

Latitudinal shift in the timing of flowering of tree species across tropical Africa: insights from field observations and herbarium collections

Research Article

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Abstract

Temporal and spatial patterns in flowering phenology were assessed for eight tropical African tree species. Specifically, the frequency and seasonality of flowering at seven sites in central Africa were determined using field data, graphical analysis and circular statistics. Additionally, spatial variation in the timing of flowering across species range was investigated using herbarium data, analysing the relative influence of latitude, longitude and timing of the dry season with a Bayesian circular generalized linear model. Annual flowering was found for 20 out of the 25 populations studied. For 21 populations located at the north of the climatic hinge flowering was occurring during the dry season. The analysis of herbarium collections revealed a significant shift in the timing of flowering with latitude for *E. suaveolens*, and with the timing of the dry season for *M. excelsa* (and to a lesser extent *L. alata*), with the coexistence of two flowering peaks near the equator where the distribution of monthly rainfall is bimodal. For the other species, none of latitude, longitude or timing of the dry season had an effect on the timing of flowering. Our study highlights the need to identify the drivers of the flowering phenology of economically important African tree species.

Introduction

Reproductive phenology, i.e. the timing of flowering and fruiting events, is a crucial element of the reproductive success of plants. Strong evidence of shifts in reproductive phenology in response to global warming has been reported worldwide and for a variety of organisms (Walther *et al.* 2002) including plant species in mid- and high northern latitudes (CaraDonna *et al.* 2014, Cleland *et al.* 2007, Rosenzweig *et al.* 2007, Zhang *et al.* 2015). In this regard it is important to identify the climatic factors that control and impact reproductive phenology.

In tropical forests, a great diversity of reproductive phenological patterns has been reported (Newstrom *et al.* 1994) ranging from continuous reproduction to more regular patterns (either annual or sub-annual) and irregular phenologies, with supra-annual patterns, and even massive, infrequent, yet synchronized masting events (Norden *et al.* 2007). In tropical Africa, annual phenologies have been found to be dominant for tree species in La Lopé, Gabon (Bush *et al.* 2017), in Luki, Democratic Republic of the Congo (Angoboy Ilondea *et al.* 2019), and across several sites from West, Central and East Africa (Adamescu *et al.* 2018). For species with relatively regular reproductive phenologies, a variety of climatic controlling factors have been identified. For instance, the seasonality of flowering was found to be correlated with seasonal changes in rainfall (Borchert *et al.* 2004), irradiance (Wright & Calderón 2018, Wright & van Schaik 1994), day length and temperature (Morellato *et al.* 2000), or temperature and relative humidity (Daïnou *et al.* 2012b). All of these studies were conducted in the Neotropics except for the study of Daïnou *et al.* (2012b) on *Milicia excelsa* in south-eastern Cameroon. As such, climatic factors controlling the flowering phenology of tropical African forest trees are still largely unidentified and are probably species-specific (as demonstrated in Panama; Wright & Calderón 2018), or associated with specific traits, such as seed size (Sun *et al.* 1996).

Rainfall seasonality is assumed to primarily control the reproductive phenology of tropical African forest tree species. Large-scale studies on the vegetative phenology of tropical African forests have revealed that the seasonality of canopy photosynthetic activity is correlated with the seasonality of rainfall (Gond *et al.* 2013, Guan *et al.* 2013). If rainfall seasonality primarily controls the reproductive phenology of tropical African forest tree species, we should expect a reverse phenology for populations located north versus south of the latitudinal area ($\sim 2^\circ\text{N}$) where rainfall seasonality reverses, i.e. the climatic hinge. The climatic hinge is also supposed to be an important discontinuity for both intra-specific genetic variation (Blatrix *et al.* 2017, Hardy *et al.* 2013) and plant communities (Gonmadje *et al.* 2012), even though the pattern is not always found (Fayolle *et al.* 2014). Wieringa (1999) showed the climatic hinge coincides with a strong disruption in the flowering pattern of *Tetraberlinia bifoliolata*.

Herbarium material provides an important source to investigate large-scale patterns in plant reproductive phenology and its putative correlation with seasonal climate variability (Davis *et al.* 2015, Willis *et al.* 2017). Herbarium specimens are mainly made from fertile material in order to improve its identification. Additionally, they are nearly always well labelled with information on collection date and locality. As a result, herbarium specimens contain valuable information on reproductive phenology. In the Neotropics, Borchert (1996) used herbarium collections to demonstrate that the flowering periodicity of 18 dry-forest tree species was correlated with the timing of the dry season. In addition, based on herbarium specimens, Zalamea *et al.* (2011) noticed that flowering phenology of *Cecropia* species across the Neotropics was strongly associated with seasonal variation in rainfall and temperature.

In this study we aimed to assess temporal patterns in flowering phenology and their spatial variation for eight tropical African tree species. The study species are of major importance as they belong to the most logged species in central Africa (Bayol *et al.* 2012), and they significantly contribute to forest regional above-ground biomass stocks (Bastin *et al.* 2015). For each species we specifically answered the following questions:

- (1) Is flowering seasonal and correlated to the seasonality of rainfall?
- (2) What is the relative importance of latitude, longitude and spatial variation in seasonality of rainfall in explaining the spatial variation in timing of flowering?

Study species

For the current study, eight tree species were selected: *Entandrophragma cylindricum* (Sprague) Sprague (Meliaceae), *Erythrophleum suaveolens* (Guill. & Perr.) Brenan (Leguminosae), *Lophira alata* Banks ex C.F.Gaertn. (Ochnaceae), *Mansonia altissima* (A.Chev.) A.Chev. (Malvaceae), *Milicia excelsa* (Welw.) C.C.Berg (Moraceae), *Pterocarpus soyauxii* Taub. (Leguminosae), *Terminalia superba* Engl. & Diels (Combretaceae) and *Triplochiton scleroxylon* K.Schum. (Malvaceae). These species are hermaphrodite (Réjou-Méchain & Cheptou 2015), large-statured canopy species, light-demanding, (briefly) deciduous, and wind-dispersed (Meunier *et al.* 2015), except for *M. excelsa* (animal dispersal, dioecious; Daïnou *et al.* 2012a) and *E. suaveolens* (unassisted and animal dispersal; Gorel *et al.* 2015). Except for *M. excelsa* which is wind-pollinated (Daïnou *et al.* 2012b), all other trees are insect-pollinated (*E. cylindricum*, Palla *et al.* 2002b; *L. alata*, Palla *et al.* 2002a) or probably

insect-pollinated species (Akinagbe *et al.* 2010, Demenou *et al.* 2018, Gorel *et al.* 2015, Palla & Louppe 2002). The extent of the spatial distribution of the species greatly varies among them. Hereafter we refer to the phytochoria defined by White (1983) to present species spatial distribution estimated from the RAINBIO database of tropical African vascular plants distributions (Dauby *et al.* 2016). Three species show a restricted distribution within the Guineo-Congolian regional centre of endemism, with *T. scleroxylon* and *M. altissima* occurring only in the northern hemisphere and *P. soyauxii* solely in central Africa. Three species widely spread over the Guineo-Congolian regional centre of endemism: *T. superba*, *L. alata* and *E. cylindricum*, the latter extending into the Lake Victoria regional mosaic. Finally, *M. excelsa* and *E. suaveolens* are the most widely distributed species, extending beyond the Guineo-Congolian regional centre of endemism into the Sudanian and Zambezi regional centres of endemism as well as the Lake Victoria and the Zanzibar-Inhambane regional mosaics.

Methods

Field flowering data

We compiled phenology data from direct observations of trees collected in seven sites (Figure 1, Table 1; Ouédraogo *et al.* 2018) across central Africa in lowland moist and wet forests (Fayolle *et al.* 2014). In all sites individual trees were tagged to be regularly monitored for phenology. In Cameroon, monitoring was conducted between 2004 and 2014 on a monthly basis in the logging concessions managed by the logging companies Pallisco (Mindourou site; Bourland *et al.* 2012, Daïnou *et al.* 2012b, Fétéké *et al.* 2016, Kouadio 2009), and Wijma (Mamfe, and Ma'an sites; Biwolé 2015). In the north of the Republic of the Congo monitoring was conducted monthly between 2005 and 2011 in two logging concessions (Pokola and Kabo sites) managed by the company CIB-Olam. Experienced forest technicians monitored trees for flowering using binoculars. They confirmed phenological activity by observing fallen flowers. In the Democratic Republic of the Congo (DRC) technicians monitored trees for flowering every 10 days between 1947 and 1958 in the Luki Forest Reserve (Luki site; Angoboy Ilondea *et al.* 2019, Couralet *et al.* 2013) located in the Mayombe forest, in the south-western-most margin of the Congo basin. In the Central African Republic, monitoring was conducted on a weekly basis between 1998 and 2003, and twice a month between 2005 and 2013, in the M'Baïki experimental site (M'Baïki site) for different subsets of trees and species over the two study periods. Technicians monitored trees for flowering and recorded the presence of flowering but only when the phenophase was dominant (when fruiting was the dominant stage of the tree, flowering was no longer recorded).

The sites correspond to semi-deciduous forests, except the Mamfe site, which corresponds to an evergreen forest and the Ma'an site, which corresponds to a transition forest between semi-deciduous and evergreen forests (Letouzey 1985). All sites were standardized for data analysis of monthly flowering phenology by scoring the presence/absence of flowering. We assumed that the comparison of phenology data from the Luki site which was monitored in the 1950s to phenology data from the other sites which were monitored in the 2000s is valid as rainfall seasonality is similar between the two periods (B. Angoboy Ilondea, unpubl. data).

In the end, information on the flowering phenology of 25 populations (a population being a species in a site) across central Africa

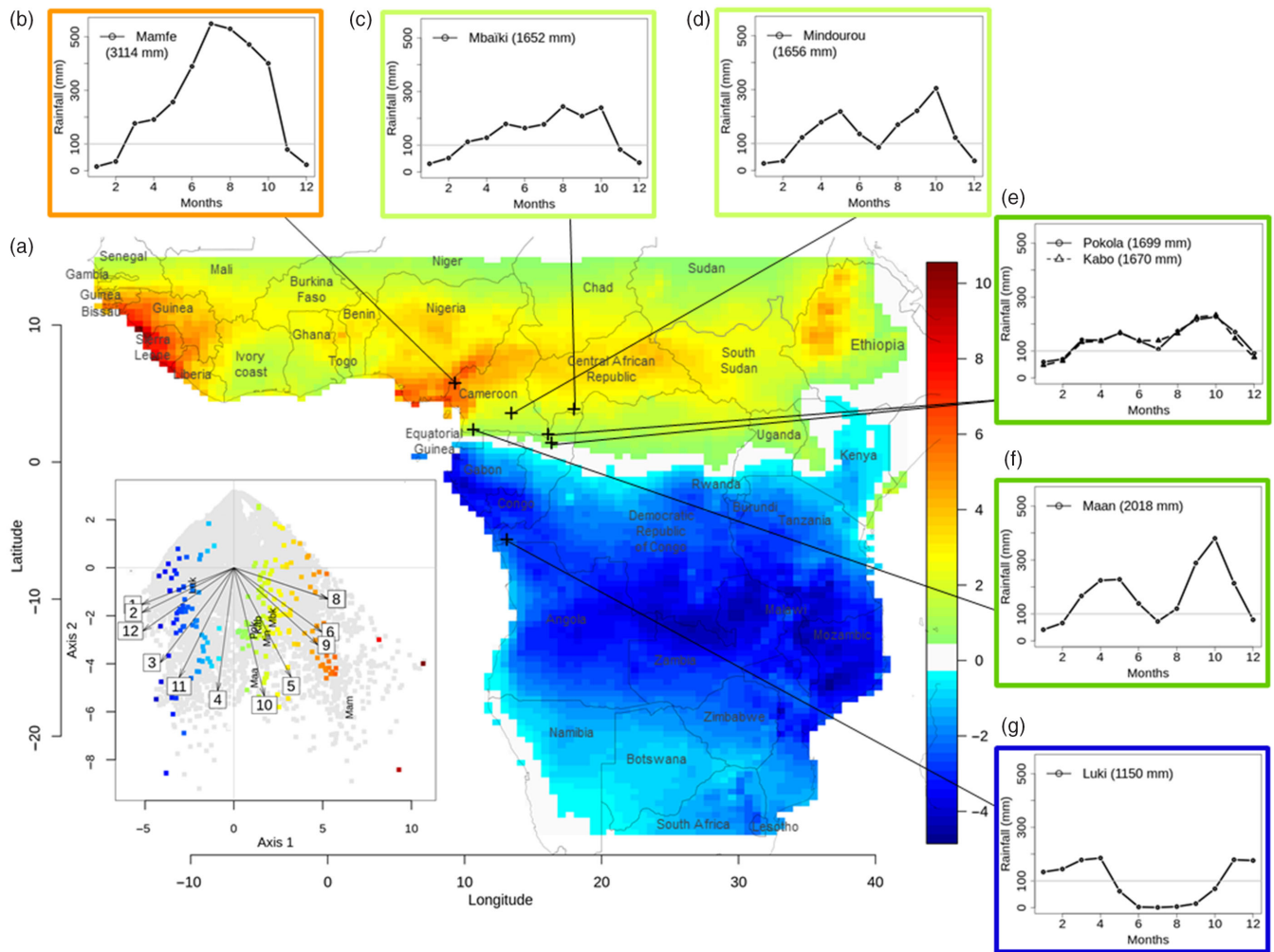


Figure 1. (a) Location of the study sites (black crosses) on a map with grid cells coloured according to the first axis scores of the principal component analysis of mean monthly rainfall (from negative scores in blue to positive scores in red). The inset shows the correlation circle of monthly rainfall (January = 1; February = 2, March = 3, April = 4, May = 5, June = 6, July = 7, August = 8, September = 9, October = 10, November = 11 and December = 12; 7 is hidden behind 8), the distribution of grid cells on the factorial plan (Axis 1 and Axis 2), as well as the position of field sites (Luki (Luk), Maan (Maa), Pokola (Pok), Kabo (Kab), Mindourou (Min), M'baïki (Mbk) and Mamfe (Mam)). Coloured grid cells are those where specimens were collected. (b, c, d, e, f, g) Field sites mean rainfall patterns with mean annual rainfall in parentheses.

was available on a monthly basis: *Entandrophragma cylindricum* (three sites; 2005–2011, 2005–2013, 2010–2013), *Erythrophleum suaveolens* (four sites; 1948–1958, 1998–2003, 2005–2011), *Lophira alata* (three sites; 2005–2011, 2011–2014, 2012–2014), *Mansonia altissima* (one site; 2004–2007), *Milicia excelsa* (four sites; 1947–1958, 2004–2010, 2005–2011, 2005–2013), *Pterocarpus soyauxii* (two sites; 1998–2003, 2005–2011), *Terminalia superba* (four sites; 1947–1958, 1998–2003, 2005–2010, 2005–2011), and *Triplochiton scleroxylon* (four sites; 2004–2008, 2005–2011, 2005–2012).

Herbarium-derived flowering data

For the eight species investigated here, we examined the herbarium collections of Meise Botanic Garden (Meise, Belgium; $n = 322$, P. Stoffelen, pers. comm.) and of the herbarium of Naturalis Biodiversity Center (Leiden, the Netherlands; $n = 206$, J.J. Wieringa, pers. comm.). Additionally, the online collections of the French National Museum of Natural History (Paris, France; $n = 197$) and of the Royal Botanical Gardens Kew (Kew, UK; $n = 23$) were examined. These four herbaria provide a very good coverage

for the studied region and hold specimens of far more than 80% of all the available material for the region (P. Stoffelen, pers. comm.), though the whole region still remains largely under-sampled (Sosef *et al.* 2017, Stropp *et al.* 2016). For all fertile specimens, the flowering status, the collection date (month-year) and geographic coordinates were recorded. Specimens with flowers just before anthesis, open flowers or old flowers were categorized as 'flowering'. Specimens annotated with a range of collection dates were discarded unless all dates belonged to the same month of the same year, in this case we used the 15th day of the month as collection date. For specimens without available coordinates but with an identifiable locality name we used this information to assign geographic coordinates using Google Earth software ($n = 173$ or 23% of all specimens). The least precise coordinates were recorded in degrees-minutes.

Overall, we gathered 53 specimens for *Entandrophragma cylindricum*, 111 specimens for *Erythrophleum suaveolens*, 31 specimens for *Lophira alata*, 17 specimens for *Mansonia altissima*, 89 specimens for *Milicia excelsa*, 56 specimens for *Pterocarpus soyauxii*, 28 specimens for *Terminalia superba* and 31 specimens for *Triplochiton scleroxylon*. The contribution of each herbarium to

Table 1. Characterization of the flowering pattern of the eight species in field sites in Cameroon (Mindourou, Mamfe, Ma'an), Central African Republic (M'Baïki), Republic of the Congo (Pokola, Kabo) and Democratic Republic of the Congo (Luki), with sampling information (period of monitoring and number N of census). The flowering cycles at population level were graphically determined following Newstrom *et al.* (1994) (Figure 2). The timing of flowering was characterized using circular statistics, with *Ntree* the number of reproductive trees, *N* the number of individual flowering observations, ρ the length of the mean vector indicating the concentration of flowering activity around a specific date, *P* the significance of ρ , and Date the mean time of occurrence of flowering

| Species | Site | Period | N census | Cycle | Circular statistics | | | | |
|------------------------------------|-----------|-----------|----------|--------------|---------------------|----------|--------|----------|--------------|
| | | | | | <i>Ntree</i> | <i>N</i> | ρ | <i>P</i> | Date |
| <i>Entandrophragma cylindricum</i> | Pokola | 2005–2011 | 71 | Supra-annual | 12 | 20 | 0.83 | <0.001 | 8 March |
| | M'Baïki | 2005–2013 | 180 | Annual | 60 | 389 | 0.92 | <0.001 | 10 February |
| | Mindourou | 2010–2013 | 36 | Annual | 65 | 194 | 0.97 | <0.001 | 5 February |
| <i>Erythrophleum suaveolens</i> | Pokola | 2005–2011 | 71 | Annual | 24 | 28 | 0.82 | <0.001 | 26 February |
| | M'Baïki | 1998–2003 | 218 | Supra-annual | 4 | 10 | 0.64 | 0.014 | 23 January |
| | Mindourou | 2005–2011 | 87 | Annual | 40 | 177 | 0.89 | <0.001 | 16 February |
| | Luki | 1948–1958 | 432 | Annual | 8 | 194 | 0.75 | <0.001 | 12 April |
| <i>Lophira alata</i> | Pokola | 2005–2011 | 71 | Annual | 22 | 43 | 0.52 | <0.001 | 26 December |
| | Ma'an | 2012–2014 | 23 | Annual | 91 | 190 | 0.96 | <0.001 | 12 December |
| | Mamfe | 2011–2014 | 24 | Annual | 80 | 115 | 0.83 | <0.001 | 17 December |
| <i>Mansonia altissima</i> | Mindourou | 2004–2007 | 46 | Annual | 47 | 244 | 0.85 | <0.001 | 12 August |
| <i>Milicia excelsa</i> | Pokola | 2005–2011 | 71 | Supra-annual | 5 | 7 | 0.77 | 0.010 | 18 March |
| | M'Baïki | 2005–2013 | 180 | Annual | 30 | 214 | 0.96 | <0.001 | 8 March |
| | Mindourou | 2004–2010 | 83 | Annual | 56 | 310 | 0.93 | <0.001 | 27 February |
| | Luki | 1947–1958 | 432 | Annual | 22 | 312 | 0.50 | <0.001 | 21 November |
| <i>Pterocarpus soyauxii</i> | Pokola | 2005–2011 | 71 | Supra-annual | 3 | 4 | 1.00 | 0.007 | 21 July |
| | M'Baïki | 1998–2003 | 218 | Supra-annual | 6 | 21 | 0.79 | <0.001 | 20 July |
| <i>Terminalia superba</i> | Pokola | 2005–2011 | 71 | Annual | 29 | 85 | 0.90 | <0.001 | 27 February |
| | M'Baïki | 1998–2003 | 218 | Annual | 25 | 334 | 0.98 | <0.001 | 14 February |
| | Mindourou | 2005–2010 | 63 | Annual | 65 | 373 | 0.58 | <0.001 | 15 February |
| | Luki | 1947–1958 | 432 | Annual | 174 | 5329 | 0.74 | <0.001 | 30 November |
| <i>Triplochiton scleroxylon</i> | Pokola | 2005–2011 | 71 | Annual | 58 | 155 | 0.55 | <0.001 | 3 January |
| | Kabo | 2005–2011 | 71 | Annual | 18 | 28 | 0.67 | <0.001 | 17 September |
| | M'Baïki | 2005–2012 | 180 | Annual | 45 | 115 | 0.75 | <0.001 | 22 February |
| | Mindourou | 2004–2008 | 47 | Annual | 36 | 78 | 0.76 | <0.001 | 26 February |

the total number of flowering specimens is detailed in Appendix 1. All specimens were collected from 1861 to 2017.

Rainfall data

We computed mean monthly rainfall over the period 1981–2000 from the CHIRPS estimates of monthly rainfall for Africa which are based on remote sensing (Funk *et al.* 2015, ftp://ftp.chg.ucsb.edu/pub/org/chg/products/CHIRPS-2.0/africa_monthly/). To model species distribution, climate data derived from remote sensing such as the CHIRPS database perform better than the widely used interpolation of ground observations such as the WorldClim database (Hijmans *et al.* 2005), especially in areas with sparse weather stations such as tropical Africa (Deblauwe *et al.* 2016). Mean monthly rainfall values were then extracted for a large area (Figure 1) which include the seven study sites for which field observations of tree phenology were available, as well as all geographic locations covered by the herbarium collections (and thus including non-forested areas).

Data analyses

First, temporal patterns in flowering phenology (frequency and seasonality) were identified using the standardized phenological data collected in field sites. Only reproductive trees were kept for analysis (i.e. trees that have flowered at least once over the study period). We used the graphical analysis developed by Newstrom *et al.* (1994) to determine the frequency of flowering (continuous, sub-annual, annual or supra-annual) at population level, based on the proportion of flowering trees across time. Flowering with sporadic brief breaks corresponds to the continuous class, flowering in more than one cycle per year corresponds to the sub-annual class, flowering in only one major cycle per year corresponds to the annual class, and flowering in one cycle over more than 1 year corresponds to the supra-annual class (Newstrom *et al.* 1994). We used circular statistics to assess the seasonality of flowering. Calendar dates (day-month) of flowering were converted to 1–360° angles to calculate in a circular manner a mean angle and vector length for each population. The length of the mean vector (which

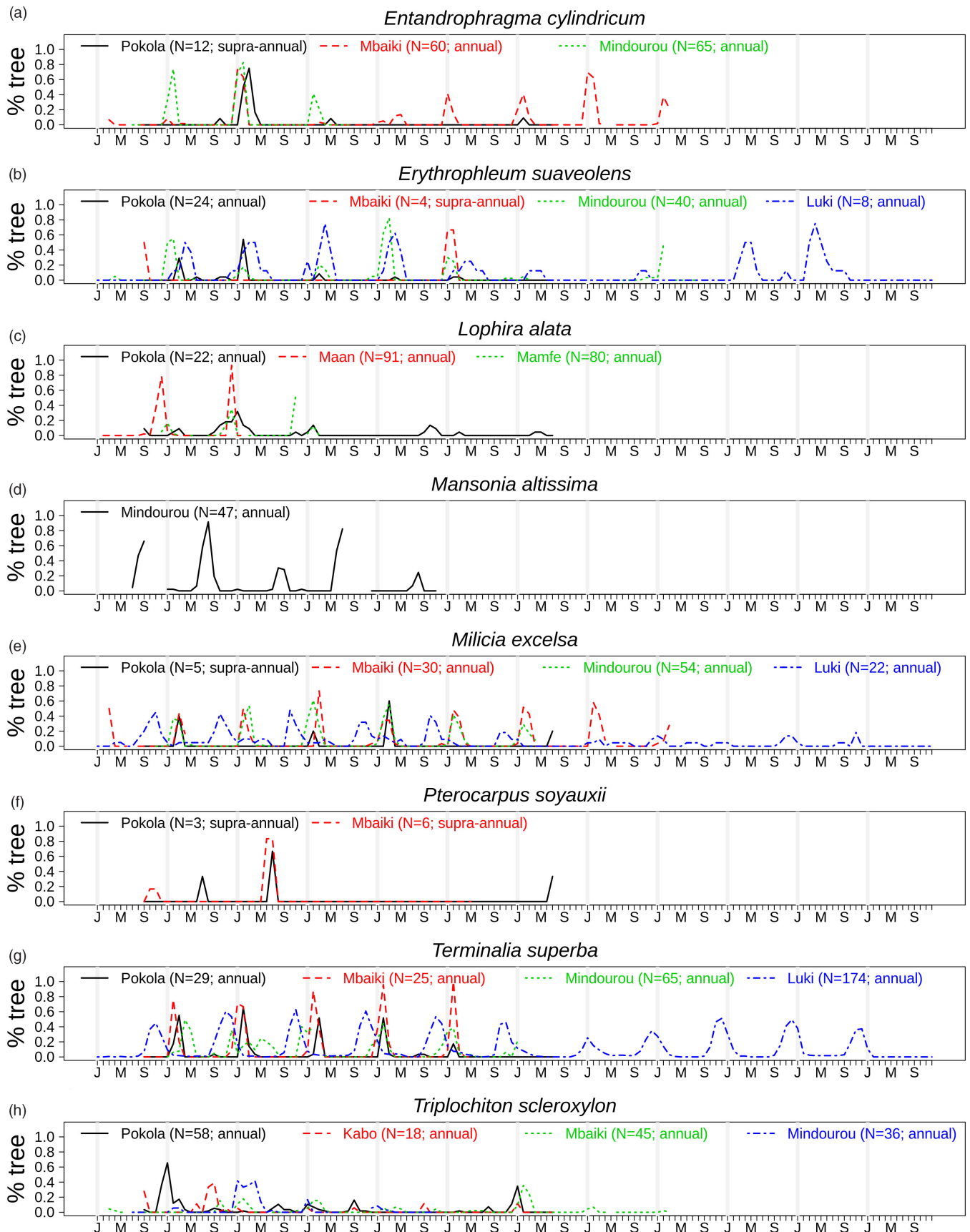


Figure 2. For the eight study species *Entandrophragma cylindricum* (a), *Erythrophleum suaveolens* (b), *Lophira alata* (c), *Mansonia altissima* (d), *Milicia excelsa* (e), *Pterocarpus soyauxii* (f), *Terminalia superba* (g) and *Triplochiton scleroxylon* (h), proportion of trees flowering in each month of each year, in the sites where the species was monitored. The total number (N) of flowering trees in each site is indicated in parentheses with flowering cycle, and grey vertical lines indicate the beginning of the year (January).

varies between 0 and 1) indicates the concentration of phenological activity around the mean date of flowering (which is the mean angle back-converted to calendar date). We performed a Rayleigh's test to test whether the flowering events were significantly aggregated around the mean date (significant mean vector length).

Second, we assessed the spatial variation in the timing of flowering using herbarium-derived flowering data and testing the relative influence of latitude, longitude and spatial variation in the seasonality of rainfall, on the collection date (in day-month) of flowering specimens. At this step we also visually checked whether the flowering specimens well covered the distribution area of the species. The latter was estimated using the RAINBIO database of tropical African vascular plants distributions (Dauby *et al.* 2016). To summarize the main pattern of rainfall variation over the area we performed a principal component analysis (PCA) on CHIRPS monthly rainfall estimates (12 variables). The first axis of the PCA (depicting the timing of the dry season) was used as an index of rainfall seasonality. Then we converted dates of collection of flowering specimens into radians, and tested the relative influence of latitude, longitude and first-axis scores of the PCA on monthly rainfall on the radians using a Bayesian circular generalized linear model (Mulder & Klugkist 2017). We also checked that year and day-month of collection were not correlated using the same model but with year as unique covariate. Given that latitude, longitude and index for the timing of dry season were often strongly correlated (absolute value of correlation coefficient > 0.7, Dormann *et al.* 2013, Appendix 2), we also ran the model for each of these variables separately and checked the consistency of the results. For all models, we performed 100 000 iterations with a burn-in of 1000 and thinning of 10. All analyses were performed using R 3.4.4 (<https://www.R-project.org/>).

Results

Flowering patterns observed in field sites

For the eight species studied, field observations demonstrated annual flowering for 20 out of the 25 populations monitored, and supra-annual flowering for the remaining five populations (Table 1, Figure 2). Four species showed annual flowering regardless of site (*Lophira alata* three sites, *Mansonia altissima* one site, *Terminalia superba* four sites and *Triplochiton scleroxylon* four sites). We identified supra-annual flowering for *Pterocarpus soyauxii* in the two sites where the species was monitored. Three species showed a variation in flowering cycle depending on site. *Entandrophragma cylindricum* flowered annually at Mindourou (N = 65 trees) and M'Baïki (N = 60), and flowered supra-annually at Pokola (N = 12). *Erythrophleum suaveolens* flowered annually at Mindourou (N = 40), Pokola (N = 24) and Luki (N = 8), and flowered supra-annually at M'Baïki (N = 4). *Milicia excelsa* flowered annually at Mindourou (N = 56), M'Baïki (N = 30) and Luki (N = 22, but the pattern was less clear at the end of the monitoring period), and flowered supra-annually at Pokola (N = 5). For these three species, supra-annual cycles may result from the small number of trees monitored (12 for *E. cylindricum* at Pokola, four for *E. suaveolens* at M'Baïki and five for *M. excelsa* at Pokola). Similarly, the supra-annual flowering identified for *P. soyauxii* may result from the small number of trees monitored (three and six trees at Pokola and M'Baïki, respectively).

Circular analysis of dates of flowering confirmed that flowering activity was significantly ($P < 0.05$) concentrated around a specific date for all population studied, with rho the length of the mean

vector ranging from 0.50 (*M. excelsa*, Luki, N = 22 trees) to 1 (*P. soyauxii*, Pokola, N = 3) (Table 1). In the northern part of central Africa (all sites but Luki), six species flowered in December–March, and two species in July–August (*M. altissima* and *P. soyauxii*, Table 2, Figure 2). A slight between-site variation in the timing of flowering was observed for three species that were monitored both at the northern sites and at the southern site Luki (*E. suaveolens*, *M. excelsa* and *T. superba*). On average *E. suaveolens* flowered in January–February at the northern sites (rho ranging between 0.64 and 0.89, Table 1) but flowered in April at the southern Luki site (rho = 0.75); *M. excelsa* flowered in February–March at the northern sites (rho ranging between 0.77 and 0.96) but flowered in November at Luki (rho = 0.50); and *T. superba* flowered in February at the northern sites (rho ranging between 0.58 and 0.98) yet flowered in November at Luki (rho = 0.74). We also found between-site variation in the timing of flowering of *T. scleroxylon* even though all populations were monitored in the northern part of central Africa. The mean flowering peak for this species was in January–February at Pokola (rho = 0.55), Mindourou (rho = 0.76) and M'Baïki (rho = 0.75), whereas flowering occurred on average in September at Kabo (rho = 0.67).

Variation in the timing of flowering: insights from herbarium specimens

The spatial distribution of flowering specimens of the eight species studied covered their species-specific distribution ranges well (Figure 3). For the three species with a narrow distribution, flowering specimens of *T. scleroxylon* were mainly collected in January (42% of the specimens), those of *M. altissima* in July–August (58%), and those of *P. soyauxii* in July (29%; Figure 3). For the species with an intermediate distribution size, flowering specimens were mainly collected in February (29%), January (38%) and December–January (67%) for *T. superba*, *E. cylindricum* and *L. alata*, respectively (Figure 3). Finally, for the most widely distributed species *M. excelsa* and *E. suaveolens*, their flowering specimens were mainly collected in March (20%) and in February (26%; Figure 3), respectively.

Rainfall seasonality and spatial variation in the timing of flowering

The principal component analysis of mean monthly rainfall separated grid cells along a first axis that explained 52% of the total variance, and along a second axis that explained 34% of the total variance. The first axis depicted the timing of the dry season that differs between the northern and southern hemisphere, with negative values indicating a southern climate with a main dry season occurring in July–August, and positive values indicating a northern climate with a main dry season occurring in December–January–February (Figure 1). The second axis was highly negatively correlated with mean annual rainfall (Pearson's correlation $r = -0.95$, $P < 0.001$). Among the sites where phenological monitoring was conducted, we found that Luki displayed a unique dry season centred around July–August (southern climate, first axis scores of -2.4) opposed to M'Baïki and Mamfe that displayed a unique dry season in December–January–February (northern climate, first axis scores of 2.1 and 6.5, respectively). The Maan, Pokola, Kabo and Mindourou sites, having positive first axis scores of 1.1, 1.1, 1.3 and 1.8, respectively, showed a major dry season from December to February, but also displayed a reduction in rainfall in July (Figure 1).

Table 2. Between-site variation in the timing of flowering for the eight species (data from Table 1). The cycle corresponds to the phenological pattern graphically determined at population level following the approach of Newstrom *et al.* (1994) (Figure 2). The most frequent cycle found among populations (i.e. a species in a site) is reported, and when another cycle was identified for one population it is indicated in parentheses. For each population, the mean date of flowering during the monitoring period is indicated with the corresponding season (long_dry = major dry season, short_dry = short dry season, wet = major wet season). Sites are ordered according to the timing of the dry season (i.e. the score on the first axis of the PCA on monthly rainfall values indicated in parentheses)

| Species | Cycle | Mean date of flowering and associated season | | | | | | |
|------------------------------------|-----------------------|--|--------------|-----------------|--------------|--------------|-------------|-------------|
| | | Mamfe (6.5) | MBaïki (2.1) | Mindourou (1.8) | Kabo (1.3) | Pokola (1.1) | Maan (1.1) | Luki (-2.4) |
| <i>Entandrophragma cylindricum</i> | Annual (Supra-annual) | - | 10 February | 5 February | - | 8 March | - | - |
| | | | long_dry | long_dry | | long_dry | | |
| <i>Erythrophleum suaveolens</i> | Annual (Supra-annual) | - | 23 January | 16 February | - | 26 February | - | 12 April |
| | | | long_dry | long_dry | | long_dry | | wet |
| <i>Lophira alata</i> | Annual | 17 December | - | - | - | 26 December | 12 December | - |
| | | long_dry | | | | long_dry | long_dry | |
| <i>Mansonias altissima</i> | Annual | - | - | 12 August | - | - | - | - |
| | | | | short_dry | | | | |
| <i>Milicia excelsa</i> | Annual (Supra-annual) | - | 8 March | 27 February | - | 18 March | - | 21 November |
| | | | long_dry | long_dry | | long_dry | | wet |
| <i>Pterocarpus soyauxii</i> | Supra-annual | - | 20 July | - | - | 21 Jul | - | - |
| | | | short_dry | | | short_dry | | |
| <i>Terminalia superba</i> | Annual | - | 14 February | 15 February | - | 27 February | - | 30 November |
| | | | long_dry | long_dry | | long_dry | | wet |
| <i>Triplochiton scleroxylon</i> | Annual | - | 22 February | 26 February | 17 September | 3 January | - | - |
| | | | long_dry | long_dry | wet | long_dry | | |

To investigate the spatial variation in the timing of flowering, we analysed the relative influence of latitude, longitude and timing of the dry season (i.e. first axis score of the PCA on monthly rainfall values) on the collection date of flowering specimens. We found significant effects (regression coefficients significantly different from 0) indicating a shift in the timing of flowering with latitude for *E. suaveolens*, and with timing of the dry season for *M. excelsa* and *L. alata* (Table 3). For *L. alata* however, the effect of timing of the dry season was not significant when included as a single variable in the model, suggesting that the effect was weak. For *E. suaveolens* and *M. excelsa* it seems that the flowering peak roughly occurred around October at low latitude (south of 1°S) and around February–March at high latitude (north of 2°N), the area around the equator showing both peaks (Figure 4a, b). Because of its more restricted distribution and lower number of specimens we could not evaluate whether *L. alata* had the same pattern (Figure 4c). For the other species studied, none of latitude, longitude or timing of the dry season had an effect (Table 3). We also did not find any significant relationship between the year of collection and timing of flowering for any species (Table 3).

Discussion

Annual flowering dominates

Studying eight large-statured (briefly) deciduous canopy tropical African tree species showed that an annual flowering phenology was the most common pattern at population level (20 out of the 25 populations monitored in time showed an annual flowering, and annual flowering was the most common pattern for seven out of the eight species examined). We identified supra-annual

flowering for the remaining five populations but this likely resulted from the small number of trees monitored. The dominance of an annual cycle in the reproductive phenology has been previously reported in central Africa for specific species in specific sites such as *Milicia excelsa* in south-eastern Cameroon (Mindourou site; Daïnou *et al.* 2012b) or *Millettia laurentii* in the Mai Ndombe area, DRC (Menga *et al.* 2012). Similar patterns were reported in Luki, western DRC at the community level (Couralet *et al.* 2013) and for most species at La Lopé National Park, Gabon (Bush *et al.* 2017) where Fourier analyses showed that 88% of the species displayed annual flowering phenology. At a larger scale, annual phenology was also reported for most trees across tropical Africa (Adamescu *et al.* 2018), including sites in West Africa (N = 1), central Africa (N = 5) and East Africa (N = 5). Elsewhere in the tropics, the predominant flowering type was the sub-annual pattern at La Selva, Costa Rica (a wet forest without a severe dry season) and the supra-annual pattern in dipterocarp forests of South-east Asia (where fluctuation in rainfall is quite unpredictable) (Sakai 2001). The strong seasonality of the African climate, and specifically rainfall seasonality, might explain the dominance of annual cycles.

Timing of flowering and its spatial variability

In our study sites located north of the climatic hinge, flowering was generally associated with the occurrence of the dry season. Flowering peaked during the major dry season for six species and during the short dry season for two species. Flowering in the dry season has been already observed for *M. excelsa* in south-eastern Cameroon (Mindourou site; Daïnou *et al.* 2012b) and *Millettia laurentii* in the Mai Ndombe area, DRC

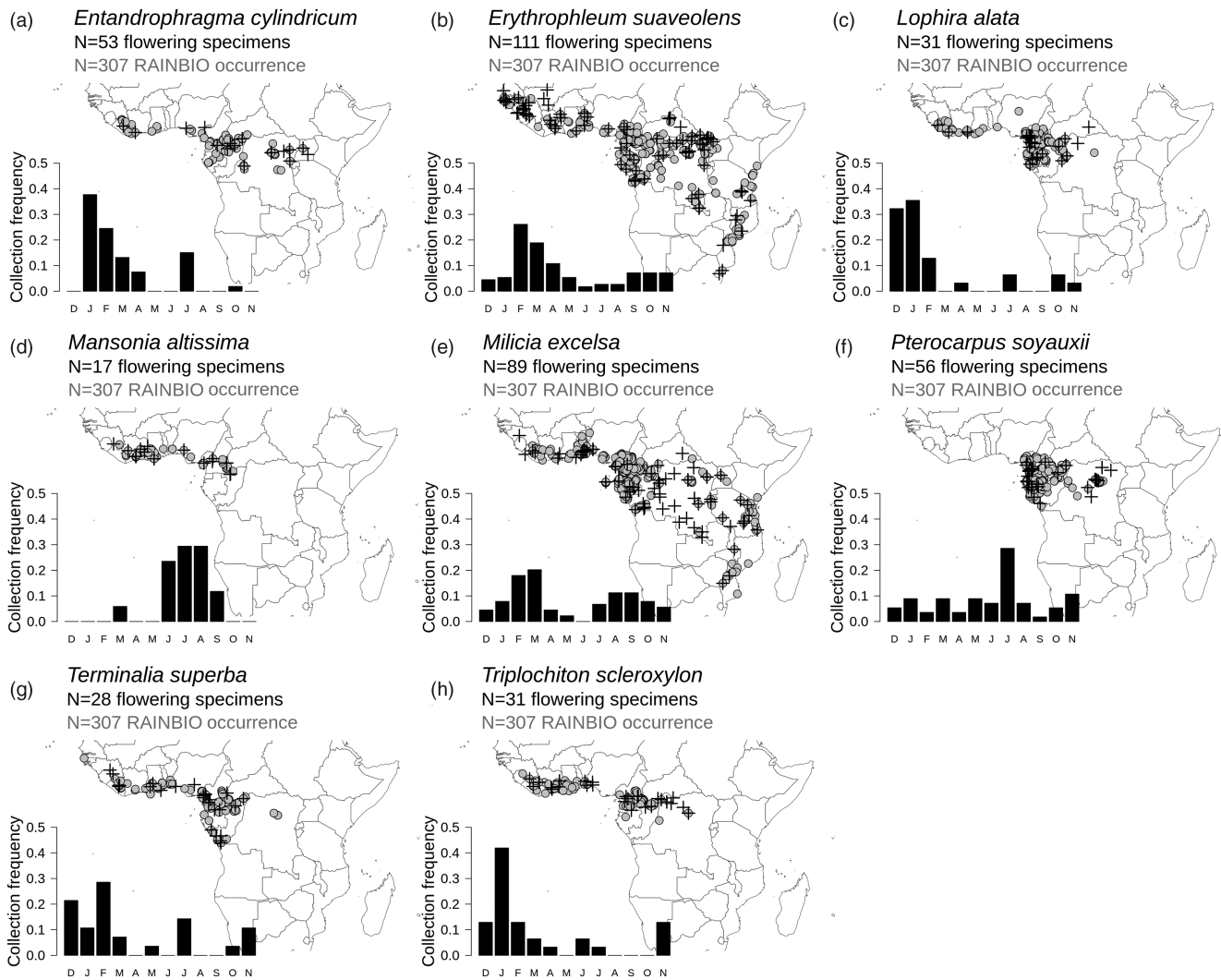


Figure 3. Location of flowering herbarium specimens (black crosses, number *n* indicated in black) across Africa for the eight species *Entandrophragma cylindricum* (a), *Erythrophleum suaveolens* (b), *Lophira alata* (c), *Mansonia altissima* (d), *Milicia excelsa* (e), *Pterocarpus soyauxii* (f), *Terminalia superba* (g) and *Triplochiton scleroxylon* (h). Species spatial distribution i.e. location of RAINBIO occurrences (Dauby *et al.* 2016) is indicated with grey circles (number *n* indicated in grey). Insets show the frequency of flowering herbarium collections by month (represented from December to November for clarity).

(Menga *et al.* 2012), and at the community level in Luki, western DRC south of the equator (Angoboy Ilondea *et al.* 2019, Couralet *et al.* 2013). Elsewhere in the tropics, flowering in the dry season has already been noticed in several neotropical forests (reviewed in Janzen 1967, Sakai 2001, Wright & van Schaik 1994). This pattern was hypothesized to be the result of selection for sexual reproduction during a period of lack of interference with vegetative processes, to allow full competitive (vegetative) activity during the rainy season (Janzen 1967). It was also hypothesized that it is the result of selection to coincide with peak irradiance when water is available (Wright & van Schaik 1994), and recently it has been shown in central Panama that high and increasing levels of irradiance are the proximate cues for flowering in many (but not all) tree species (Wright & Calderón 2018). Increasing levels of irradiance during the dry season intuitively result from lack of clouds, but may also result from particular cloudy conditions that increase diffuse light (Pau *et al.* 2013). Indeed the light-use efficiency of forests can be higher under cloudy or partly cloudy conditions (low irradiance conditions) because diffuse light is scattered more uniformly throughout the canopy and understorey, whereas on

clear-sky days sunlight comes from a single direction and many leaves remain in shade. Another hypothesis to explain flowering during the dry season is the availability of pollinators. Since most herbs will not flower in this period there are in general fewer flowers available so flowers may need to produce less nectar to be competitive for attracting pollinators.

The flowering during dry season at the north of the climatic hinge suggests a correlation between the timing of flowering and rainfall seasonality. However, for the three species *Erythrophleum suaveolens*, *Milicia excelsa* and *Terminalia superba* that were also monitored south of the climatic hinge (i.e. in site Luki), flowering occurred at the beginning or the end of the wet season. As such the north-south between-site variation in flowering phenology for these species does not perfectly match with the inversion of the timing of the dry season. Also, in Gabon, Doucet (2003) observed that the majority of the tree species monitored (16 out of 19 species) flowered during the wet season. Likewise, all nine Gabonese tree legume species tested by Wieringa (1999) that showed a significant flowering period flowered during the rainy season. This suggests that other factors partially correlated

Table 3. For the eight species, latitudinal range (in decimal degrees) of collected fertile specimens in square brackets, total number of specimens (N), and results of the Bayesian circular generalized linear model testing the relative influence of latitude, longitude, and timing of the dry season (first axis score of the PCA on monthly rainfall) on dates of collection (day-month) of flowering herbarium specimens converted in radians (Latitude + Longitude + Rainfall). Results of the models testing the influence of year of collection (Year), latitude (Latitude), longitude (Longitude) and timing of the dry season (Rainfall) are also reported. For each model, the posterior means of the regression coefficients are given with their credible intervals in square brackets, as well as the Widely Applicable Information Criterion (WAIC, first formulation of the WAIC as given in Bayesian Data Analysis; Gelman *et al.* 2003). Posterior means of regression coefficients significantly different from zero are indicated with symbols (*).

| Species | Model | WAIC | Estimates |
|---|---------------------------------|---------|--|
| <i>Entandrophragma cylindricum</i> ([-2.2, 8.0]) (N = 53) | Year | 151.6 | -0.039 [-0.181; 0.087] |
| | Latitude | 151.73 | -0.018 [-0.158; 0.118] |
| | Longitude | 151.639 | 0.005 [-0.118; 0.132] |
| | Rainfall | 151.762 | -0.025 [-0.183; 0.120] |
| | Latitude + Longitude + rainfall | 154.693 | Latitude: 0.131 [-0.762; 0.507] Longitude: -0.107 [-0.491; 0.284] Rainfall: -0.008 [-0.459; 0.393] |
| <i>Erythrophleum suaveolens</i> ([-26.8, 14.9]) (N = 111) | Year | 378.471 | 0.015 [-0.145; 0.175] |
| | Latitude | 323.541 | 0.611 [0.441; 0.808]* |
| | Longitude | 356.103 | -0.342 [-0.491; -0.204]* |
| | Rainfall | 334.924 | 0.607 [0.422; 0.830]* |
| | Latitude + Longitude + rainfall | 325.274 | Latitude: 0.586 [0.225; 1.011]* Longitude: 0.082 [-0.100; 0.278] Rainfall: 0.145 [-0.148; 0.437] |
| <i>Lophira alata</i> ([-1.9, 8.0]) (N = 31) | Year | 79.42 | -0.084 [-0.246; 0.069] |
| | Latitude | 80.248 | 0.052 [-0.099; 0.206] |
| | Longitude | 79.621 | 0.091 [-0.071; 0.281] |
| | Rainfall | 78.224 | 0.107 [-0.033; 0.249] |
| | Latitude + Longitude + rainfall | 77.182 | Latitude: -0.244 [-0.627; 0.132] Longitude: 0.124 [-0.060; 0.336] Rainfall: 0.355 [0.014; 0.712]* |
| <i>Mansonia altissima</i> ([2.0, 8.6]) (N = 17) | Year | 41.544 | -0.092 [-0.314; 0.103] |
| | Latitude | 42.289 | 0.003 [-0.186; 0.195] |
| | Longitude | 41.541 | 0.106 [-0.088; 0.310] |
| | Rainfall | 42.374 | 0.016 [-0.170; 0.218] |
| | Latitude + Longitude + rainfall | 41.663 | Latitude: 0.286 [-0.077; 0.659] Longitude: 0.357 [-0.008; 0.744] Rainfall: -0.075 [-0.298; 0.151] |
| <i>Milicia excelsa</i> ([-21.6, 10.4]) (N = 89) | Year | 327.765 | 0.760 [-1.536; 2.929] |
| | Latitude | 296.612 | 0.792 [0.499; 1.180]* |
| | Longitude | 324.699 | 0.804 [-0.708; 2.227] |
| | Rainfall | 287.096 | 0.899 [0.625; 1.236]* |
| | Latitude + Longitude + rainfall | 288.941 | Latitude: 0.439 [-0.190; 1.309] Longitude: 0.294 [-0.052; 0.676] Rainfall: 0.698 [0.021; 1.373]* |

(Continued)

Table 3. (Continued)

| Species | Model | WAIC | Estimates |
|---|--|---------|---|
| <i>Pterocarpus soyauxii</i> ([-5.1, 5.2]) (N = 56) | Year | 204.431 | -0.023 [-2.155; 2.109] |
| | Latitude | 207.23 | -0.005 [-1.698; 1.615] |
| | Longitude | 197.65 | 0.180 [-1.373; 1.713] |
| | Rainfall | 196.998 | 1.065 [-1.250; 2.363] |
| | Latitude + Longitude + rainfall | 198.614 | Latitude: 0.141 [-1.596; 1.483] Longitude: 0.590 [-1.475; 2.127] Rainfall: 0.305 [-1.099; 2.140] |
| | <i>Terminalia superb</i> ([-5.9, 10]) (N = 28) | Year | 96.319 |
| Latitude | | 93.994 | 0.210 [-0.085; 0.581] |
| Longitude | | 94.894 | 0.090 [-0.486; 2.654] |
| Rainfall | | 95.927 | 0.123 [-0.254; 0.504] |
| Latitude + Longitude + rainfall | | 92.797 | Latitude: -0.991 [-2.341; 0.722] Longitude: 1.600 [-0.485; 3.036] Rainfall: 0.762 [-1.788; 2.107] |
| <i>Triplochiton scleroxylon</i> ([0.8, 8.1]) (N = 31) | | Year | 90.381 |
| | Latitude | 88.478 | -0.122 [-0.298; 0.042] |
| | Longitude | 88.281 | 0.120 [-0.037; 0.285] |
| | Rainfall | 88.836 | -0.119 [-0.309; 0.056] |
| | Latitude + Longitude + rainfall | 91.706 | Latitude: 0.025 [-0.432; 0.500] Longitude: 0.109 [-0.286; 0.530] Rainfall: -0.078 [-0.359; 0.183] |

with rainfall seasonality drive the flowering phenology of these species. For instance, Daïnou *et al.* (2012b) showed that flowering of *M. excelsa* at Mindourou in Cameroon was significantly correlated with a decrease in relative air humidity 3 mo prior to flowering. If the decrease in relative air humidity during the dry season differs either north or south of the climatic hinge due to the influence of other factors than rainfall (e.g. wind or temperature), this may explain why we did not observe a shift in flowering that matches the inversion of the dry season.

Van Schaik *et al.* (1993) reported for tropical forests around the equator (in Africa, Asia and America) a 6-month shift in community-level peak flowering linked to the month of peak irradiance (when the sun passes directly over the localities). Here we showed at population level a slightly different pattern. The analysis of herbarium collections revealed a shift in flowering peak from northern sites toward southern sites for *E. suaveolens* and *M. excelsa* (and to a lesser extent *L. alata*), with the coexistence of two flowering peaks near the equator where monthly rainfall is bimodal with two dry seasons and two rainy seasons. These results suggest that the spatial variation in the timing of flowering could be explained by the spatial variation in rainfall seasonality, but this was true only for *M. excelsa* (and to a lesser extent *L. alata*). For *M. excelsa*, we may even expect a stronger correlation with the spatial variation in seasonal patterns of air relative humidity. For *E. suaveolens*, the spatial variation in the timing of reproduction may be due to the spatial

variation in a climatic factor other than rainfall seasonality. In this context, the role of light in particular should be further explored.

Conclusion

The analysis of field observations of flowering for the eight species studied showed a strong seasonality of flowering, which usually occurred during dry seasons. Our field sites were however almost all located at the north of the climatic hinge, and the pattern is likely to be different at the south (as observed here for three species). Although rainfall seasonality may play a role in driving the flowering for some species, more discriminating climatic variables such as air humidity have to be explored. Further research is needed to identify the drivers (either abiotic or biotic) of flowering of these economically important species. In particular, the influence of soil fertility on the probability of flowering should be explored, with lower probabilities of flowering (e.g. supra-annual flowering) expected on low-fertility sites (Monks *et al.* 2016). Finally, the analysis of herbarium collections revealed for two widely distributed species a shift in flowering peak from northern sites toward southern sites, with the coexistence of two flowering peaks near the equator where precipitation is bimodal. This indicates that the hypothesis of genetic discontinuities due to a 6-month north-south shift in flowering phenology preventing gene

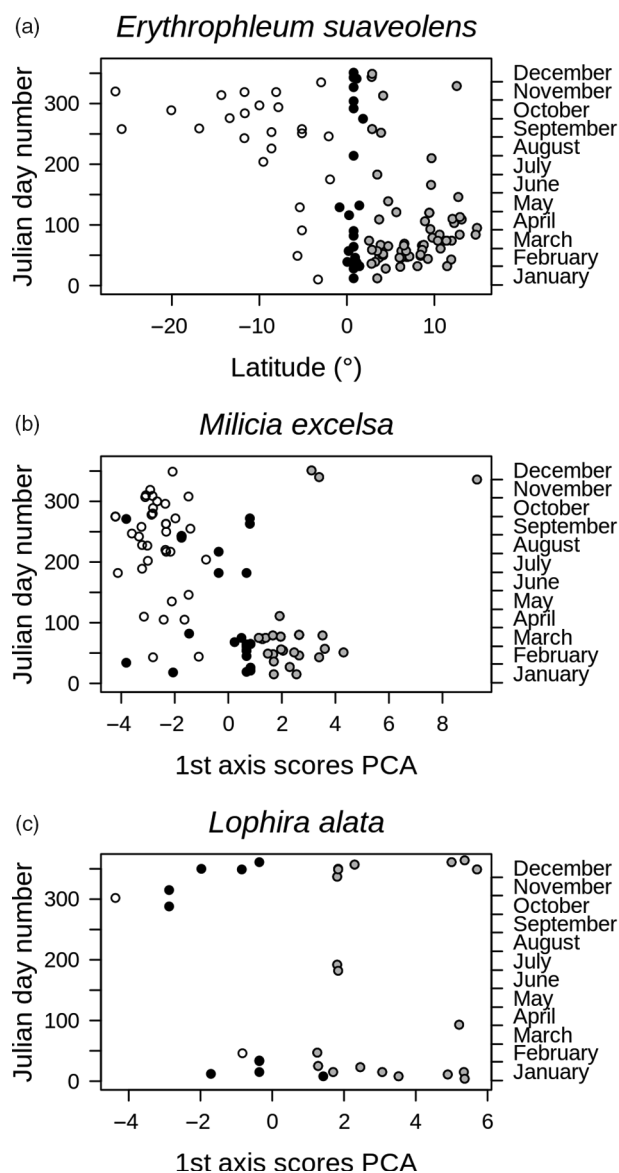


Figure 4. Relationship between calendar dates of flowering herbarium specimens (in Julian days) and the variable explaining their variation, that is latitude for *Erythrophleum suaveolens* (a) and timing of the dry season (first axis score of the PCA on monthly rainfall) for *Milicia excelsa* (b) and *Lophira alata* (c). In a, b and c, open circles represent specimens collected at south of 1°S, black circles those collected between 1°S and 2°N, and grey circles those collected at north of 2°N. For clarity, the second y-axis indicates the months corresponding to Julian days.

flow between northern and southern populations (Hardy *et al.* 2013) is not supported for the species here studied.

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Literature cited

- Adamescu GS, Plumtre AJ, Abernethy KA, Polansky L, Bush ER, Chapman CA, Shoo LP, Fayolle A, Janmaat KRL, Robbins MM, Ndangalasi HJ, Cordeiro NJ, Gilby IC, Wittig RM, Breuer T, Breuer-Ndoundou Hockemba M, Sanz CM, Morgan DB, Pusey AE, Mugerwa B, Gilagiza B, Tutin C, Ewango CEN, Sheil D, Dimoto E, Baya F, Bujo F, Ssali F, Dikangadissi JT, Jeffery K, Valenta K, White L, Masozera M, Wilson ML, Bitariho R, Ndolo Ebika ST, Gourlet-Fleury S and Beale CM (2018) Annual cycles dominate reproductive phenology of African tropical trees. *Biotropica* 50, 418–430.
- Akinngabe A, Gailing O and Finkeldey R (2010) Genetic diversity of *Mansonia altissima* A. Chev. under different regimes of human impact in the Akure Forest Reserve, Nigeria. *Forestry Studies in China* 12, 193–200.
- Angoboy Ilondea B, Beckman H, Ouédraogo DY, Bourland N, De Mil T, Van den Bulcke J, Van Acker J, Couralet C, Ewango C, Hubau W, Toirambe B, Doucet JL and Fayolle A (2019) Une forte saisonnalité du climat et de la phénologie reproductive dans la forêt du Mayombe : l'apport des données historiques de la Réserve de Luki en République démocratique du Congo. *Bois et Forêts des Tropiques* 341, 39–53.
- Bastin JF, Barbier N, Réjou-Méchain M, Fayolle A, Gourlet-Fleury S, Maniatis D, De Haulleville T, Baya F, Beeckman H, Beina D, Couteron P, Chuyong G, Dauby G, Doucet JL, Droissart V, Dufrêne M, Ewango C, Gillet JF, Gonmadje C, Hart T, Kavali T, Kenfack D, Libalah M, Malhi Y, Makana JR, Péliissier R, Ploton P, Serckx A, Sonké B, Stevart T, Thomas DW, De Cannière C and Bogaert J (2015) Seeing Central African forests through their largest trees. *Scientific Reports* 5, 13156.
- Bayol N, Demarquez B, De Wasseige C, Atyi RE, Fisher JF, Nasi R, Pasquier A, Rossi X, Steil M and Vivien C (2012) Forest management and the timber sector in central Africa. In de Wasseige C, de Marcken P, Bayol N, Hiol Hiol F, Mayaux Ph, Desclée B, Nasi R, Billand A, Defourny P and Eba'a R (eds), *The Forests of the Congo Basin: State of the Forests 2010*. Luxembourg: Publications Office of the European Union, pp. 43–61.
- Biwolé A (2015) Origine et dynamique des populations d'arbres des forêts denses humides d'Afrique Centrale, le cas de *Lophira alata* Banks ex Gaertn C.F. (Ochnaceae). PhD Dissertation: Université de Liège – Gembloux Agro-Bio Tech, Gembloux, Belgique.
- Blatrix R, Peccoud J, Born C, Piatscheck F, Benoit L, Sauve M, Djiéto-Lordon C, Atteke C, Wieringa JJ and Harris DJ (2017) Comparative analysis of spatial genetic structure in an ant-plant symbiosis reveals a tension zone and highlights speciation processes in tropical Africa. *Journal of Biogeography* 44, 1856–1868.
- Borchert R (1996) Phenology and flowering periodicity of Neotropical dry forest species: evidence from herbarium collections. *Journal of Tropical Ecology* 12, 65–80.

- Borchert R, Meyer SA, Felger RS and Porter-Bolland L (2004) Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* **13**, 409–425.
- Bourland N, Kouadio YL, Lejeune P, Sonké B, Phillipart J, Daïnou K, Fétéké F and Doucet JL (2012) Ecology of *Pericopsis elata* (Fabaceae), an endangered timber species in Southeastern Cameroon. *Biotropica* **44**, 840–847.
- Bush ER, Abernethy KA, Jeffery K, Tutin C, White L, Dimoto E, Dikangadissi JT, Jump AS and Bunnefeld N (2017) Fourier analysis to detect phenological cycles using long-term tropical field data and simulations. *Methods in Ecology and Evolution* **8**, 530–540.
- CaraDonna PJ, Iler AM and Inouye DW (2014) Shifts in flowering phenology reshape a subalpine plant community. *PNAS* **111**, 4916–4921.
- Cleland EE, Chuine I, Menzel A, Mooney HA and Schwartz MD (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- Couralet C, Van Den Bulcke J, Ngoma LM, Van Acker J and Beekman H (2013) Phenology in functional groups of Central African rainforest trees. *Journal of Tropical Forest Science* **25**, 361–374.
- Daïnou K, Doucet JL, Sinsin B and Mahy G (2012a) Identité et écologie des espèces forestières commerciales d'Afrique centrale: le cas de *Milicia* spp. (synthèse bibliographique). *Biotechnologie, Agronomie, Société et Environnement* **16**, 229–241.
- Daïnou K, Laurenty E, Mahy G, Hardy OJ, Brostaux Y, Tagg N and Doucet JL (2012b) Phenological patterns in a natural population of a tropical timber tree species, *Milicia excelsa* (Moraceae): evidence of isolation by time and its interaction with feeding strategies of dispersers. *American Journal of Botany* **99**, 1453–1463.
- Dauby G, Zaiss R, Blach-Overgaard A, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V, Duarte MC, Engledow H, Fadeur G, Figueira R, Gereau RE, Hardy OJ, Harris DJ, De Heij J, Janssens S, Klomberg Y, Ley AC, Mackinder BA, Meerts P, Van de Poel JL, Sonké B, Sosef MSM, Stévant T, Stoffelen P, Svenning JC, Sepulchre P, Van Der Burgt X, Wieringa JJ and Couvreur TLP (2016) RAINBIO: a mega-database of tropical African vascular plants distributions. *PhytoKeys* **74**, 1–18.
- Davis CC, Willis CG, Connolly B, Kelly C and Ellison AM (2015) Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* **102**, 1599–1609.
- Deblauwe V, Droissart V, Bose R, Sonké B, Blach-Overgaard A, Svenning JC, Wieringa JJ, Ramesh BR, Stévant T and Couvreur TLP (2016) Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Global Ecology and Biogeography* **25**, 443–454.
- Demenou BB, Doucet JL and Hardy OJ (2018) History of the fragmentation of the African rain forest in the Dahomey Gap: insight from the demographic history of *Terminalia superba*. *Heredity* **120**, 547–561.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D and Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46.
- Doucet JL (2003) L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. PhD Dissertation: Université Gembloux Agro-Bio Tech, Gembloux, Belgique.
- Fayolle A, Swaine MD, Bastin JF, Bourland N, Comiskey JA, Dauby G, Doucet JL, Gillet JF, Gourlet-Fleury S, Hardy OJ, Kirunda B, Kouamé FN and Plumptre AJ (2014) Patterns of tree species composition across tropical African forests. *Journal of Biogeography* **41**, 2320–2331.
- Fétéké F, Fayolle A, Daïnou K, Bourland N, Dié A, Lejeune P, Doucet JL and Beekman H (2016) Variations saisonnières de la croissance diamétrique et des phénomènes foliaire et reproductive de trois espèces ligneuses commerciales d'Afrique centrale. *Bois et Forêts des Tropiques* **330**.
- Funk C, Peterson P, Landsfeld M, Pedreros D, Verdin J, Shukla S, Husak G, Rowland J, Harrison L, Hoell A and Michaelsen J (2015) The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. *Scientific Data* **2150066**.
- Gelman A, Carlin JB, Stern HS and Rubin DB (2003) *Bayesian Data Analysis*. Boca Raton, FL: CRC Press.
- Gond V, Fayolle A, Pennec A, Cornu G, Mayaux P, Camberlin P, Doumenge C, Fauvet N and Gourlet-Fleury S (2013) Vegetation structure and greenness in Central Africa from Modis multi-temporal data. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**20120309.
- Gonmadje CF, Doumenge C, Sunderland TCH, Balinga MPB and Sonké B (2012) Analyse phytogéographique des forêts d'Afrique Centrale: le cas du massif de Ngovayang (Cameroun). *Plant Ecology and Evolution* **145**, 152–164.
- Gorel AP, Fayolle A and Doucet JL (2015) Ecologie et gestion des espèces multi-usages du genre *Erythrophleum* (Fabaceae-Caesalpinioideae) en Afrique (synthèse bibliographique). *Biotechnologie, Agronomie, Société et Environnement* **19**, 415–429.
- Guan K, Wolf A, Medvigy D, Caylor KK, Pan M and Wood EF (2013) Seasonal coupling of canopy structure and function in African tropical forests and its environmental controls. *Ecosphere* **4**, 1–21.
- Hardy OJ, Born C, Budde K, Daïnou K, Dauby G, Duminiel J, Ewédjé EEB, Gomez C, Heuertz M and Koffi GK (2013) Comparative phylogeography of African rain forest trees: a review of genetic signatures of vegetation history in the Guineo-Congolian region. *Comptes rendus Geoscience* **345**, 284–296.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG and Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.
- Janzen DH (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* **21**, 620–637.
- Kouadio YL (2009) Mesures sylvicoles en vue d'améliorer la gestion des populations d'essences forestières commerciales de l'Est du Cameroun. PhD Dissertation: Université de Liège – Gembloux Agro-Bio Tech, Gembloux, Belgique. 241 pp.
- Letouzey R (1985) Notice de la carte phytogéographique du Cameroun au 1:500,000 (1985). *Institut de la Carte Internationale de la Végétation, Toulouse and Institut de la Recherche Agronomique, Yaoundé Cameroun*.
- Menga P, Nasi R, Bayol N and Fayolle A (2012) Phénologie et diamètre de fructification du wengé, *Millettia laurentii* De Wild: implications pour la gestion. *Bois et Forêts des Tropiques* **312**.
- Meunier Q, Moubogou C and Doucet JL (2015) *Les arbres utiles du Gabon*. Gembloux: Presses Agronomiques de Gembloux.
- Monks A, Monks JM and Tanentzap AJ (2016) Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist* **210**, 419–430.
- Morelato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC and Zipparro VB (2000) Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* **32**, 811–823.
- Mulder K and Klugkist I (2017) Bayesian estimation and hypothesis tests for a circular generalized linear model. *Journal of Mathematical Psychology* **80**, 4–14.
- Newstrom LE, Frankie GW and Baker HG (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* **26**, 141–159.
- Norden N, Chave J, Belbenoit P, Caubère A, Châtelet P, Forget PM and Thébaud C (2007) Mast fruiting is a frequent strategy in woody species of Eastern South America. *PLoS ONE* **2**, e1079.
- Ouédraogo DY, Doucet JL, Daïnou K, Baya F, Biwolé AB, Bourland N, Fétéké F, Gillet JF, Kouadio YL and Fayolle A (2018) The size at reproduction of canopy tree species in central Africa. *Biotropica* **50**, 465–476.
- Palla F and Louppe D (2002) *Obéché. Fiche technique, écologique et sylvicole*. Montpellier: Cirad-Forêt.
- Palla F, Louppe D and Doumenge C (2002a) *Azobé. Fiche technique, écologique et sylvicole*. Montpellier: Cirad-Forêt.
- Palla F, Louppe D and Forni E (2002b) *Sapelli. Fiche technique, écologique et sylvicole*. Montpellier: Cirad-Forêt.
- Pau S, Wolkovich EM, Cook BI, Nyctch CJ, Regetz J, Zimmerman JK and Wright SJ (2013) Clouds and temperature drive dynamic changes in tropical flower production. *Nature Climate Change* **3**, 838–842.
- Réjou-Méchain M and Cheptou PO (2015) High incidence of dioecy in young successional tropical forests. *Journal of Ecology* **103**, 725–732.
- Rosenzweig C, Casassa G, Karoly DJ, Imeson A, Liu C, Menzel A, Rawlins S, Root TL, Seguin B and Tryjanowski P (2007) Assessment of observed changes and responses in natural and managed systems. In Parry ML,

- Canziani OF, Palutikof JP, van der Linden PJ and Hanson CE (eds), *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press, pp. 79–131.
- Sakai S** (2001) Phenological diversity in tropical forests. *Population Ecology* **43**, 77–86.
- Van Schaik CP, Terborgh JW and Wright SJ** (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* **24**, 353–377.
- Sosef MSM, Dauby G, Blach-Overgaard A, Van Der Burg X, Catarino L, Damen T, Deblauwe V, Dessein S, Dransfield J, Droissart V, Duarte MC, Engledow H, Fateur G, Figueira R, Gereau RE, Hardy OJ, Harris DJ, De Heij J, Janssens S, Klomberg Y, Ley AC, Mackinder BA, Meerts P, Van De Poel JL, Sonké B, Stévant T, Stoffelen P, Svenning JC, Sepulchre P, Zaiss R, Wieringa JJ and Couvreur TLP** (2017) Exploring the floristic diversity of tropical Africa. *BMC Biology* **15**, 15.
- Stropp J, Ladle RJ, Malhado ACM, Hortal J, Gaffuri J, Temperley WH, Skoien JO and Mayaux P** (2016) Mapping ignorance: 300 years of collecting flowering plants in Africa. *Global Ecology and Biogeography* **25**, 1085–1096.
- Sun C, Kaplin BA, Kristensen KA, Munyaligoga V, Mvukiyumwami J, Kajondo KK and Moermond TC** (1996) Tree phenology in a tropical montane forest in Rwanda. *Biotropica* **28**, 668–681.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O and Bairlein F** (2002) Ecological responses to recent climate change. *Nature* **416**, 389–395.
- White F** (1983) *The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. Paris: UNESCO.
- Wieringa JJ** (1999) *Monopetalanthus* exit.: a systematic study of Aphanocalyx, Bikinia, Icuria, Michelsonia and Tetraberlinia (Leguminosae, Casalpinoideae). *Wageningen Agricultural University Papers* **99 4**, 1–320.
- Willis CG, Ellwood ER, Primack RB, Davis CC, Pearson KD, Gallinat AS, Yost JM, Nelson G, Mazer SJ, Rossington NL, Sparks TH and Soltis PS** (2017) Old plants, new tricks: phenological research using herbarium specimens. *Trends in Ecology and Evolution* **32**, 531–546.
- Wright SJ and Calderón O** (2018) Solar irradiance as the proximate cue for flowering in a tropical moist forest. *Biotropica* **50**, 374–383.
- Wright SJ and van Schaik CP** (1994) Light and the phenology of tropical trees. *American Naturalist* **143**, 192–199.
- Zalamea PC, Munoz F, Stevenson PR, Paine CET, Sarmiento C, Sabatier D and Heuret P** (2011) Continental-scale patterns of *Cecropia* reproductive phenology: evidence from herbarium specimens. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20102259.
- Zhang H, Yuan W, Liu S, Dong W and Fu Y** (2015) Sensitivity of flowering phenology to changing temperature in China. *Journal of Geophysical Research: Biogeosciences* **120**, 1658–1665.

Appendices

Appendix 1

For the flowering herbarium specimens of the eight species, number of specimens coming from each herbarium (Meise: Meise Botanic Garden; Paris: National Museum of Natural History in Paris; Leiden: Naturalis Biodiversity Center in Leiden; Kew: Royal Botanical Gardens Kew) and total number of specimens (N Total).

| Species | Meise | Paris | Leiden | Kew | N Total |
|------------------------------------|-------|-------|--------|-----|---------|
| <i>Entandrophragma cylindricum</i> | 40 | 8 | 4 | 1 | 53 |
| <i>Erythrophleum suaveolens</i> | 38 | 37 | 35 | 1 | 111 |
| <i>Lophira alata</i> | 7 | 8 | 15 | 1 | 31 |
| <i>Mansonia altissima</i> | 0 | 10 | 7 | 0 | 17 |
| <i>Milicia excelsa</i> | 39 | 27 | 15 | 8 | 89 |
| <i>Pterocarpus soyauxii</i> | 29 | 10 | 16 | 1 | 56 |
| <i>Terminalia superba</i> | 7 | 11 | 8 | 2 | 28 |
| <i>Triplochiton scleroxylon</i> | 7 | 13 | 9 | 2 | 31 |

Appendix 2

For the eight study species *Entandrophragma cylindricum* (a), *Erythrophleum suaveolens* (b), *Lophira alata* (c), *Mansonia altissima* (d), *Milicia excelsa* (e), *Pterocarpus soyauxii* (f), *Terminalia superba* (g) and *Triplochiton scleroxylon* (h), correlation matrix of the variables used to explain the variation in the collection month of flowering herbarium specimens. 'Year' corresponds to the year of collection, 'Latitude' to specimen's latitude coordinate, 'Longitude' to specimen's longitude coordinate, and 'Timing dry season' corresponds to the first axis scores of a principal component analysis on monthly rainfall, with positive scores indicating that the major dry season occurs in December–January–February, and negative scores indicating that the major dry season occurs in July–August. Pearson's correlation coefficients are displayed below the diagonal, and associated P values above the diagonal.

| (a) <i>Entandrophragma cylindricum</i> (N = 53 specimens) | | | | |
|--|-------|----------|-----------|-------------------|
| | Year | Latitude | Longitude | Timing dry season |
| Year | – | 0.295 | 0.559 | 0.494 |
| Latitude | 0.15 | – | 0 | 0 |
| Longitude | –0.08 | –0.84 | – | 0 |
| Timing dry season | 0.10 | 0.92 | –0.67 | – |
| (b) <i>Erythrophleum suaveolens</i> (N = 111 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | – | 0.241 | 0.852 | 0.022 |
| Latitude | –0.11 | – | 0 | 0 |
| Longitude | 0.02 | –0.72 | – | 0 |
| Timing dry season | –0.22 | 0.82 | –0.6 | – |
| (c) <i>Lophira alata</i> (N = 31 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | – | 0.220 | 0.087 | 0.043 |
| Latitude | –0.23 | – | 0.006 | 0 |

(Continued)

(Continued)

| | | | | |
|---|-------|----------|-----------|-------------------|
| Longitude | -0.31 | -0.49 | - | 0.126 |
| Timing dry season | -0.37 | 0.88 | -0.28 | - |
| (d) <i>Mansonia altissima</i> (N = 17 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | - | 0.540 | 0.558 | 0.836 |
| Latitude | -0.16 | - | 0 | 0.187 |
| Longitude | -0.15 | -0.81 | - | 0.912 |
| Timing dry season | 0.05 | 0.34 | -0.03 | - |
| (e) <i>Milicia excelsa</i> (N = 89 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | - | 0.423 | 0.010 | 0.566 |
| Latitude | -0.09 | - | 0 | 0 |
| Longitude | 0.27 | -0.70 | - | 0 |
| Timing dry season | 0.06 | 0.80 | -0.56 | - |
| (f) <i>Pterocarpus soyauxii</i> (N = 56 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | - | 0.167 | 0.366 | 0.859 |
| Latitude | -0.19 | - | 0.528 | 0 |
| Longitude | -0.12 | -0.09 | - | 0.101 |
| Timing dry season | -0.02 | 0.79 | 0.22 | - |
| (g) <i>Terminalia superba</i> (N = 28 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | - | 0.885 | 0.777 | 0.892 |
| Latitude | 0.03 | - | 0 | 0 |
| Longitude | 0.06 | -0.67 | - | 0.038 |
| Timing dry season | -0.03 | 0.84 | -0.39 | - |
| (h) <i>Triplochiton scleroxylon</i> (N = 31 specimens) | | | | |
| | Year | Latitude | Longitude | Timing dry season |
| Year | - | 0.235 | 0.350 | 0.912 |
| Latitude | -0.22 | - | 0 | 0 |
| Longitude | 0.17 | -0.89 | - | 0.002 |
| Timing dry season | 0.02 | 0.66 | -0.53 | - |