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

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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.* 2012*b*). All of these studies were conducted in the Neotropics except for the study of Daïnou *et al.* (2012*b*) 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).

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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 (~2°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.* 2012*a*) and *E. suaveolens* (unassisted and animal dispersal; Gorel *et al.* 2015). Except for *M. excelsa* which is wind-pollinated (Daïnou *et al.* 2012*b*), all other trees are insect-pollinated (*E. cylindricum*, Palla *et al.* 2002*b*; *L. alata*, Palla *et al.* 2002*a*) or probably insect-pollinated species (Akinnagbe *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 Zambezian 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.* 2012*b*, 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

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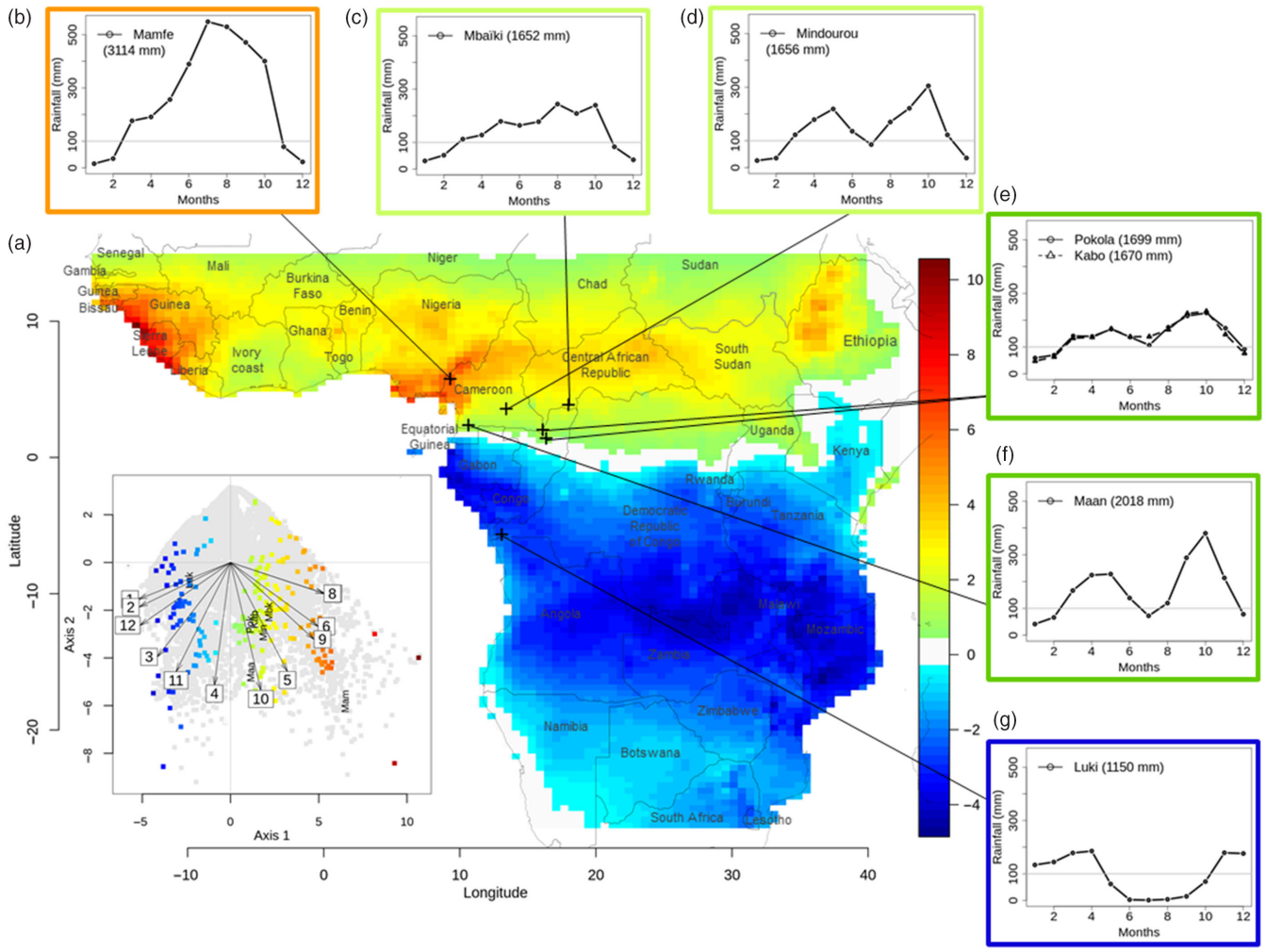

Figure 1. (a) Location of the study sites (black crosses) on a map with grid cells coloured according to the first axis scores of the principal component analysis of mean monthly rainfall (from negative scores in blue to positive scores in red). The inset shows the correlation circle of monthly rainfall (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

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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, rho the length of the mean vector indicating the concentration of flowering activity around a specific date, P the significance of rho, and Date the mean time of occurrence of flowering

					Circular statistics				
Species	Site	Period	N census	Cycle	*Ntree*	*N*	rho	P	Date
Entandrophragma cylindricum	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
Erythrophleum suaveolens	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
Lophira alata	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
Mansonia altissima	Mindourou	2004–2007	46	Annual	47	244	0.85	<0.001	12 August
Milicia excelsa	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
Pterocarpus soyauxii	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
Terminalia superba	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
Triplochiton scleroxylon	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

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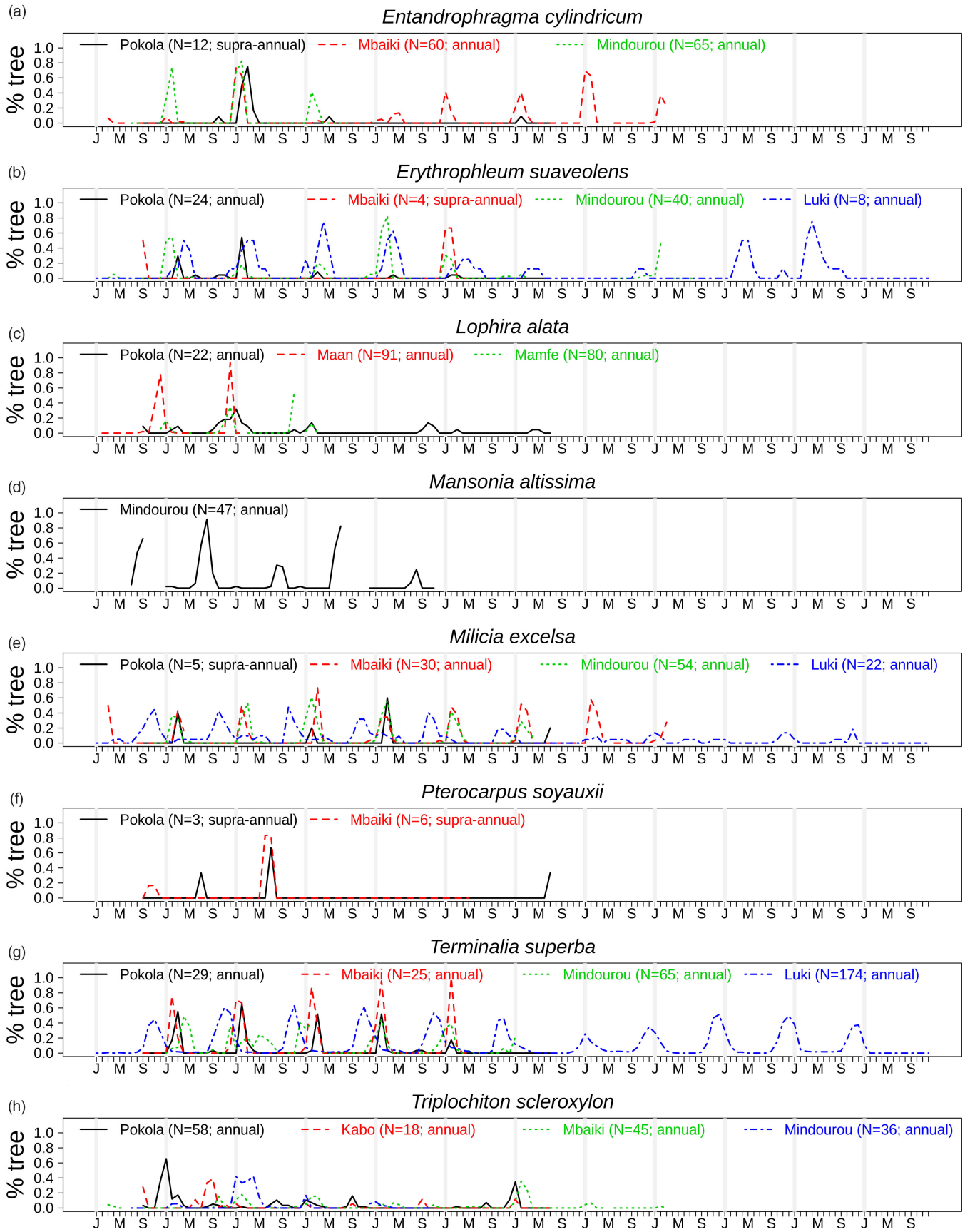

Figure 2. For the eight study species *Entandrophragma cylindricum* (a), *Erythrophleum suaveolens* (b), *Lophira alata* (c), *Mansonia altissima* (d), *Milicia excelsa* (e), *Pterocarpus soyauxii* (f), *Terminalia superba* (g) and *Triplochiton scleroxylon* (h), proportion of trees flowering in each 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).

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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).

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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)

		Mean date of flowering and associated season						
Species	Cycle	Mamfe (6.5)	MBaïki (2.1)	Mindourou (1.8)	Kabo (1.3)	Pokola (1.1)	Maan (1.1)	Luki (−2.4)
Entandrophragma cylindricum	Annual (Supra-annual)	-	10 February	5 February	–	8 March	–	–
			long_dry	long_dry		long_dry		
Erythrophleum suaveolens	Annual (Supra-annual)	–	23 January	16 February	–	26 February	–	12 April
			long_dry	long_dry		long_dry		wet
Lophira alata	Annual	17 December	–	–	–	26 December	12 December	–
		long_dry				long_dry	long_dry	
Mansonia altissima	Annual	–	–	12 August	–	–	–	–
				short_dry				
Milicia excelsa	Annual (Supra-annual)	–	8 March	27 February	–	18 March	–	21 November
			long_dry	long_dry		long_dry		wet
Pterocarpus soyauxii	Supra-annual	–	20 July	–	–	21 Jul	–	–
			short_dry			short_dry		
Terminalia superba	Annual	–	14 February	15 February	–	27 February	–	30 November
			long_dry	long_dry		long_dry		wet
Triplochiton scleroxylon	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.* 2012*b*) 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 Fourrier 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.* 2012*b*) and *Millettia laurentii* in the Mai Ndombe area, DRC

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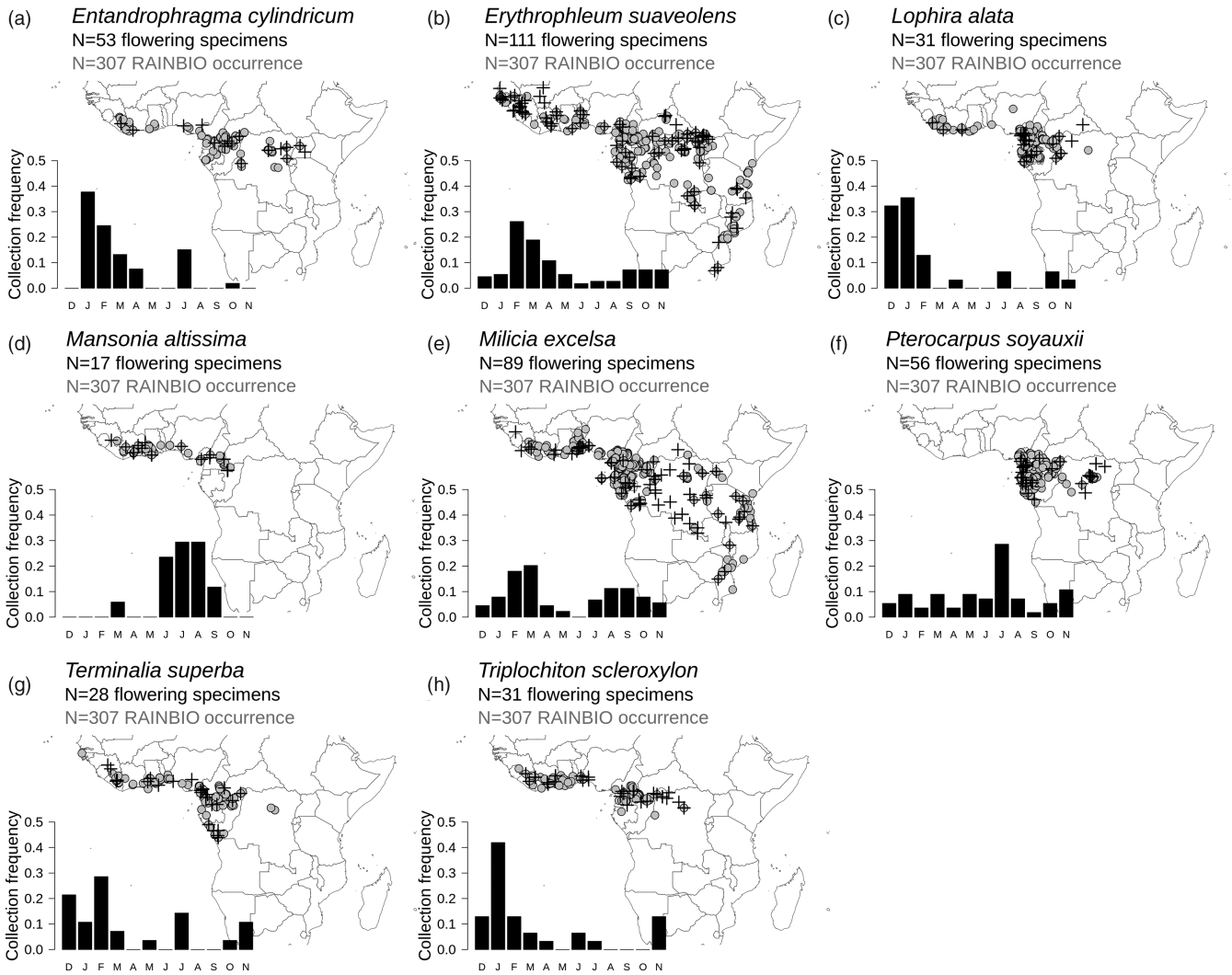

Figure 3. Location of flowering herbarium specimens (black crosses, number n indicated in black) across Africa for the eight species *Entandrophragma cylindricum* (a), *Erythrophleum suaveolens* (b), *Lophira alata* (c), *Mansonia altissima* (d), *Milicia excelsa* (e), *Pterocarpus soyauxii* (f), *Terminalia 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

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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
Entandrophragma cylindricum ([−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]
Erythrophleum suaveolens ([−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]
Lophira alata ([−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]*
Mansonia altissima ([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]
Milicia excelsa ([−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*)

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Table 3. (*Continued*)

Species	Model	WAIC	Estimates
Pterocarpus soyauxii ([−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]
Terminalia superb ([−5.9, 10]) (N = 28)	Year	96.319	0.450 [−0.323; 1.288]
	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]
Triplochiton scleroxylon ([0.8, 8.1]) (N = 31)	Year	90.381	0.044 [−0.139; 0.232]
	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.* (2012*b*) 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

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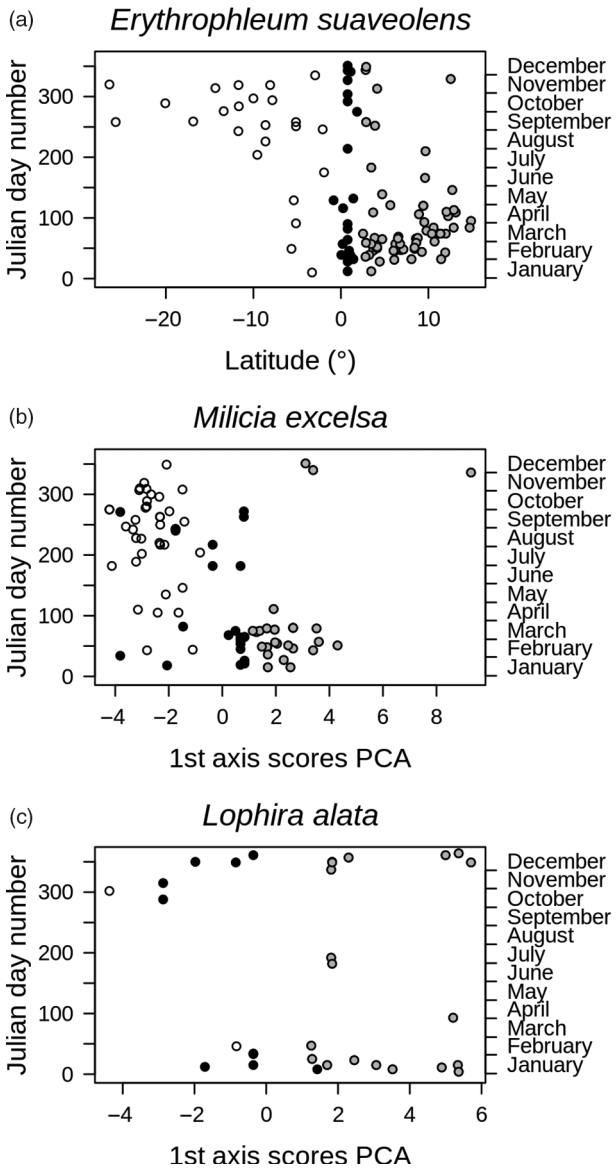

Figure 4. Relationship between calendar dates of flowering herbarium specimens (in Julian days) and the variable explaining their variation, that is latitude for *Erythrophleum suaveolens* (a) and timing of the dry season (first axis score of the PCA on monthly rainfall) for *Milicia excelsa* (b) and *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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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
Entandrophragma cylindricum	40	8	4	1	53
Erythrophleum suaveolens	38	37	35	1	111
Lophira alata	7	8	15	1	31
Mansonia altissima	0	10	7	0	17
Milicia excelsa	39	27	15	8	89
Pterocarpus soyauxii	29	10	16	1	56
Terminalia superba	7	11	8	2	28
Triplochiton scleroxylon	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) *Entandrophragma cylindricum* (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) *Erythrophleum suaveolens* (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) *Lophira alata* (N = 31 specimens)				
	Year	Latitude	Longitude	Timing dry season
Year	–	0.220	0.087	0.043
Latitude	−0.23	–	0.006	0

(*Continued*)

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(*Continued*)

Longitude	−0.31	−0.49	–	0.126
Timing dry season	−0.37	0.88	−0.28	–
(d) *Mansonia altissima* (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) *Milicia excelsa* (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) *Pterocarpus soyauxii* (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) *Terminalia superba* (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) *Triplochiton scleroxylon* (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	–

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