.31	15 (1997–2011)	Diverse moist evergreen and semi-evergreen forest	80 m	68 (SD = 4.1)	68 (4.1) SD = 4.1

FL, flowering; RF, fruiting; SD, standard deviation.

Sources: Amani Nature Reserve, Tanzania—Henry Ndangalasi and Norbert Cordeiro; Gombe Stream National Park, Tanzania—Ian Gilby, Anne Pusey, Michael Wilson, and Baraka Gilagiza; Nyungwe National Park, Rwanda—Felix Mulindahabi; Bwindi Impenetrable National Park, Uganda—Badru Mugerwa, Frederick Ssali, Douglas Sheil, and Martha Robbins; Kibale National Park, Uganda—Colin Chapman; Okapi Wildlife Reserve, Democratic Republic of Congo—Flory Bujo, Corneille Ewango, and Terese Hart; Lopé Reserve, Gabon—Kate Abernethy, Emma Bush, Edmond Dimoto, Jean-Thoussaint Dikangadissi, Kath Jeffery, Caroline Tutin, and Lee White; Mbeli Bai, Nouabalé-Ndoki National Park, Republic of Congo—Mireille Breuer-Ndoundou Hockemba and Thomas Breuer; M'Baïki, Central African Republic—Adeline Fayolle; Taï National Park, Ivory Coast—Christophe Boesch and Leo Polansky; Goualougo, Republic of Congo—Sydney Ndolo, Dave Morgan, and Crickette Sanz.

sites were located within protected areas. Site elevation and total protected area around the study trees varied from 80 to 3000 m and from 35 km^2 to approximately 13,000 km^2, respectively. Each site experiences two main seasons, dry and wet, each present once or twice a year, depending on the site location. Average minimum and maximum monthly temperatures were between 12 and 30°C, with maximum rainfall ranging between 200 mm and 700 mm per month (Table 2). Data collection of flowering and fruiting events (data for ripe fruit only are used in these analyses) at each site was carried out monthly and was accomplished by the investigators and trained field assistants. Each tree was visually monitored for the presence/absence of flowers or ripe fruits. In some sites, the phenophase response was quantified, but as different scoring methods were used at different sites, we restricted our analyses to presence/absence. Monitored individuals were originally selected based on different research questions at each site, and thus, most sites represent a non-random subset of the total forest coverage and species diversity (further information on species diversity in Table S1). One site (M'Baïki) selected species important in the timber trade, but with the exception of Amani in Tanzania where phenological transects were randomly located, all other sites preferentially sampled species producing fleshy fruits, as original research questions focused on resource availability for large mammals, mainly primates or elephants. Although the sample at any site is not limited to fleshy fruit-producing species and includes other traits, such as abiotically dispersed species, the systematic selection for fleshy fruits means that our total sample is likely to overrepresent this trait at a community level.

DATA PREPARATION.—Fourier analysis requires continuous regular data. However, due to the logistical challenges of field data collection, including civil unrest in some regions, there are occasional gaps in the data we have available for individual time series. If gaps were shorter than three months, we interpolated the missing data using a linear estimator. If gaps were longer than three months, we split the data at the gap. Bush *et al.* (2017) show that time series length is a significant predictor of identifying cyclic activity in phenological data. To account for this, we only included trees with time series longer than 60 consecutive months after linear interpolation, with a minimum of 10 individuals for each species. We also excluded trees that died or never flowered or fruited.

TABLE 2. *Monthly minimum and maximum temperature and precipitation values at each of the 12 African sites taken from CHIRPS.*

	Minimum precipitation (mm)	Maximum precipitation (mm)	Minimum temperature (°C)	Maximum temperature (°C)
Amani	49	341	18	33
Kibale	45	209	15	30
Okapi	57	221	17	31
Bwindi	21	161	9	23
Nyungwe	13	203	11	24
Gombe	1	212	15	30
M'Baïki	29	232	17	34
Goualougo	47	224	18	32
Mbeli	46	226	18	31
Lope	0	349	18	30
Taï	10	380	19	34

FOURIER ANALYSIS OF INDIVIDUAL VARIATION.—To assess the major cyclic patterns for flowering and fruiting at the sites, we used Fourier analysis to identify dominant cycles per individual tree. Fourier is a spectral analysis method used to decompose a time series into a sum of sine waves of different frequencies and is a robust analysis for determining plants' dominant cycles (Platt & Denman 1975). Bush *et al.* (2017) showed how it could be used to statistically assess the cycle length and predictability of phenological activity in tropical trees at the individual level.

We calculated the Fourier spectrum for each individual tree using the *R* function spectrum from the *R* base package 'stats' (R Core Team 2015). Following the guidelines in Bush *et al.* (2017), we smoothed the raw spectrum using a Daniell kernel (a moving average smoother) with varying spans depending on the time series length to give a bandwidth of 0.1. The 0.1 bandwidth represents one-tenth of the length of the available time series of each tree and gives sufficient resolution in the spectral estimate to assess dominant cycles while suppressing irrelevant fine-scale structure (Bush *et al.* 2017).

We assessed the smoothed spectral estimate for each individual tree and extracted the cycle frequency with the highest power, representing the strongest cycle in the data. Bush *et al.* (2017) warn that time series with little cyclic activity can sometimes produce Fourier transforms with high power in non-relevant low frequencies (*e.g.,* the full length of the time series). To account for this, we screened out individuals where the dominant cycle identified from the spectrum was greater than half the length of the time series (resulting in exclusion of 9% of trees for flowering and 13% of trees for fruiting). Although 9% of individuals that showed non-cyclical flowering were excluded from our analyses, the bias away from shorter cycles is likely to be minimal, as individuals only flowered once or twice during the whole study period at the site, rather than continuously.

These data exclusions following Fourier analysis resulted in final samples of 5446 individuals (196 species) for the flowering analysis and 4595 individuals (191 species) for the fruiting analysis. Prior to the application of the minimum 60-month threshold, numbers were 11,211 individuals (469 unique species) for the flowering analysis and 10,517 individuals (453 unique species) for the fruiting analysis (Table 3). Individual time series ranged from 60 to 339 months long (median = 199.5 months) with site differences in data length.

TESTING FOR DIFFERENCES IN CYCLIC ACTIVITY AMONG SITES.—We used the Fourier-derived estimates for dominant cycle length for each individual tree to determine the differences among sites. To describe the most common flowering and fruiting cycles found at each site and to compare among sites, we plotted the distribution of dominant cycles at each site using violin plots. We treated flowering and fruiting events separately and not as a dependent process. Hence, it is worth noting that not all individuals considered in the flowering analysis were shared in the fruiting analysis. For 851 trees, fruiting was more erratic than flowering and these individuals were excluded from analysis of fruiting, but retained in the flowering analysis. This also led to five species from the

TABLE 3. *Number of individual trees and species at each African site in the original and Fourier datasets. A total number of species do not match the ones presented in the text because in this summary we considered all species, including the ones present at multiple sites (therefore species may appear more than once).*

	Original sample		Detected cycle sample		Characteristics of detected cycles					
					Sub-annual		Annual		Supra-annual	
Site (Southeast to northwest)	N Species	N trees	N Species	N trees	N Species	N trees	N Species	N trees	N Species	N trees
Amani	70	935	14	410	14	252	7	23	14	135
Gombe	13	277	11	192	7	13	10	146	7	33
Nyungwe	74	1000	45	794	35	187	43	326	42	245
Bwindi	33	319	8	80	6	40	6	18	8	22
Kibale	75	311	10	85	8	29	7	13	10	43
Okapi Lenda	49	570	27	354	17	60	27	251	19	43
Okapi Edoro	61	850	30	439	27	111	24	140	29	188
M’Baïki	30	769	6	155	6	55	5	36	6	64
Goualougo	28	284	3	43	2	19	3	20	1	4
Mbeli	44	438	12	112	10	24	11	55	11	33
Lope	84	940	48	733	33	167	45	478	30	88
Taï	108	1000	44	2049	43	663	43	973	39	413
Total	669	7693	258	5446	208	1620	231	2479	216	1311

flowering analysis to being excluded from the fruiting analysis as <10 individuals showed regular fruiting.

COMMUNITY-LEVEL SEASONALITY.—We assessed the seasonal rainfall pattern at each site by calculating a mean monthly rainfall value (Table 3) over the maximum phenological data collection period (28 years starting in 1986 and finishing in 2014) using rainfall data from the Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) dataset (Funk *et al.* 2015: http://chg.geog.ucsb.edu/data/chirps/). This dataset combines ground-based monitoring with satellite-derived rainfall data starting in 1986 and finishing in 2014. For the two sites (Lopé and Mbeli) for which rainfall data were available locally, the empirically observed monthly time series data were poorly matched in the CHIRPS dataset. However, seasonal patterns (average monthly rainfall across all years) were strongly correlated ($r > 0.9$ observed at Lopé and Mbeli sites) (data not shown). To standardize across sites, we defined the dry season as any months where rainfall was <60 mm (after van Schaik *et al.* 1993). We assessed canopy-level flowering and fruiting status for trees at each site, by calculating at each site the proportion of trees in the phenological sample flowering and fruiting within each month and year. To test for seasonality in flowering, fruiting and rainfall data, we used Rayleigh tests implemented in the R package circular (Agostinelli & Lund 2011) with the null hypothesis of uniformity (no seasonality) (Morellato *et al.* 2010). As the Rayleigh test can fail in the presence of strong and symmetric multimodality, we first visually inspected seasonal patterns to identify potential multimodality. We then used the function ‘Rayleigh.test’ from the R package ‘circular’ (Agostinelli & Lund 2011). At some sites (*e.g.,* Kibale and Amani), rainfall is strongly bimodal, but not symmetrical. Significant seasonality could be identified by the Rayleigh test in such circumstances, although the angle identified is likely to be meaningless (Morellato *et al.* 2010).

RESULTS

SITE-LEVEL FLOWERING AND FRUITING CYCLES.—Across 12 sites and 5446 individuals (196 species) for which all data quality control conditions were met, we found 46% of all individual trees showed dominant annual flowering cycles (between 11 and 13 months), 29% of individuals showed sub-annual cycles (typically between 5 and 7 months), and supra-annual cycles (above 13 months) were seen in 25% of trees, with 24-month cycles being the most common.

The overall prevalence of annual cycles in individuals was reflected at the site level in Gombe, Nyungwe, Bwindi, Okapi Lenda, Okapi Edoro, Goualougo, Mbeli, Lopé, and Taï. Elsewhere, annual cycles were not most common, with M’Baïki showing mainly supra-annual cycles, Kibale showing a very diverse profile with sub-annual, annual, and a variety of mainly supra-annual cycles, and Amani showing mainly sub-annual cycles (Fig. 2). Remarkably, despite being only 35 km apart and in the same forest type, Okapi Lenda and Edoro showed different dominant cycles with far greater diversity in cycle length in Okapi Lenda.

Across the 11 sites and 191 species (4595 individuals), 42% of individuals showed annual fruiting cycles. In contrast to the flowering analysis, supra-annual fruiting cycles were nearly as common as annual cycles (35% of individual trees), with the most frequent dominant fruiting cycle being 24 months. Sub-annual cycles were encountered only in 23% of individuals with the most common cycle being six months. At most sites, we found species with differing cycle lengths (Fig. 3). In sites in West

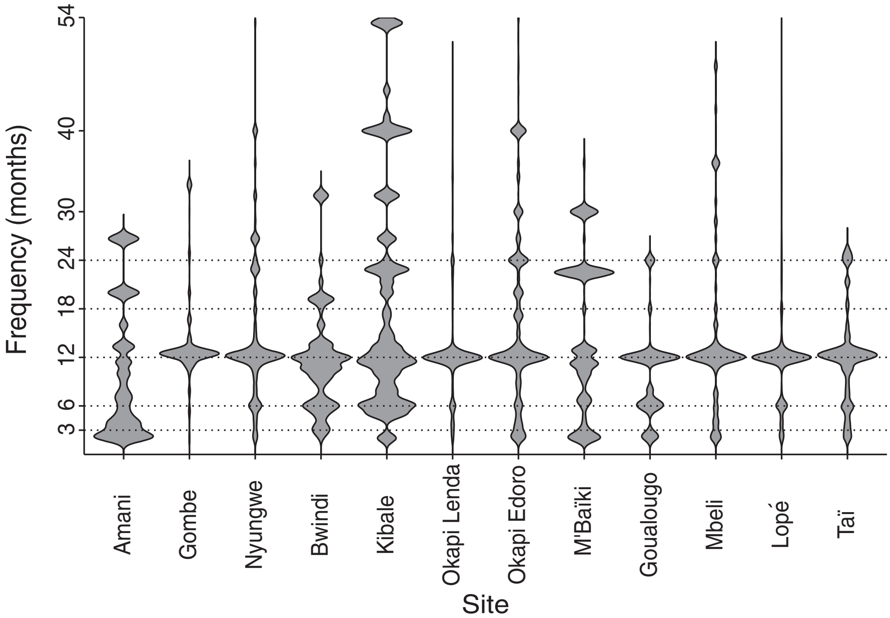

FIGURE 2. Violin plot showing the density of flowering frequency of all individual trees present at 12 African sites ordered from east to west. (Species present after Fourier analysis was applied for each site: Amani = 14, Gombe = 11, Nyungwe = 45, Bwindi = 8, Kibale = 10, Okapi Lenda = 27, Okapi Edoro = 30, M'Baïki = 6, Goualougo = 3, Mbeli = 12, Lopé 48, Taï = 44; Number of trees present at each site: Amani = 410, Gombe = 192, Nyungwe = 792, Bwindi = 80, Kibale = 85, Okapi Lenda = 354, Okapi Edoro = 439, M'Baïki = 155, Goualougo = 43, Mbeli = 112, Lopé = 733, and Taï = 2049).

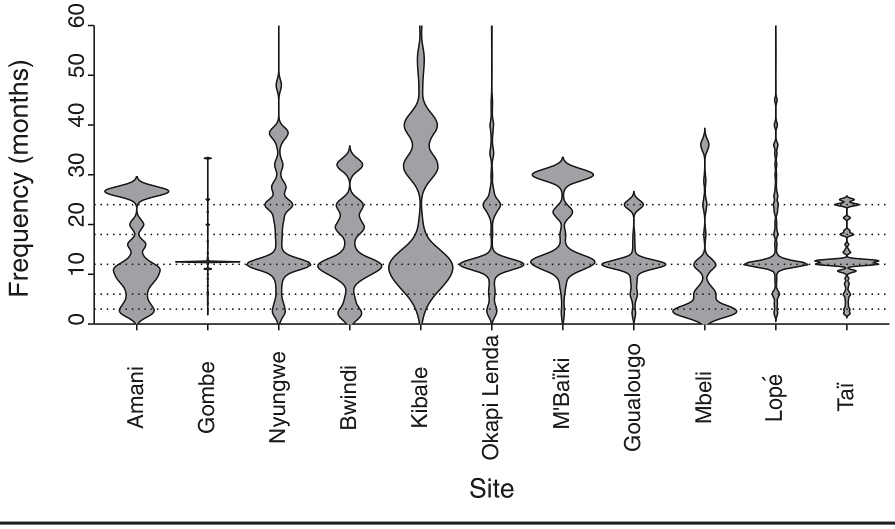

FIGURE 3. Violin plot showing the density of fruiting frequency of all individual trees present at each African site. (Species present after Fourier analysis was applied for each site: Amani = 11, Gombe = 10, Nyungwe = 49, Bwindi = 7, Kibale = 7), Okapi Lenda = 20, M'Baïki = 6, Goualougo = 6, Mbeli = 9, Lopé = 48, Taï = 49; Number of trees present at each site: Amani = 321, Gombe = 165, Nyungwe = 842, Bwindi = 60, Kibale = 57, Okapi Lenda = 265, M'Baïki = 132, Goualougo = 64, Mbeli = 66, Lopé = 709, and Taï = 1914). Okapi Edoro was not included in the fruiting analysis because it did not pass the condition of the 60-month threshold.

and West Central Africa, we found that most trees recorded an annual fruiting cycle.

FLOWERING AND FRUITING SEASONALITY.—Due to considerable variation between individuals and both within and between species, flowering patterns at the community level at most sites showed weak seasonality (some trees flower during both wet and dry seasons) despite considerable seasonal differences in rainfall between sites (Figs 4, 5 and Table 5). Seasonality in flowering (flowering triggered by a certain environmental cue, such as heat or rainfall) was not observed in Amani, Kibale, Nyungwe, Bwindi, and Taï, while we detected significant flowering seasonality at the canopy level in the rest of sites (Fig. 4 and Table 5). Among the remaining seven sites, the strongest seasonal flowering patterns were encountered at Gombe, M'Baïki, Lope, Goualougo, Okapi Lenda, and Okapi Edoro sites (Fig. 5). All sites showed significant seasonality in rainfall (Table 4).

With regard to fruiting, we found constant fruit patterns a feature of several sites. Amani, Kibale, Nyungwe, and Bwindi were sites that exhibited no significant seasonality in flowering and also showed no statistically significant seasonality in fruiting patterns ($P > 0.01$, Table 5). However, although Lope showed strong significant seasonality in flowering, it did not show seasonality in fruiting (although the P value = 0.01). In contrast, Taï, which showed no seasonality in flowering, showed strong seasonality in fruiting. Most inter-month variation (the highest seasonality) in fruiting was found in Tai, Okapi Lenda, M'Baïki, and Gombe. For Amani, Nyungwe, M'Baïki, Mbeli, and Taï, peak fruiting occurred during the dry season. At Kibale, peak fruiting was at the transition from wet to dry seasons, and for the rest of the sites, peak fruiting occurred during the wet season (Fig. 5).

DISCUSSION

Using Fourier-based analysis, we effectively estimated flowering patterns for 5446 individual trees of 196 species and fruiting patterns for 4595 trees of 191 species, across 12 and 11 sites, respectively. This was performed both at the site level and among tropical forests spanning from West to East Africa. We found that across all sites, more trees flowered and fruited annually than supra- or sub-annually; however, sub-annual flowering cycles and supra-annual fruiting patterns were present at all sites and common in many. Although some sites had few individual trees reproducing annually, all sites had some annually reproductive trees, as expected from previous analyses of dominant reproductive cycles in Lopé (Bush *et al.* 2017) and Kibale (Chapman *et al.* 1999).

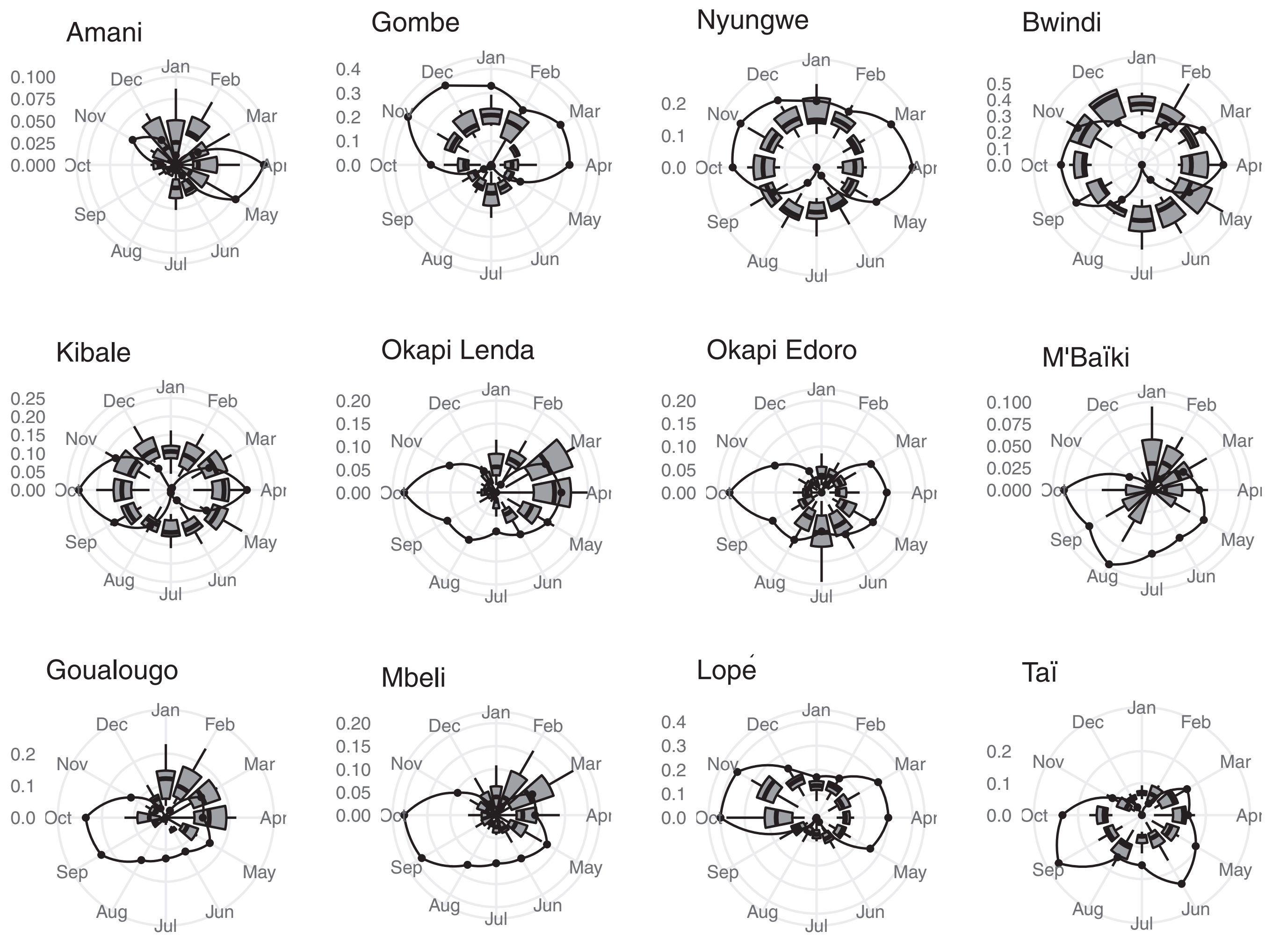

FIGURE 4. Flowering seasonality at 12 different sites in Africa. Black graph represents the rainfall for each month normalized to the rainfall of the wettest month. Circular plots indicate the proportion of individual trees flowering in each month for 12 sites. Sites are labeled above each circular plot.

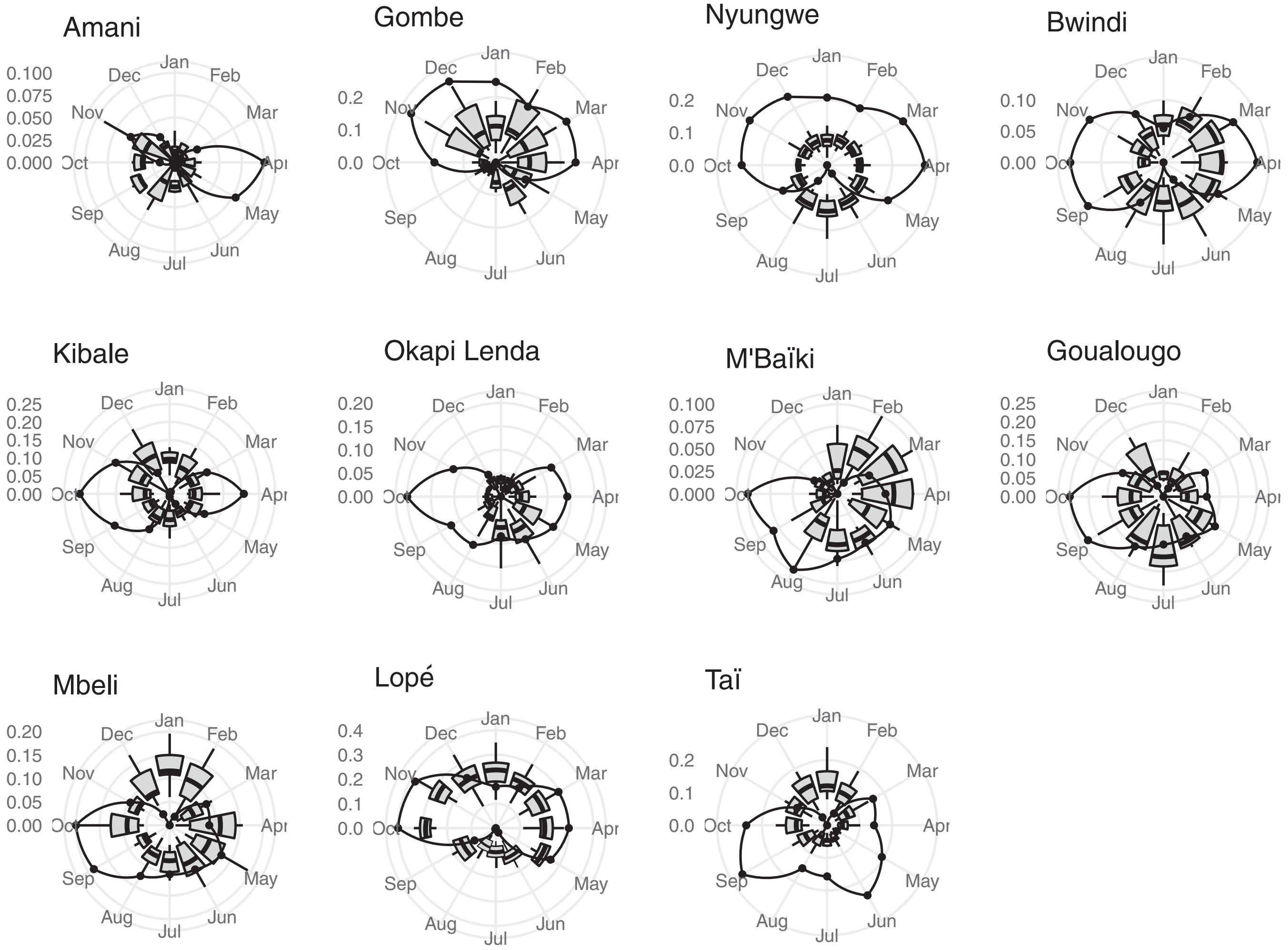

FIGURE 5. Fruiting seasonality at 11 sites in Africa. Black graph represents the rainfall for each month normalized to the rainfall of the wettest month. Circular plots show the proportion of individual trees flowering in each month for 11 sites. Sites are labeled above each circular plot. Okapi Edoro was not included in the fruiting analysis because it did not pass the condition of the 60-month threshold.

TABLE 4. *Rayleigh test of uniformity (Z) and* P *value for non-uniformity of monthly precipitation at 12 sites in tropical Africa. All sites show significant seasonality.*

Site	Z	*P* value
Amani	0.206	0
Kibale	0.113	0
Okapi	0.120	0
Bwindi	0.092	0
Nyungwe	0.243	0
Gombe	0.458	0
M'Baïki	0.312	0
Goualougo	0.190	0
Mbeli Bai	0.206	0
Lopé	0.078	0
Taï	0.288	0

Overall, 46% of trees showed annual flowering frequencies across all 12 sites. Our results contrast with those previously reported from tropical forests of Central and South America, as well as Southeast Asia, where, depending on the region, sub-annual and supra-annual frequencies have previously been reported as the most frequent strategies (Newstrom *et al.* 1994, Sakai 2001, McEwan & McCarthy 2005, Wright *et al.* 2005). However, more recent work in South America has now shown some sites where annual cycles in fruiting are dominant (Norden *et al.* 2007, Mendoza *et al.* 2018). Evolutionary histories and pressures driving flowering and fruiting are likely to be different in forests on different continents and, equally, even at a continental scale, may contrast greatly between West and East Africa (Slik *et al.* 2018). There is certainly room for further work on the evolution of cyclicity and current drivers of cyclicity on all continents before robust intercontinental comparisons can be made.

TABLE 5. *Rayleigh test of uniformity (Z) and* P *value of significance of deviation from uniformity.* P *values of* <0.01 *are considered significant.*

Site	Z	*P* value
Flowering		
Amani	0.248	0.039
Kibale	0.034	0.80
Okapi Edoro	0.238	0.001
Okapi Lenda	0.551	0.001
Bwindi	0.039	0.308
Nyungwe	0.117	0.02
Gombe	0.193	0.001
M'Baïki	0.448	0.001
Goualougo	0.294	0.001
Mbeli Bai	0.316	0.003
Lopé	0.275	0.001
Taï	0.057	0.389
Fruiting		
Amani	0.246	0.03
Kibale	0.105	0.210
Okapi Lenda	0.256	0.001
Bwindi	0.160	0.05
Nyungwe	0.181	0.012
Gombe	0.238	0.001
M'Baïki	0.182	0.009
Goualougo	0.201	0.001
Mbeli Bai	0.168	0.002
Lopé	0.104	0.010
Taï	0.304	0.001

Fruiting showed similar patterns to flowering, with 42% of trees at 11 sites showing annual cycles, also as previously reported for Africa (Chapman *et al.* 1999, Takenoshita *et al.* 2008, Bush *et al.* 2017). This result was not as strong as the annual flowering pattern, presumably because many flowering cycles do not result in the production of mature fruit. Our dataset shows that fruiting cycles are slightly more likely to be supra-annual than flowering cycles, which may be the result of resource deficiencies, stochastic weather events, flower or fruit predation, or disease, all playing a role in modifying annual cycles by preventing fruiting after a flowering event.

SITE-LEVEL FLOWERING AND FRUITING PATTERNS.—We assume that the prevalence of annual cycles suggests that a regular, external annual cycle, sometimes moderated by the resource base available to each individual, and additional extra-annual environmental variation, perhaps, such as the El Niño phenomenon (Chapman *et al.* 2018, Dunham *et al.* 2018), drive the observed phenological pattern in many trees. Annual phenological cycles have previously been reported to be initiated by annual cycles in environmental conditions such as day length, seasonal rainfall, and temperature (Borchert 1983, Pau *et al.* 2013). It is difficult to disentangle exactly which cues were responsible for triggering phenological events at our sites due to the lack of data on environmental conditions. Factors mediating the trees' ability to respond to an environmental cue, such as carbohydrate storage (Borchert 1983), or phosphorus accumulation (Corlett 2016), have not been measured at any of our sites. The lack of data on local weather at a sufficient level of precision (Maidment *et al.* 2015, Abernethy *et al.* 2016) is also problematic for robust definition of environmental cues in African sites. However, despite these limitations, we did find annual cycles in rainfall in most sites and consider it likely that annually cycling local environmental cues are important in driving African tree phenology across the continent. It is important to remember that although annual cycles were the most common patterns at most sites, annual cycles were not shown by a majority of trees: There were individuals at every site showing either sub- or super-annual cycles, and across the whole dataset, more trees showed non-annual than annual cycles. African forests show a high level of diversity in phenological behaviors both within and between species. Although there was no clear effect of forest type, longitude, latitude, or altitude on the phenological profile at a site, the more westerly sites showed stronger dominance of annual cycles than those in the west and south, and sites closest to the current edge of the rain forest extent showed the highest diversity in cyclic behavior.

Our results underscore the complexity and inter-individual variation in flowering and fruiting at the community level, previously reported at different sites in Africa (Tutin & Fernandez 1993, Plumptre 1995). In this analysis, a different set of species was monitored at each site. As species are not distributed at random among sites and tree selection criteria varied at different sites (see *Methods*), it is plausible that differences among sites are more reflective of differences in species selection than fundamental differences in geography. Unfortunately, we cannot estimate the degree of bias this generates *post-hoc*, but further research into functional or taxonomic group responses to environmental triggers may elucidate the potential effects of each. We saw variability in flowering and fruiting patterns among species within the same forest site, presumably associated with selection for responses to differing environmental drivers. This may be expected when different functional traits mediate the response to environmental drivers of phenological patterns: *for example,* different animal–plant relationships (Takenoshita *et al.* 2008), different modes of seed dispersal (*e.g.,* wind-dispersed seeds tend to ripen during drier periods and fleshy fruits in wetter ones: Chapman *et al.* 2005), or differences in endogenous factors mediating the response (which may reflect genetic differences: Staggemeier *et al.* 2015). Although our study is the first to present and compare the range of phenological profiles at tropical forest sites across Africa, the question of *why* predominant cycle length varies across the continent remains unanswered. Further analyses including factors such as climate change, rare weather events, soil types, interspecific interactions, genetic variation, forest history, and geographic position should be considered by researchers wishing to advance this discipline.

Flowering and fruiting seasonality.—As reported elsewhere in Africa (Chapman *et al.* 1999), we found that timing of flowering and fruiting between species was highly variable at most sites, such that at the canopy level, some individuals may always be found in flower or in fruit. Visually, Bwindi and Kibale showed the least seasonal flowering patterns (Fig. 4), but even here there may be some slightly bimodal seasonal patterns that cannot be detected by the Rayleigh test. We confirmed that for the majority of sites, flowering activity peaked at the beginning or during the middle of one of the two wet seasons (Anderson *et al.* 2005, Polansky & Boesch 2013). In five of our sites, peak fruiting occurred during the wet season (c.f. Sun *et al.* 1996), a pattern also common in South and Central America (Smythe 1970) and Asia (Medway 1972). However, in another five sites, peak fruiting occurred in the dry season, and for one site, fruiting peaked in the transition from wet to dry. There was no discernible pattern in the geographic distribution, seasonality, or rainfall characteristics of wet- vs. dry-season fruiting sites.

Phenological complementarity between plants and animals is crucial for ecosystem organization, process, and function (Cleland *et al.* 2007), and the importance of phenological events in understanding the ecology and evolution of species within their communities has been previously demonstrated (Chapman *et al.* 2005, Visser & Both 2005). Changes in plant phenology can lead to cascading effects across the entire ecosystem by causing phenological mismatches between the cycles followed by plants and the animals that rely on them (Newstrom *et al.* 1994, Sakai 2001, Morellato *et al.* 2016). Mismatches have already been observed in temperate regions where phenology has changed differently for animals and plant communities, due to recent rapid changes in climate (Brown *et al.* 2016). Morellato *et al.* (2016) and Mendoza *et al.* (2017) review the evidence and likelihood of such mismatches arising in Neotropical forests. Chapman *et al.* (2005), Polansky and Boesch (2013), Dunham *et al.* (2018), and Chapman *et al.* (2018) consider the consequences of mismatches in African forests. All conclude that primate foragers have developed behavioral patterns in response to the predictability of fruit resources and are likely to suffer population declines if fruit phenological cycles become less regular.

Concluding remarks.—Our study shows that annual cycling, as opposed to supra- or sub-annual cycling, is the most common flowering and fruiting strategy in African tree reproduction across the continent. However, both supra- and sub-annual strategies exist in every site alongside annually cycling trees, and non-annual patterns (of supra- and sub-annual combined) are common overall and at many individual sites. Seasonality at most sites covers two wet and two dry seasons, providing potential for environmental cues at a sub-annual cycle length, but we found relatively low frequencies of sub-annual cycling. Our results provide an important baseline from which future changes in seasonality, community phenological profiles, and individual or species average cycle length can be assessed. We show for the first time that there is considerable variation in the frequency of phenological cycle types at different tropical African sites and that there is some geographic patterning in the distribution of site-specific phenological cycle profiles, although trends are not strong.

With this study, we bring African data to bear in global comparisons of tropical forest behavior. We show similarities and differences in flower and fruit cycles between African, Asian, and Neotropical forests. We also show the complexity of observed phenological cycles within and among sites in Africa and the lack of explanatory power found in the currently available environmental data. In order for the environmental drivers of phenological patterns in Afrotropical forests to be more clearly understood, we make the following research recommendations: (1) Encourage the collection of more detailed and precise environmental data (weather, soils, nutrient flux, etc.) at phenological data collection sites; (2) assess and improve the potential of African climate models to provide interpolated climate data for specific sites; (3) resolve differences in observational methodologies such that inter-site comparisons become more robust; (4) expand data collection to include a more representative selection of tree species; and (5) increase the collection of functional trait data for the species targeted for phenological data collection. Furthermore, we encourage future work that addresses questions of variability within tree species. Finally, we note that although more work has been undertaken in Asian and Neotropical forests than in Africa to date, it seems likely that the application of new analytical methods such as those used here may identify previously overlooked patterns in these better known forests too.

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DATA AVAILABILITY

The summary data from this study is available via the WCS Data Archives website (https://doi.org/10.19121/2018.dse.dmx3404800000). Data for the Lopé site is stored at (DataSTORRE; http://hdl.handle.net/11667/103), under a 10-year open-access embargo. Access to embargoed data may be requested by contacting the relevant authors (see affiliations).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Species characteristics.*

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