



Deposited via The University of York.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/129767/>

Version: Accepted Version

Article:

Adamescu, Gabriela Simina, Plumptre, Andrew J., Abernethy, Katharine A. et al. (2018)
Annual cycles are the most common reproductive strategy in African tropical tree
communities. *Biotropica*. pp. 418-430. ISSN: 0006-3606

<https://doi.org/10.1111/btp.12561>

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



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

Journal:	<i>Biotropica</i>
Manuscript ID	BITR-17-100.R3
Manuscript Type:	Paper
Date Submitted by the Author:	24-Mar-2018
Complete List of Authors:	<p>Adamescu, Gabriela; University of York, Department of Biology Plumptre, Andrew; WCS, Albertine Rift; Abernethy, Katharine; University of Stirling, School of Natural Sciences; CENAREST, Institut de Recherche en Ecologie Tropicale Polansky, Leo; Max-Planck-Institut für evolutionäre Anthropologie, Department of Primatology Bush, Emma; University of Stirling, Biological and Environmental Sciences Chapman, Colin; McGill University, Anthropology/School of Environment Shoo, Luke; The University of Queensland, School of Biological Sciences Fayolle, Adeline; Gembloux Agro-Bio Tech / ULg, Unit of Forest and Nature Management Janmaat, Karline; Max-Planck-Institut für evolutionäre Anthropologie, Department of Primatology Robbins, Martha; Max Planck Institute of Evolutionary Anthropology, Primatology Ndangalasi, Henry; University of Dar es Salaam, Botany Cordeiro, Norbert; Roosevelt University, Biology Aud 520; The Field Museum, Departments of Zoology & Botany Glibly, Ian; Arizona State University School of Human Evolution and Social Change Wittig, Roman; Max-Planck-Institut für evolutionäre Anthropologie Breuer, Thomas; Wildlife Conservation Society - Congo Program, Mbeli Bai Study; Max Planck Institute for Evolutionary Anthropology, Primatology Ndoundou Hockemba, Mireille; Wildlife Conservation Society - Congo Program, Mbeli Bai Study; Sanz, Crickette; Washington University in St Louis, Anthropology Morgan, David; Lester E. Fisher Center for the Study and Conservation of Apes Pusey, Anne; Duke University, Department of Evolutionary Anthropology Mugerwa, Badru ; University of Dar es Salaam Gilagiza , Baraka ; Gombe Stream Research Centre Tutin, Caroline; University of Stirling, Biological and Environmental Sciences Ewango, Corneille; Wildlife Conservation Society Sheil, Douglas; Center for International Forestry Research, Dimoto, Edmond; Agence Nationale des Parcs Nationaux (ANPN) Baya, Fidèle; Agence Nationale des Parcs Nationaux (ANPN) Flort, Bujo; Wildlife Conservation Society Ssali, Fredrick; University of Dar es Salaam, Department of Botany</p>

	<p>Dikangadissi, Jean-Thoussaint ; Agence Nationale des Parcs Nationaux (ANPN)</p> <p>Jeffery, Kathryn; University of Stirling, Biological and Environmental Sciences; Institut de Recherche en Écologie Tropicale, CENAREST; Agence Nationale des Parcs Nationaux (ANPN)</p> <p>Valenta, Kim; University of Toronto, Anthropology</p> <p>White, Lee; Agence Nationale des Parcs Nationaux (ANPN); University of Stirling, Biological and Environmental Sciences; Institut de Recherche en Écologie Tropicale, CENAREST</p> <p>Masozera, Michel; Wildlife Conservation Society</p> <p>Wilson, Michael; University of Minnesota, Department of Ecology, Evolution and Behavior</p> <p>Bitariho, Robert; University of Dar es Salaam</p> <p>Ndolo Ebika, Sydney ; Initiative des Champignons et des Plantes du Congo (ICPC)</p> <p>Gourlet-Fleury, Sylvie; CIRAD, FORESTRY</p> <p>Mulindahabi , Felix; Wildlife Conservation Society</p> <p>Beale, Colin; University of York, Department of Biology</p>
Keywords:	Phenology, Annual cycles, Seasonality, Flowers, Fruits, Tropical forest, Africa

SCHOLARONE™
Manuscripts

Review Only

BIOTROPICA

THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

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

Authors: Gabriela S. Adamescu¹, Andrew J. Plumptre^{2,3}, Katharine A. Abernethy^{4,5}, Leo Polansky⁶, Emma R. Bush⁴, Colin A. Chapman⁷, Luke P. Shoo⁸, Adeline Fayolle⁹, Karline R. L. Janmaat⁶, Martha M. Robbins⁶, Henry J. Ndangalasi²⁴, Norbert J. Cordeiro¹⁰, Ian C. Gilby¹¹, Roman M. Wittig^{6, 12}, Thomas Breuer^{2, 13}, Mireille Breuer-Ndoundou Hockemba¹³, Crickette M. Sanz^{14, 15}, David B. Morgan¹⁶, Anne E. Pusey¹⁷, Badru Mugerwa²⁵, Baraka Gilagiza¹⁸, Caroline Tutin⁴, Corneille E.N. Ewango², Douglas Sheil²⁵, Edmond Dimoto¹⁹, Fidèle Baya²⁰, Flort Bujo², Fredrick Ssali²⁵, Jean-Thoussaint Dikangadissi¹⁹, Kathryn Jeffery^{4,19}, Kim Valenta⁷, Lee White^{4,5,19}, Michel Masozera², Michael L. Wilson²¹, Robert Bitariho²⁵, Sydney T. Ndolo Ebika²², Sylvie Gourlet-Fleury²³, Felix Mulindahabi² and Colin M. Beale¹

1. Department of Biology, University of York, Wentworth Way, York, YO10 5DD, UK
2. Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA
3. Conservation Science Group, Department of Zoology, Cambridge University, Pembroke Rd, Cambridge, United Kingdom
4. Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, Scotland, UK

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 26 5. Institut de Recherche en Ecologie Tropicale, CENAREST, BP 842, Libreville, Gabon
- 4
5 27 6. Department of Primatology, Max Planck Institute for Evolutionary Anthropology,
6
7 28 Leipzig, Deutscher Platz 6, 04103, Leipzig, Germany
- 8
9 29 7. Department of Anthropology and McGill School of Environment, McGill University,
10
11 30 Montreal, Quebec, Canada, and Wildlife Conservation Society, Bronx, NY, U.S.A.
- 12
13
14 31 8. School of Biological Sciences, The University of Queensland, Brisbane, Queensland,
15
16 32 Australia
- 17
18 33 9. TERRA Teaching and Research Center, Gembloux Agro-Bio Tech, Liège University, Passage des
19
20 34 Déportés 2, 5030 Gembloux, Belgium
- 21
22
23
24 35 10. Roosevelt University, Dept. of Biology, 430 Michigan Ave, Chicago, IL 60605, U.S.A.
25
26 36 & Science and Education, The Field Museum, 1400 S. Lake Shore Dr., Chicago, IL
27
28 37 60605, U.S.A.
- 29
30
31 38 11. School of Human Evolution and Social Change, Arizona State University
- 32
33 39 12. Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, BP 1303, Abidjan 01, Ivory
34
35 40 Coast
- 36
37
38 41 13. Mbeli Bai Study, Wildlife Conservation Society – Congo Program, 151 Avenue Charles de
39
40 42 Gaulle, 14537 Brazzaville, Republic of Congo
- 41
42 43 14. Washington University in St. Louis, Department of Anthropology, 1 Brookings Drive, Saint Louis,
43
44 44 MO 63130, U.S.A.
- 45
46
47 45 15. Congo Program, Wildlife Conservation Society, 151 Avenue de Gaulle, Brazzaville, Republic of
48
49 46 Congo
- 50
51 47 16. Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, 2001 North
52
53 48 Clark Street, Chicago, IL 60614, U.S.A.

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 49 17. Department of Evolutionary Anthropology, Duke University
4
5 50 18. Gombe Stream Research Centre, Tanzania
6
7
8 51 19. Agence Nationale des Parcs Nationaux (ANPN), B.P. 20379, Libreville, Gabon
9
10 52 20. Ministère des Eaux, Forêts, Chasse et Pêche, BP 3314 Bangui, Central African Republic
11
12 53 21. Departments of 1) Anthropology and 2) Ecology, Evolution & Behavior, University of Minnesota
13
14 54 22. Initiative des Champignons et des Plantes du Congo (ICPC), B.P. 2300, Brazzaville, Republic of
15
16 Congo
17 55
18
19 56 23. UPR Bsef, CIRAD, Montpellier, France
20
21 57 24. Department of Botany, University of Dar es Salaam, P.O. Box 35060, Dar es Salaam, Tanzania
22
23 58 25. Institute of Tropical Forest Conservation (ITFC), PO BOX 44, Kabale, Uganda
24
25
26 59 26. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of
27
28 Life Sciences.
29 60
30
31 61
32
33 62
34
35
36 63
37
38
39 64 **Corresponding author:** Gabriela S. Adamescu, adamescusimina@gmail.com
40
41
42 65
43
44
45 66 Received _____; revision accepted _____.
46
47
48 67
49
50
51
52
53
54
55
56
57
58
59
60

68 ABSTRACT


69
70 We present the first cross continental comparison of the flowering and fruiting phenology of
71 tropical forests across Africa. Flowering events of 5,446 trees from 196 species across 12 sites,
72 and fruiting events of 4,595 trees from 191 species, across 11 sites were monitored over periods
73 of 6 to 29 years, and analysed to describe phenology at the continental level. To study phenology
74 we used Fourier analysis to identify the dominant cycles of flowering and fruiting for each
75 individual tree and we identified the time of year African trees bloom and bear fruit and their
76 relationship to local seasonality. Reproductive strategies were diverse and no single regular cycle
77 was found in >50% of individuals across all 12 sites. Additionally, we found annual flowering
78 and fruiting cycles to be the most common. Sub-annual cycles were the next most common for
79 flowering whereas supra-annual patterns were the next most common for fruiting. We also
80 identify variation in different subsets of species, with species exhibiting mainly annual cycles
81 most common in West and West-Central African tropical forests, while more species at sites in
82 East-Central and Eastern African forests showed cycles ranging from sub-annual to supra-annual.
83 Despite many trees showing strong seasonality, at most sites some flowering and fruiting
84 occurred all year round. Environmental factors with annual cycles are likely to be important
85 drivers of seasonal periodicity in trees across Africa, but proximate triggers are unlikely to be
86 constant across the continent.

87
88 Key words: Phenology; Annual cycles; Seasonality; Flowers; Fruits; Tropical forest; Africa

89
90 Word count: 5096

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 91 PLANT PHENOLOGY, THE TIMING OF CYCLICAL BIOLOGICAL EVENTS (PHENOPHASES) SUCH AS
4
5 92  flowering and fruiting, is essential for the reproductive success of plants, and equally
6
7 93 important for animals that rely on plant resources to survive and reproduce (van Schaik *et al.*
8
9 94 1993, Sakai 2001). Phenology is well studied in northern, temperate systems (Visser & Both
10
11 95 2005) and changes in phenology associated with climate warming are widespread (Parmesan &
12
13 96 Yohe 2003). However, the phenology of tropical plants is poorly understood, due both to the
14
15 97 paucity of long-term data sets and the complexity of individual patterns (Gentry 1974, Hudson &
16
17 98 Keatley 2009). Ultimately, if we are to understand how phenology is changing in the tropics, it is
18
19 99 vitally important to establish how canopy-level patterns emerge from variation at the levels of
20
21
22
23
24 100 species and communities.

25
26 101
27
28 102 Globally, tropical forests are characterised by an exceptionally high diversity of plant species,
29
30 103 which can flower or fruit at any time of the year, often with very different patterns to other
31
32 104 species within the same forest, including closely related taxa (Bawa *et al.* 2003, Zhou *et al.*
33
34 105 2014). Flowering and fruiting events in tropical forests vary from complete intraspecific
35
36 106 synchrony to extreme asynchrony, and from constant activity to recurrent short pulses (van
37
38 107 Schaik *et al.* 1993). Depending on the environmental conditions, species, individual tree
39
40 108 characteristics, location and sometimes year, different phenophases occur at different times of
41
42 109 the year, in different seasons, and vary in their frequencies and duration (Sakai *et al.* 1999, Pau *et*
43
44 110 *al.* 2013, Bush *et al.* 2017).

45
46 111
47
48
49
50 112 To produce leaves, flowers, or fruits, an adult tree needs to accumulate sufficient nutritional
51
52 113 resource before a phenophase onset can be triggered (Opler *et al.* 1976). Consequently, weather
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 114 conditions that could trigger phenophase onset cannot do so if the tree has not first acquired
4
5 115 sufficient resources to enable it to respond (Bullock & Solis-Magallanes 1990). Fruiting events
6
7
8 116 also do not necessarily always follow flowering, as flowers may not be pollinated, may be
9
10 117 damaged by weather and herbivores, or trees may abort unripe fruits (Stephenson 1981). These
11
12 118 factors make the study of phenological responses in relation to climate extremely challenging.
13
14 119 Large and long-term datasets are therefore required to study general phenological patterns, and
15
16
17 120 this is especially needed to offset the high heterogeneity of individual tree responses.
18
19 121
20
21 122 Regular patterns in phenophase expression can be a first indicator of the factors that drive and
22
23 123 mediate plant responses. Analysis of both cycle length and timing of regular patterns in
24
25 124 phenology at annual (including supra-annual and sub-annual variants) and seasonal scales is a
26
27 125 first step to elucidating potential environmental triggers for various phenophases. In tropical
28
29 126 forests, climate is not as seasonally restrictive for plant growth as in temperate areas, with the
30
31 127 exceptions of dry forests, which have little or no rainfall for months. Seasonality in the tropics
32
33 128 is dominated by the intertropical convergence zone (ITCZ), a band of warm air, which carries
34
35 129 precipitation north and south over the equator in annual cycles (National Weather Service 2010),
36
37 130 but regular seasonal differences in rainfall and temperature are relatively small for the majority
38
39 131 of forests (van Schaik *et al.* 1993).
40
41 132
42
43 133 Asian and South American studies dominate our current knowledge of tropical phenology (Sakai
44
45 134 2001, Chambers *et al.* 2013, Mendoza *et al.* 2017, Morellato *et al.* 2013). In these regions,
46
47 135 phenology has been described in terms of timing, duration, synchronicity, and dominant cycles
48
49 136 (McEwan & McCarthy 2005). In South-East Asia and South America the highly variable
50
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 137 phenology patterns of trees can be triggered by various cues, including sudden drops in solar
4
5 138 radiation, plant moisture availability, heavy rain or increased temperatures (Corlett & Lafrankie
6
7 139 1998, Sakai *et al.* 1999, Butt *et al.* 2015.). Compared to Asian and Neotropical forests, tropical
8
9
10 140 forests in Africa have been little studied in terms of phenology, and this is mainly because of the
11
12 141 relative lack of long-term data sets. As a stark comparison, a recent review of Neotropical
13
14 142 phenology studies compiled data from 218 phenology study sites, with 10 sites yielding
15
16 143 information from more than a decade (Mendoza *et al.* 2017). In contrast, our efforts to analyse
17
18 144 phenological patterns across tropical Africa produced data from just 17 sites, of which only nine
19
20 145 have data from more than a decade (Plumptre *et al.* 2012; this study).
21
22
23
24 146

25
26 147 Despite the shortcomings of scant long-term phenological datasets from tropical Africa, what we
27
28 148 do know from the few African forests (East and West Africa) that have been previously studied
29
30 149 in detail, is that (i) flowering and fruiting frequencies vary from sub-annual to supra-annual
31
32 150 (Chapman *et al.* 1999, Polansky & Boesch 2013, Janmaat *et al.* 2016, Bush *et al.* 2017), and (ii)
33
34 151 annual flowering cycles were found to be the most common. These important findings from less
35
36 152 than a handful of studies representing a narrow range of tropical Africa beckoned for a more in-
37
38 153 depth analysis across the continent. In an effort to undertake initial steps towards describing
39
40 154 continental patterns in phenological responses and defining likely environmental cues for
41
42 155 phenological behaviour in African forests, we here (i) analyze cycles observed in phenophases at
43
44 156 different sites, and (ii) examine the site-based relationships between phenophases and seasonal
45
46 157 weather cycles that can reliably be extracted from global datasets.
47
48
49
50

51 158

52 159

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 160 Understanding phenology in African forests has become a fundamental issue in tropical forest
4
5 161 ecology and conservation of trees and inter-dependent fauna whose survival is threatened by
6
7 162 climate change and other anthropogenic pressures such as logging and hunting (Butt *et al.* 2015).
8
9
10 163 We therefore consider this continental wide analysis as a vital step towards understanding and
11
12 164 elucidating phenological patterns of African forest tree species. As such, this study provides a
13
14 165 first overview of variability in cycle profiles within and between African sites. It allows initial
15
16 166 comparisons between the general characteristics of phenological profiles from African forests
17
18 167 with those observed on other continents or outside the tropics. Furthermore, this study lays the
19
20 168 foundation for future analyses of the climatic conditions that may be driving phenological
21
22 169 responses in flowering and fruiting across different African sites. We use a Fourier analysis of
23
24 170 trees from 12 long-term studies in tropical forests to examine the dominant pattern of flowering
25
26 171 and fruiting cycles at each site and compare cycle profiles across the African continent. We also
27
28 172 explore the seasonal phase of flowering and fruiting events of individual trees at each site.
29
30
31
32

173

174

METHODS

DATA COLLECTION — We assembled data from 12 long-term research sites across East, Central and West Africa (Fig. 1), including montane, submontane, semi-deciduous, evergreen and swamp forests (Table 1). With the exception of M'baiki which was in a conservation area within a logging concession, all forest sites were located within protected areas. Site elevation and total protected area around the study trees varied between 80 to 3000 m and from 35 km² to approximately 13,000 km², respectively. Each site experiences two main seasons, dry and wet, each present once or twice a year, depending on the site location. Average minimum and maximum monthly temperatures were between 12 and 30 °C, with maximum rainfall ranging between 200 mm and 700 mm per month (Table 2). Data collection of flowering and fruiting events (data for ripe fruit only are used in these analyses) at each site was done monthly and was accomplished by the investigators and trained field assistants. Each tree was visually monitored for the presence/absence of flowers or ripe fruits. In some sites the phenophase response was quantified, but as different scoring methods were used at different sites, we restricted our analyses to presence/absence. Monitored individuals were originally selected based on different research questions at each site and thus most sites represent a non-random subset of the total forest coverage and species diversity (More information on species diversity in Supplementary material A). One site (M'baiki) selected species important in the timber trade, but with the exception of Amani in Tanzania where phenological transects were randomly located, all other sites preferentially sampled species producing fleshy fruits, as original research questions focussed on resource availability for large mammals, mainly primates or elephants. Although the sample at any site is not limited to fleshy fruit-producing species and includes other traits, such

Adamescu *et al.*

Annual reproduction in African tropical trees

197 as abiotically-dispersed species, the systematic selection for fleshy fruits means that our total
198 sample is likely to over-represent this trait at a community level.

199
200 DATA PREPARATION — Fourier analysis requires continuous regular data. However, due to the
201 logistical challenges of field data collection, including civil unrest in some regions, there are
202 occasional gaps in the data we have available for individual time series. If gaps were shorter than
203 three months, we interpolated the missing data using a linear estimator. If gaps were longer than
204 3 months we split the data at the gap. Bush *et al.* (2017) show that time series length is a
205 significant predictor of identifying cyclic activity in phenology data. To account for this we only
206 included trees with time series longer than 60 consecutive months after linear interpolation, with
207 a minimum of 10 individuals for each species. We also excluded trees that died or never
208 flowered or fruited.

209
210 FOURIER ANALYSIS OF INDIVIDUAL VARIATION — To assess the major cyclic patterns for
211 flowering and fruiting at the sites, we used Fourier analysis to identify dominant cycles per
212 individual tree. Fourier is a spectral analysis method used to decompose a time series into a sum
213 of sine waves of different frequencies and is a robust analysis for determining plants' dominant
214 cycles (Platt & Denman 1975). Bush *et al.* (2017) showed how it could be used to statistically
215 assess the cycle length and predictability of phenology activity in tropical trees at the individual-
216 level.

217 We calculated the Fourier spectrum for each individual tree using the *R* function spectrum from
218 the *R* base package 'stats' (*R* Core Team 2015). Following the guidelines in Bush *et al.* (2017)
219 we smoothed the raw spectrum using a Daniell kernel (a moving average smoother) with varying

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 220 spans depending on the time series length to give a bandwidth of 0.1. The 0.1 bandwidth
4
5 221 represents one 10th of the length of the available time series of each tree and gives sufficient
6
7 222 resolution in the spectral estimate to assess dominant cycles while suppressing irrelevant fine-
8
9 223 scale structure (Bush *et al.* 2017).

11 224 We assessed the smoothed spectral estimate for each individual tree and extracted the cycle
12
13 225 frequency with the highest power, representing the strongest cycle in the data. Bush *et al.* (2017)
14
15 226 warn that time series with little cyclic activity can sometimes produce Fourier transforms with
16
17 227 high power in non-relevant low frequencies (e.g. the full length of the time series). To account
18
19 228 for this, we screened out individuals where the dominant cycle identified from the spectrum was
20
21 229 greater than half the length of the time series (resulting in exclusion of 9% of trees for flowering
22
23 230 and 13% of trees for fruiting). Although 9% of individuals that showed non-cyclical flowering
24
25 231 were excluded from our analyses, the bias away from shorter cycles is likely to be minimal, as
26
27 232 individuals only flowered once or twice during the whole study period at the site, rather than
28
29 233 continuously.

31 234 These data exclusions following Fourier analysis resulted in final samples of 5,446 individuals
32
33 235 (196 species) for the flowering analysis and 4,595 individuals (191 species) for the fruiting
34
35 236 analysis. Prior to application of the minimum 60-month threshold, numbers were 11,211
36
37 237 individuals (469 unique species) for the flowering analysis and 10,517 individuals (453 unique
38
39 238 species) for the fruiting analysis (Table 3). Individual time series ranged from 60 to 339 months
40
41 239 long (median= 199.5 months) with site differences in data length.

42
43
44
45
46
47
48
49 240

50
51 241 TESTING FOR DIFFERENCES IN CYCLIC ACTIVITY AMONG SITES — We used the Fourier-derived
52
53 242 estimates for dominant cycle length for each individual tree to determine the differences among
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 243 sites. To describe the most common flowering and fruiting cycles found at each site and to
4
5 244 compare among sites, we plotted the distribution of dominant cycles at each site using violin
6
7
8 245 plots. We treated flowering and fruiting events separately and not as a dependent process. Hence,
9
10 246 it is worth noting that not all individuals considered in the flowering analysis were shared in the
11
12 247 fruiting analysis. For 851 trees, fruiting was more erratic than flowering and these individuals
13
14 248 were excluded from analysis of fruiting, but retained in the flowering analysis. This also led to
15
16 249 five species from the flowering analysis to being excluded from the fruiting analysis as less than
17
18
19 250 10 individuals showed regular fruiting.
20
21
22 251

23
24 252 COMMUNITY LEVEL SEASONALITY - We assessed the seasonal rainfall pattern at each site by
25
26 253 calculating a mean monthly rainfall value (Table 3) over the maximum phenology data collection
27
28 254 period (28 years starting in 1986 and finishing in 2014) using rainfall data from the Climate
29
30 255 Hazards Group InfraRed Precipitation with Station dataset (CHIRPS) (Funk *et al.* 2015:
31
32 256 <http://chg.geog.ucsb.edu/data/chirps/>). This dataset combines ground-based monitoring with
33
34 257 satellite derived rainfall data starting in 1986 and finishing in 2014. For the two sites (Lopé and
35
36 258 Mbeli) for which rainfall data were available locally the empirically observed monthly time-
37
38 259 series data were poorly matched in the CHIRPS dataset. However, seasonal patterns (average
39
40 260 monthly rainfall across all years) were strongly correlated ($r > 0.9$ observed at Lopé and Mbeli
41
42 261 sites) (data not shown). To standardise across sites, we defined the dry season as any months
43
44 262 where rainfall was less than 60 mm (after van Schaik *et al.* 1993). We assessed canopy level
45
46 263 flowering and fruiting status for trees at each site, by calculating at each site the proportion of
47
48 264 trees in the phenology sample flowering and fruiting within each month and year. To test for
49
50
51
52
53 265 seasonality in flowering, fruiting and rainfall data we used Rayleigh tests implemented in the R

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 266 package **circul** (Agostinelly & Lund 2011) with the null hypothesis of uniformity (no
4
5 267 seasonality) (Morellato *et al.* 2010). As the Rayleigh test can fail in the presence of strong and
6
7 268 symmetric multi-modality, we first visually inspected seasonal patterns to identify potential
8
9
10 269 multi-modality. We then used the function ‘Rayleigh.test’ from the R package ‘circular’
11
12 270 (Agostinelly & Lund 2011). At some sites (e.g. Kibale and Amani) rainfall is strongly bimodal,
13
14 271 but not symmetrical. Significant seasonality could be identified by the Rayleigh test in such
15
16 272 circumstances, although the angle identified is likely to be meaningless (Morellato *et al.* 2010).
17
18
19 273

274 RESULTS

275
276 SITE LEVEL FLOWERING AND FRUITING CYCLES - Across 12 sites and 5446 individuals (196
277 species) for which all data quality control conditions were met, we found 46% of all individual
278 trees showed dominant annual flowering cycles (between 11 and 13 months), 29% of individuals
279 showed sub-annual cycles (typically between 5 and 7 months) and supra-annual cycles (above 13
280 months) were seen in 25% of trees, with 24-month cycles being the most common.
281 The overall prevalence of annual cycles in individuals was reflected at the site-level in Gombe,
282 Nyungwe, Bwindi, Okapi Lenda, Okapi Egoro, Goualougo, Mbeli, Lopé and Taï. Elsewhere
283 annual cycles were not most common, with **M’Baiki** showing mainly supra-annual cycles, Kibale
284 showing a very diverse profile with sub-annual, annual and a variety of mainly supra-annual
285 cycles and Amani showing mainly sub-annual cycles (Fig 2). Remarkably, despite being only 35
286 km apart and in the same forest type, Okapi Lenda and Egoro showed different dominant cycles
287 with far greater diversity in cycle length in Okapi Lenda.

288

Adamescu et al.

Annual reproduction in African tropical trees

289 Across the 11 sites and 191 species (4,595 individuals), 42% of individuals showed annual
290 fruiting cycles. In contrast to the flowering analysis, supra-annual fruiting cycles were nearly as
291 common as annual cycles (35% of individual trees), with the most frequent dominant fruiting
292 cycle being 24 months. Sub-annual cycles were encountered only in 23% of individuals with the
293 most common cycle being 6 months. At most sites we found species with differing cycle lengths
294 (Fig. 4). In sites in West and West Central Africa we found that most trees recorded an annual
295 fruiting cycle.

297 FLOWERING AND FRUITING SEASONALITY - Due to considerable variation between individuals
298 and both within and between species, flowering patterns at the community level at most sites
299 showed weak seasonality (some trees flower during both the wet and dry season) despite
300 considerable seasonal differences in rainfall between sites (Fig 5 and Table 5). Seasonality in
301 flowering (flowering triggered by a certain environmental cue, such as heat or rainfall) was not
302 observed in Amani, Kibale, Nyungwe, Bwindi, and Tai, while we detected significant flowering
303 seasonality at the canopy level in the rest of sites (Fig 3 and Table 5). Among the remaining
304 seven sites, the strongest seasonal flowering patterns were encountered at Gombe, M'Baiki,
305 Lope, Goualougo, Okapi Lenda and Okapi Egoro sites (Fig 5). All sites showed significant
306 seasonality in rainfall (Table 4).

307
308 With regard to fruiting, we found constant fruit patterns a feature of several sites. Amani, Kibale,
309 Nyungwe and Bwindi were sites that exhibited no significant seasonality in flowering, and also
310 showed no statistically significant seasonality in fruiting patterns ($p > 0.01$, Table 5). However,
311 although Lope showed strong significant seasonality in flowering, it did not show seasonality in

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 312 fruiting (although the p value = 0.01). In contrast, Taï, which showed no seasonality in
4
5 313 flowering, showed strong seasonality in fruiting. Most inter-month variation (highest seasonality)
6
7 314 in fruiting was found in Tai, Okapi Lenda, M’Baïki, and Gombe. For Amani, Nyungwe,
8
9 315 M’Baïki, Mbeli and Taï, peak fruiting occurred during the dry season. At Kibale, peak fruiting
10
11 316 was at the transition from wet to dry seasons, and for the rest of the sites, peak fruiting occurred
12
13 317 during the wet season (Fig 5).
14
15
16
17
18
19
20
21
22

320 **DISCUSSION**

23
24 321
25
26 322 Using Fourier based analysis we effectively estimated flowering patterns for 5446 individual
27
28 323 trees of 196 species, and fruiting patterns for 4595 trees of 191 species, across 12 and 11 sites,
29
30 324 respectively. This was performed both at the site level and among tropical forests spanning from
31
32 325 western to eastern Africa. We found that across all sites, more trees flowered and fruited
33
34 326 annually than supra or sub-annually; however, sub-annual flowering cycles and supra-annual
35
36 327 fruiting patterns were present at all sites and common in many. Although some sites had few
37
38 328 individual trees reproducing annually, all sites had some annually reproductive trees, as expected
39
40 329 from previous analyses of dominant reproductive cycles in Lopé (Bush *et al.* 2017) and Kibale
41
42 330 (Chapman *et al.* 1999).
43
44
45
46
47
48

49 332 Overall, 46% of trees showed annual flowering frequencies across all 12 sites. Our results
50
51 333 contrast with those previously reported from tropical forests of Central and South America, as
52
53 334 well as Southeast Asia, where, depending on the region, sub-annual and supra-annual
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 335 frequencies have previously been reported as the most frequent strategies (Newstrom *et al.* 1994,
4
5 336 Sakai 2001, McEwan & McCarthy 2005, Wright *et al.* 2005). However, more recent work in
6
7 337 South America has now shown some sites where annual cycles in fruiting are dominant (Norden
8
9 338 *et al.* 2007, Mendoza *et al.* 2018). Evolutionary histories and pressures driving flowering and
10
11 339 fruiting are likely to be different in forests on different continents and, equally, even at a
12
13 340 continental scale, may contrast greatly between western and eastern Africa (Slik *et al.* 2018).
14
15 341 There is certainly room for further work on the evolution of cyclicity and current drivers of
16
17 342 cyclicity on all continents before robust inter-continental comparisons can be made.
18
19 343 Fruiting showed similar patterns to flowering, with 42% of trees at 11 sites showing annual
20
21 344 cycles, also as previously reported for Africa (Chapman *et al.* 1999, Takenoshita *et al.* 2008,
22
23 345 Bush *et al.* 2017). This result was not as strong as the annual flowering pattern, presumably
24
25 346 because many flowering cycles do not result in production of mature fruit. Our dataset shows
26
27 347 that fruiting cycles are slightly more likely to be supra-annual than flowering cycles, which may
28
29 348 be the result of resource deficiencies, stochastic weather events, flower or fruit predation, or
30
31 349 disease all playing a role in modifying annual cycles by preventing fruiting after a flowering
32
33 350 event.
34
35
36
37
38
39

40 351
41
42 352 SITE LEVEL FLOWERING AND FRUITING PATTERNS — We assume that the prevalence of annual
43
44 353 cycles suggests that a regular, external annual cycle, sometimes moderated by the resource base
45
46 354 available to each individual, and additional extra-annual environmental variation, perhaps, such
47
48 355 as the El Niño phenomenon (Chapman *et al.* 2018, Dunham *et al.* 2018) drives the observed
49
50 356 phenological pattern in many trees. Annual phenological cycles have previously been reported to
51
52 357 be initiated by annual cycles in environmental conditions such as day length, seasonal rainfall
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 358 and temperature (Borchert 1983, Pau *et al.* 2013). It is difficult to disentangle exactly which cues
4
5 359 were responsible for triggering phenological events at our sites due to the lack of data on
6
7 360 environmental conditions. Factors mediating the trees' ability to respond to an environmental
8
9 361 cue, such as carbohydrate storage (Borchert 1983), or phosphorus accumulation (Corlett 2016),
10
11 362 have not been measured at any of our sites. The lack of data on local weather at a sufficient level
12
13 363 of precision (Maidment *et al.* 2015, Abernethy *et al.* 2016) is also problematic for robust
14
15 364 definition of environmental cues in African sites. However, despite these limitations, we did find
16
17 365 annual cycles in rainfall in most sites and consider it likely that annually cycling local
18
19 366 environmental cues are important in driving African tree phenology across the continent. It is
20
21 367 important to remember that although annual cycles were the most common patterns at most sites,
22
23 368 annual cycles were not shown by a majority of trees: there were individuals at every site showing
24
25 369 either sub- or super-annual cycles, and across the whole dataset more trees showed non-annual
26
27 370 than annual cycles. African forests show a high level of diversity in phenological behaviours
28
29 371 both within and between species. Although there was no clear effect of forest type, longitude,
30
31 372 latitude or altitude on the phenological profile at a site, the more westerly sites showed stronger
32
33 373 dominance of annual cycles than those in the west and south, and sites closest to the current edge
34
35 374 of the rainforest extent showed the highest diversity in cyclic behaviour.
36
37
38
39
40
41
42
43

44 376 Our results underscore the complexity and inter-individual variation in flowering and fruiting at
45
46 377 the community level, previously reported at different sites in Africa (Tutin & Fernandez 1993,
47
48 378 Plumptre 1995). In this analysis a different set of species was monitored at each site. Since
49
50 379 species are not distributed at random among sites and tree selection criteria varied at different
51
52 380 sites (see Methods), it is plausible that differences among sites are more reflective of differences
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 381 in species selection than fundamental differences in geography. Unfortunately, we cannot
4
5 382 estimate the degree of bias this generates post hoc, but further research into functional or
6
7 383 taxonomic group responses to environmental triggers may elucidate the potential effects of each.
8
9
10 384 We saw variability in flowering and fruiting patterns among species within the same forest site,
11
12 385 presumably associated with selection for responses to differing environmental drivers. This may
13
14 386 be expected when different functional traits mediate the response to environmental drivers of
15
16 387 phenological patterns: e.g. different animal-plant relationships (Takenoshita *et al.* 2008);
17
18 388 different modes of seed dispersal (e.g. wind dispersed seeds tend to ripen during drier periods,
19
20 389 fleshy fruits in wetter ones: Chapman *et al.* 2001) or differences in endogenous factors mediating
21
22 390 the response (which may reflect genetic differences: Staggemeier *et al.* 2015). Although our
23
24 391 study is the first to present and compare the range of phenological profiles at tropical forest sites
25
26 392 across Africa, the question of *why* predominant cycle length varies across the continent remains
27
28 393 unanswered. Further analyses including factors such as climate change, rare weather events, soil
29
30 394 types, interspecific interactions, genetic variation, forest history and geographical position should
31
32 395 be considered by researchers wishing to advance this discipline.
33
34
35
36
37
38
39

40 397 FLOWERING AND FRUITING SEASONALITY — As reported elsewhere in Africa (Chapman *et al.*
41
42 398 1999), we found that timing of flowering and fruiting between species was highly variable at
43
44 399 most sites, such that at the canopy level some individuals may always be found in flower or in
45
46 400 fruit. Visually, Bwindi and Kibale showed the least seasonal flowering patterns (Fig 3), but even
47
48 401 here there may be some slightly bimodal seasonal patterns that cannot be detected by the
49
50 402 Rayleigh test. We confirmed that for the majority of sites, flowering activity peaked at the
51
52 403 beginning or during the middle of one of the two wet seasons (Anderson *et al.* 2005, Polansky &
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 404 Boesch 2013). In five of our sites, peak fruiting occurred during the wet season (c.f. Sun *et al.*
4
5 405 1996), a pattern also common in South and Central America (Smythe 1970) and Asia (Medway
6
7 406 1972). However, in another five sites, peak fruiting occurred in the dry season, and for one site,
8
9
10 407 fruiting peaked in the transition from wet to dry. There was no discernible pattern in the
11
12 408 geographic distribution, seasonality, or rainfall characteristics of wet vs. dry season fruiting sites.
13
14
15 409
16
17 410 Phenological complementarity between plants and animals is crucial for ecosystem organisation,
18
19 411 process and function (Cleland *et al.* 2007), and the importance of phenological events in
20
21 412 understanding the ecology and evolution of species within their communities has been previously
22
23 413 demonstrated (Chapman *et al.* 2005, Visser & Both 2005). Changes in plant phenology can lead
24
25 414 to cascading effects across the entire ecosystem by causing phenological mismatches between
26
27 415 the cycles followed by plants and the animals that rely on them (Newstrom *et al.* 1994, Sakai
28
29 416 2001, Morellato *et al.* 2016). Mismatches have already been observed in temperate regions
30
31 417 where phenology has changed differently for animals and plant communities, due to recent rapid
32
33 418 changes in climate (Brown *et al.* 2016). Morellato *et al.* (2016) and Mendoza *et al.* (2017) review
34
35 419 the evidence and likelihood of such mismatches arising in neotropical forests. Chapman *et al.*
36
37 420 (2005), Polansky & Boesch (2013), Dunham *et al.* (this issue) and Chapman *et al.* (this issue)
38
39 421 consider the consequences of mismatches in African forests. All conclude that primate foragers
40
41 422 have developed behavioural patterns in response to the predictability of fruit resources, and are
42
43 423 likely to suffer population declines if fruit phenology cycles become less regular.
44
45
46
47
48

49 424

50
51 425 CONCLUDING REMARKS - Our study shows that annual cycling, as opposed to supra- or sub-
52
53 426 annual cycling, is the most common flowering and fruiting strategy in African tree reproduction
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 427 across the continent. However, both supra- and sub-annual strategies exist in every site alongside
4
5 428 annually cycling trees, and non-annual patterns (of supra and sub-annual combined) are common
6
7
8 429 overall and at many individual sites. Seasonality at most sites covers two wet and two dry
9
10 430 seasons, providing potential for environmental cues at a sub-annual cycle length, but we found
11
12 431 relatively low frequencies of sub-annual cycling. Our results provide an important baseline from
13
14 432 which future changes in seasonality, community phenological profiles and individual or species
15
16 433 average cycle length can be assessed. We show for the first time that there is considerable
17
18 434 variation in the frequency of phenological cycle types at different tropical African sites and that
19
20 435 there is some geographic patterning in the distribution of site-specific phenological cycle
21
22 436 profiles, although trends are not strong.
23

24
25
26 437
27
28 438 With this study, we bring African data to bear in global comparisons of tropical forest behaviour.
29
30 439 We show similarities and differences in flower and fruit cycles between African, Asian and
31
32 440 Neotropical forests. We also show the complexity of observed phenology cycles within and
33
34 441 among sites in Africa and the lack of explanatory power found in the currently available
35
36 442 environmental data. In order for the environmental drivers of phenology patterns in Afrotropical
37
38 443 forests to be more clearly understood we make the following research recommendations: 1)
39
40 444 encourage the collection of more detailed and precise environmental data (weather, soils, nutrient
41
42 445 flux etc.) at phenology data collection sites; 2) assess and improve the potential of African
43
44 446 climate models to provide interpolated climate-data for specific sites; 3) resolve differences in
45
46 447 observational methodologies such that inter-site comparisons become more robust; 4) expand
47
48 448 data collection to include a more representative selection of tree species and 5) increase the
49
50 449 collection of functional trait data for the species targeted for phenology data collection.
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 450 Furthermore, we encourage future work that addresses questions of variability within tree
4
5 451 species. Finally, we note that although more work has been undertaken in Asian and Neotropical
6
7 452 forests than in Africa to date, it seems likely that application of new analytical methods such as
8
9 453 those used here may identify previously overlooked patterns in these better known forests too.
10
11

12 454


14 455 **ACKNOWLEDGEMENTS**

16
17 456 We thank ESA CCI Land Cover project for permission to use the land cover data to create our
18
19 457 map. Thanks are due to the following organisations and individuals for assistance with funding,
20
21 458 permits, permissions and fieldwork at each of the sites:
22
23

24 459

25
26 460 AMANI - Permits and permissions from COSTECH and Amani Nature Reserve; fieldwork from
27
28 461 University of Dar es Salaam, Roosevelt University and the Field Museum, Thomas Challenge,
29
30 462 Bakari Mtui, and Mwanaidi Kijazi.
31
32

33 463

34
35 464  We thank the Tanzania Wildlife Research Institute (TAWIRI) and Commission on
36
37 465 Science and Technology (COSTECH) for permission to conduct this research, and Gen
38
39 466 Yamakoshi, who initiated collection of phenology data at Gombe. We thank the Jane Goodall
40
41 467 Institute, NSF grants IOS-1052693 and BCS-0648481, the University of Minnesota, Harris Steel,
42
43 468 and Duke University for supporting fieldwork and data entry.
44
45
46

47 469

48
49 470 KIBALE - Funding from Canada Research Chairs Program, Wildlife Conservation Society,
50
51 471 Natural Science and Engineering Research Council of Canada, National Geographic, National
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

472 Science Foundation, and Fonds Québécois de la Recherche sur la Nature et les Technologies.

473 Fieldwork: Richard Wrangham.

474 LOPÉ - Funding from the International Centre for Medical Research in Franceville (CIRMF)

475 (1986-2010), the University of Stirling (1986-present) and Gabon's National Parks Agency

476 (ANPN) (2011-present). Permission and permits from the CIRMF Scientific Council and the

477 Ministry of Water and Forests (1986 – 2010), and by ANPN and the National Centre for

478 Research in Science and Technology (CENAREST) (2011 – present). We also thank Richard

479 Parnell, Liz Williamson, Rebecca Ham and Patricia Peignot for significant periods of data

480 collection.

481

482 M'BAÏKI - Fieldwork by ARF Project (Appui la Recherche Forestière) funded by six partners:

483 AFD (Agence Française de Développement), CIRAD (Centre de Coopération Internationale en

484 Recherche Agronomique pour le Développement), ICRA (Institut Centrafricain de Recherche

485 Agronomique), MEFCP (Ministère centrafricain des Eaux, Forêts, Chasse et Pêche),

486 SCAC/MAE (Service de Coopération et d'Actions Culturelles, Ministère des Affaires

487 Etrangères), and SCAD (Société Centrafricaine de Déroulage).

488

489 MBELI BAI - Funding from The Columbus Zoo and Aquarium, Cincinnati Zoo and Botanical

490 Garden, Cologne Zoo, Disney Worldwide Conservation Fund, Dublin Zoo, Sea World and Busch

491 Gardens Conservation Fund, Toronto Zoo, Wildlife Conservation Society and Woodland Park

492 Zoo. Permits from Ministry of Sustainable Development, Forest Economy and Environment and

493 the Ministry of Scientific Research of the Republic of Congo.

494

Adamescu *et al.*


Annual reproduction in African tropical trees

1
2
3 495 Tai - Funding from Max Planck Institute for Evolutionary Anthropology. Permits from the
4
5 496 Ministère de la Recherches Scientifiques, the Ministère de l'Environnement et des Eaux et
6
7 497 Forêts, the Office Ivoirien des Parcs et Réserves. Support in the field from the staff of the Tai
8
9 498 Chimpanzee Project, Centre Suisse de Recherche Scientifique, C. Boesch, D. P. Anderson, and
10
11 499 Z.B. Goné Bi.
12
13
14

15 500

16
17 501 **DATA AVAILABILITY STATEMENT**

18 502 The summary data from this study will be available via the WCS data portal website (doi: xxx

19
20
21 503  Data for the Lopé site is stored at (DataSTORRE; <http://hdl.handle.net/11667/103>),
22

23 504 under a 10 year open-access embargo. Access to embargoed data may be requested by contacting

24
25 505 the relevant authors (see affiliations).
26
27

28 506
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

507 **LITERATURE CITED**

- 508
- 509 ABERNETHY, K., F. MAISELS AND L. J. T. WHITE. 2016. Environmental Issues in Central Africa.
510 *Annu. Rev. Environ. Resour.* 41: 1-33.
- 511 AGOSTINELLI C. AND U. LUND. 2011. R package 'circular': Circular statistics (version 0.4-3).
512 URL <https://rforge.r-project.org/projects/circular>.
- 513 ANDERSON, D. P., E. V. NORDHEIM, T. C. MOERMOND, Z. B. GONE BI, AND C. BOESCH. 2005.
514 Factors Influencing Tree Phenology in Taï National Park, Côte d'Ivoire. *Biotropica* 37:
515 631–640.
- 516 ARINO, O., P. BICHERO, F. ACHA, J. LATHAM, R. WITT AND J. L. WEBER. 2009. Globcover: the
517 most detailed portrait of Earth. *ESA Bulletin* 136, European Space Agency.
- 518 BAWA, K. S., H. KANG AND M. H. GRAYUM. 2003. Relationships among time, frequency, and
519 duration of flowering in tropical rain forest trees. *Am. J. Bot.* 90: 877–887.
- 520 BORCHERT, R. 1983. Phenology and control of flowering in tropical trees. *Biotropica* 15: 81–89.
- 521 BROWN, C. J., M. I. O'CONNOR, E. S. POLOCZANSKA, D. S. SCHOEMAN, L. B. BUCKLEY, M. T.
522 BURROWS, C. M. DUARTE, B. S. HALPERN, J. M. PANDOLFI, C. PARMESAN AND A. J.
523 RICHARDSON. 2016. Ecological and methodological drivers of species' distribution and
524 phenology responses to climate change. *Glob. Change Biol.* 22: 1548–1560.
- 525 BULLOCK, S. H. AND J. A. SOLIS-MAGALLANES. 1990. Phenology of canopy trees of a tropical
526 deciduous forest in Mexico. *Biotropica* 22: 22–35.
- 527 BUSH, E. R., K. A. ABERNETHY, K. JEFFERY, C.E. G. TUTIN, L. J. T. WHITE, E. DIMOTO, J.-T.
528 DIKANGADISSI, A. S. JUMP AND N. BUNNEFELD. 2017. Fourier analysis to detect
529 phenological cycles using long-term tropical field data and simulations. *Methods Ecol.*
530 *Evol.* 8: 530-540

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 531
4
5 532 BUTT, N., L. SEABROOK, M. MARON, B. S. LAW, T. P. DAWSON, J. SYKTUS AND C. A. MCALPINE.
6
7 533 2015. Cascading effects of climate extremes on vertebrate fauna through changes to low-
8
9 latitude tree flowering and fruiting phenology. *Glob. Change Biol.* 21: 3267–3277.
10 534
11 535 CHAMBERS, L.E., R. ALTWEG, C. BARBRAUD, P. BARNARD, L.J. BEAUMONT, R.J.M. CRAWFORD,
12
13 536 J.M. DURANT, L. HUGHES, M. R. KEATLEY, M. LOW, P. MORELLATO, E. S. POLOCZANSKA,
14
15 537 V. RUOPOLLO, R.E.T. VANSTREELS, E.J. WOehler, A.C. WOLFAARDT, B. HÉRAULT.
16
17 538 2013. Phenological Changes in the Southern Hemisphere. *PloSOne* 8: e75514.
18
19 539 CHAPMAN, C. A., L. J. CHAPMAN, A. E. ZANNE, J. R. POULSEN, AND C. J. CLARK. 2005. A 12-
20
21 540 Year Phenological Record of Fruiting: Implications for Frugivore Populations and
22
23 541 Indicators of Climate Change. In J. L. Dew and J. P. Boubli (Eds.) *Tropical Fruits and*
24
25 542 *Frugivores: The Search for Strong Interactors*, pp. 75–92. Springer Netherlands,
26
27 543 Dordrecht.
28
29 544 CHAPMAN, C. A., K. VALENTA, T.M. BONNELL, K. BROWN, L.J. CHAPMAN. 2018. Solar radiation
30
31 545 and ENSO predict fruiting phenology patterns in a 16-Year record from Kibale National
32
33 546 Park, Uganda. *Biotropica*, this issue.
34
35 547 CHAPMAN, C. A., R. W. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD AND A. E. ZANNE. 1999.
36
37 548 Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J. Trop. Ecol.*
38
39 549 15: 189–211.
40
41 550 CLELAND, E. E., I. CHUINE, A. MENZEL, H. A. MOONEY, AND M. D. SCHWARTZ. 2007. Shifting
42
43 551 plant phenology in response to global change. *Trends Ecol. Evol.* 22: 357–365.
44
45 552 CORLETT, R. T. AND J. V. LAFRANKIE. 1998. Potential impacts of climate change on tropical
46
47 553 Asian forests through an influence on phenology. *Clim. Change* 39: 439–453.
48
49
50
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 554 DUNHAM, A., O.H. RAZAFINDRATSIMA, P. RAKOTONIRINA AND P.C. WRIGHT. 2018. ENSO and
4
5 555 Rainfall Variability Impact Fruiting Phenology in a Madagascar Rainforest. *Biotropica*,
6
7 556 this issue.
8
9
10 557 FUNK, C., P. PETERSON, M. LANDSFELD, D. PEDREROS, J. VERDIN, S. SHUKLA, G. HUSAK, J.
11
12 558 ROWLAND, L. HARRISON AND A. HOELL. 2015. The climate hazards infrared precipitation
13
14 559 with stations—a new environmental record for monitoring extremes. *Sci. Data* 2: 150066.
15
16
17 560 GENTRY, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6:
18
19 561 64–68.
20
21 562 HUDSON, I. L. AND M. R. KEATLEY. 2010. *Phenological Research: methods for environmental*
22
23 563 *and climate change analysis*. Springer, The Netherlands.
24
25
26 564 JANMAAT, K. R., C. BOESCH, R. BYRNE, C. A. CHAPMAN, G. BI, B. ZORO, J. S. HEAD, M. M.
27
28 565 ROBBINS, R. W. WRANGHAM AND L. POLANSKY. 2016. Spatio-temporal complexity of
29
30 566 chimpanzee food: How cognitive adaptations can counteract the ephemeral nature of ripe
31
32 567 fruit. *Am. J. Primatol.* 78 : 626-645.
33
34
35 568 MAIDMENT, R. I., R. P. ALLAN AND E. BLACK. 2015. Recent observed and simulated changes in
36
37 569 precipitation over Africa. *Geophys. Res. Lett.* 42: 8155–8164.
38
39
40 570 MCEWAN, R. W., AND B. C. MCCARTHY. 2005. Phenology: An integrative environmental
41
42 571 science. *BioOne*.
43
44
45 572 MEDWAY, L. 1972. Phenology of a tropical rain forest in Malaya. *Biol. J. Linn. Soc.* 4: 117–146.
46
47 573 MENDOZA, I., C. A. PERES AND L. P. C. MORELLATO. 2017. Continental-scale patterns and
48
49 574 climatic drivers of fruiting phenology: A quantitative Neotropical review. *Glob. Planet.*
50
51 575 *Change* 148: 227–241.
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 576 MORELLATO, L. P. C., L. F. ALBERTI AND I. L. HUDSON. 2010. Applications of circular statistics
4
5 577 in plant phenology: a case studies approach. *In* Hudson, I. L. and M. R. Keatley (Eds).
6
7 578 *Phenological research: methods for environmental and climate change analysis*. pp.
8
9 579 339–359. Springer, The Netherlands.
- 11
12 580 MORELLATO, L.P.C., CAMARGO, M.G.G. AND GRESSLER, E., 2013. A review of plant phenology
13
14 581 in South and Central America. *In* Schwartz, M.D. (Ed.), *Phenology: An Integrative*
15
16 582 *Environmental Science*, pp. 91–113. Springer, The Netherlands.
- 18
19 583 NATIONAL WEATHER SERVICE (2010) Inter-tropical convergence zone. Jet Stream. Available at:
20
21 584 <http://www.srh.noaa.gov/jetstream/tropics/itcz.htm> [Accessed July 29, 2017].
- 23
24 585 NEWSTROM, L. E., G. W. FRANKIE, AND H. G. BAKER. 1994. A new classification for plant
25
26 586 phenology based on flowering patterns in lowland tropical rain forest trees at La Selva,
27
28 587 Costa Rica. *Biotropica* 26: 141–159.
- 30
31 588 OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1976. Rainfall as a factor in the release, timing,
32
33 589 and synchronization of anthesis by tropical trees and shrubs. *J. Biogeogr.* 3: 231–236.
- 35
36 590 PARMESAN, C. AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts
37
38 591 across natural systems. *Nature* 421: 37.
- 40
41
42 592 PAU, S., E. M. WOLKOVICH, B. I. COOK, C. J. NYTCH, J. REGETZ, J. K. ZIMMERMAN AND S. J.
43
44 593 WRIGHT. 2013. Clouds and temperature drive dynamic changes in tropical flower
45
46 594 production. *Nat. Clim Change* 3: 838–842.
- 48
49 595 PLATT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology. *Annu. Rev. Ecol. Syst.* 6:
50
51 596 189–210.
- 53
54 597 PLUMPTRE, A. J. 2012. Changes in Tree Phenology across Africa : A comparison across 17 sites.
55
56 598 Technical Report or the Wildlife Conservation Society, New York.

Adamescu *et al.*

Annual reproduction in African tropical trees

- 1
2
3 599 POLANSKY, L., AND C. BOESCH. 2013. Long-term changes in fruit phenology in a West African
4
5 600 lowland tropical rain forest are not explained by rainfall. *Biotropica* 45: 434–440.
6
7 601 SAKAI, S. 2001. Phenological diversity in tropical forests. *Popul. Ecol.* 43: 77–86.
8
9 602 SAKAI, S., K. MOMOSE, T. YUMOTO, T. NAGAMITSU, H. NAGAMASU, A. A. HAMID, AND T.
10
11 NAKASHIZUKA. 1999. Plant reproductive phenology over four years including an episode
12
13 603 of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *Am. J. Bot.* 86:
14
15 604 1414–1436.
16
17 605
18
19 606 SLIK, F., J. FRANKLIN, V. ARROYO-RODRÍGUES, R. FIELD, S. AGUILAR, N. AGUIRRE, J.
20
21 AHUMADA, S.-I. AIBA, L. F. ALVES, K. ANITHA, ET AL. 2018. Phylogenetic Classification
22
23 607 of the world's tropical forests. *Proc. Nat. Acad. Sci. USA.* 115: 1837–1842
24
25 608
26 609 SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a
27
28 610 neotropical forest. *Am. Nat.* 104: 25–35.
29
30 611 STAGGEMEIER, V.G., J. A. F., DINIZ-FILHO, V. B. ZIPPARRO, E. GRESSLER, E. R. DE CASTRO, F.
31
32 MAGAZINE, I. R. DA COSTA, E. LUCAS, L. P. C. MORELLATO. 2015. Clade-specific
33
34 612 responses regulate phenological patterns in Neotropical Myrtaceae. *Perspect. Plant Ecol.*
35
36 613 17: 476–490.
37
38 614
39
40 615 STEPHENSON, A. G. 1981. Flower and Fruit Abortion: Proximate causes and ultimate functions.
41
42 616 *Annu. Rev. Ecol. Syst.* 12: 253–279.
43
44 617 SUN, C., B. A. KAPLIN, K. A. KRISTENSEN, V. MUNYALIGOGA, J. MVUKIYUMWAMI, K. K.
45
46 KAJONDO, AND T. C. MOERMOND. 1996. Tree phenology in a tropical montane forest in
47
48 618 Rwanda. *Biotropica* 28: 668–681.
49
50 619
51 620 TAKENOSHITA, Y., C. ANDO AND J. YAMAGIWA. 2008. Fruit phenology of the great ape habitat in
52
53 621 the Moukalaba-Doudou National Park, Gabon. *Afr. Study. Monogr. Suppl.* 39 : 23–39.
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 622 TUTIN, C. E. G. AND M. FERNANDEZ. 1993. Relationships between minimum temperature and
4
5 623 fruit production in some tropical forest trees in Gabon. *J. Trop. Ecol.* 9: 241-248
6

7 624 VAN SCHYNDEN, C. P., J. W. TERBORGH AND S. J. WRIGHT. 1993. The phenology of tropical forests:
8
9
10 625 adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.*
11
12 626 24: 353–377.
13

14 627 VISSER, M. E. AND C. BOTH. 2005. Shifts in phenology due to global climate change: the need for
15
16
17 628 a yardstick. *Proc. R. Soc. B Biol. Sci.* 272: 2561.
18

19 629 WRIGHT, S. J., M. A. JARAMILLO, J. PAVON, R. CONDIT, S. B. HUBBELL AND R. B. FOSTER. 2005.
20
21 630 Reproductive size thresholds in tropical trees: variation among individuals, species and
22
23
24 631 forests. *J. Trop. Ecol.* 21: 307-315
25

26 632 ZHOU, L., Y. TIAN, R. B. MYNENI, P. CIAIS, S. SAATCHI, Y. Y. LIU, S. PIAO, H. CHEN, E. F.

27
28 633 VERMOTE, C. SONG, AND T. HWANG. 2014. Widespread decline of Congo rainforest
29
30
31 634 greenness in the past decade. *Nature* 509: 86–9.
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

635

For Peer Review Only

Adamescu *et al.*

Annual reproduction in African tropical trees

636 **TABLES**

637

638 TABLE 1. Characteristics of the 12 African study sites, including country, geographical coordinates and monitoring period for
 639 flowering and fruiting phenology of tropical trees. Sites are organised from East to West. Latitude and longitude are expressed in
 640 decimal degrees. FL = flowering; RF= fruiting; SD= Standard deviation.

641

642

643

	Study site	Country	Latitude	Longitude	Length (years)	Vegetation	Mean Altitude	Mean time series length for flower	Mean time series length for fruit
1	Amani Nature Reserve	Tanzania	-5.13	38.62	7 (2006 – 2012)	Moist submontane forest	950 m	78 (SD=0)	78 (SD=0)
2	Kibale Forest National Park	Uganda	0.56	30.36	11 (2005 – 2015)	Moist submontane forest	1500 m	148 (SD=23.7)	142 (SD=27.9)
3	Okapi Wildlife Reserve Lenda site	Democratic Republic of the Congo	1.26	28.64	20 (1993 – 2012)	Humid mixed evergreen forest	750 m	OL: 200 (SD= 53.3)	OL: 200.9 (SD=53.1)
4	Okapi Wildlife Reserve Edoro sites	Democratic Republic of the Congo	1.26	28.64	20 (1993 – 2012)	Humid mixed evergreen forest	750 m	152 (SD=57.9)	No data

Adamescu *et al.*

Annual reproduction in African tropical trees

5	Bwindi Impenetrable National Park	Uganda	-1.05	29.77	6 (2008 – 2014)	Montane forests	2240 m	93 (SD=5.9)	93 (SD=7.4)
6	Nyungwe Forest National Park	Rwanda	-2.43	29.26	13 (1996 – 2008)	Montane forest	2260 m	150 (SD=15.3)	184 (SD=21.6)
7	Gombe National Park	Tanzania	-4.61	29.64	13 (1997 – 2009)	Evergreen riverine forest, deciduous woodland, and grassland	1000 m	98 (SD=5.4)	97 (SD=5.5)
8	M’Baïki forest	Central African Republic	3.90	17.90	21 (1991 – 1995, 1998 – 2003, 2005 – 2011)	Semi- deciduous - tropical forest	560 m	82 (SD=0.9)	81 (SD=0.4)
9	Goualougo Triangle Nouabalé- Ndoki National Park	Republic of Congo	2.21	16.52	11 (2002 – 2012)	Semi- deciduous rain forest	300 m	69 (SD=2.7)	70 (SD=2.1)

Adamescu *et al.*

Annual reproduction in African tropical trees

10	Mbeli Bai Nouabalé- Ndoki National Park	Republic of Congo	2.26	16.41	12 (2004 – 2015)	Semi- deciduous rain forest	300 m	134 (SD=22.8)	140 (SD=13.6)	644
										645
										646
11	Lopé National Park	Gabon	-1.09	11.16	29 (1986 – 2014)	Semi- evergreen, tropical lowland rainforest	300 m	237 (SD=91.1)	236 (SD=90.5)	647
										648
										649
										650
12	Taï National Park	Côte d'Ivoire	5.84	-7.31	15 (1997 – 2011)	Diverse moist evergreen and semi- evergreen forest	80 m	68 (SD=4.1)	68 (4.1)	651
										652
										653

654

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

664

665

666

667

668 TABLE 2. Monthly minimum and maximum temperature and precipitation values at each of the 12 African sites taken from CHIRPS.
669

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

For Peer Review Only

Adamescu *et al.*

Annual reproduction in African tropical trees

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

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

Adamescu *et al.*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

673
674
675
676
677
678
679
680
681
682
683
684
685
686
687
688
689
690
691
692
693
694
695
696
697
698
699
700

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

Site	<i>Z</i>	<i>P</i> value
Amani	0.206	0
Kibale	0.113	0
Okapi	0.120	0
Bwindi	0.092	0
Nyungwe	0.243	0
Gombe	0.458	0
M’Baiki	0.312	0
Goualago	0.190	0
Mbeli Bai	0.206	0
Lopé	0.078	0
Taï	0.288	0

For Peer Review Only

701 TABLE 5. Rayleigh test of uniformity (Z), and p value of significance of deviation from uniformity. P values of less than 0.01 are
 702 considered significant.
 703

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

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

Goualougo	0.201	0.001
Mbeli Bai	0.168	0.002
Lopé	0.104	0.010
Taï	0.304	0.001

704

For Peer Review Only

Adamescu *et al.*

Annual reproduction in African tropical trees

705 **FIGURE LEGENDS**

706

707 FIGURE 1. Geographical position of the 12 long-term, cross-continental phenology studies in

708 Africa. Okapi Wildlife Reserve is represented by two sites: Okapi Lenda and Edo. Due to the

709 scale of the map, dots for Goualogo and Mbeli overlap, as do the dots for Bwindi and Nyungwe.

710 Colors indicate spatial variation in land cover on a spectrum of high (green) to low (orange)

711 cover (data downloaded from ESA at 5° x 5° resolution no *et al.* 2009).

712

713 FIGURE 2. Violin plot showing the density of flowering frequency of all individual trees present

714 at 12 African sites ordered from East to West. (Species present after Fourier analysis was applied

715 for each site: Amani = 14, Gombe = 11, Nyungwe = 45, Bwindi = 8, Kibale = 10, Okapi Lenda =

716 27, Okapi Edo = 30, M'ba  = 6, Goualougo = 3, Mbeli = 12, Lopé 48, Taï = 44; Number of

717 trees present at each site: Amani = 410, Gombe = 192, Nyungwe = 792, Bwindi = 80, Kibale =

718 85, Okapi Lenda = 354, Okapi Edo = 439, M'Baiki = 155, Goualougo = 43, Mbeli = 112, Lopé

719 = 733, Taï = 2049)

720

721 FIGURE 3. Flowering seasonality at 12 different sites in Africa. Black graph represents the

722 rainfall for each month normalised to the rainfall of the wettest month. Circular plots indicate the


723 proportion of individual trees flowering in each month in each month for 12 sites. Sites are

724 labelled above each circular plot.

725


726 FIGURE 4. Violin plot showing the density of fruiting frequency of all individual trees present at

727 each African site. (Species present after Fourier analysis was applied for each site: Amani = 11,

728 Gombe = 10, Nyungwe = 49, Bwindi = 7, Kibale = 7), Okapi Lenda = 20, M'  ki = 6,

Adamescu *et al.*

Annual reproduction in African tropical trees

1
2
3 729 Goualougo = 6, Mbeli = 9, Lopé = 48, Taï = 49; Amani = 321, Gombe = 165, Nyungwe = 842,
4
5 730 Bwindi = 60, Kibale = 57, Okapi Lenda = 265, M'ba  = 132, Goualougo = 64, Mbeli = 66,
6
7 731 Lopé = 709, Taï = 1914). Okapi Egoro was not included in the fruiting analysis because it did
8
9
10 732 not pass the condition of the 60-month threshold.

11
12 733

13
14 734 FIGURE 5. Fruiting seasonality at 11 sites in Africa. Black graph represents the rainfall for
15
16 735 each month normalised to the rainfall of the wettest month. Circular plots show the proportion
17
18 736 of individual trees flowering in each month for 11 sites. Sites are labelled above each circular
19
20 737 plot. Okapi Egoro was not included in the fruiting analysis because it did not pass the
21
22 738 condition of the 60-month threshold.

23 739
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Adamescu *et al.*

Annual reproduction in African tropical trees

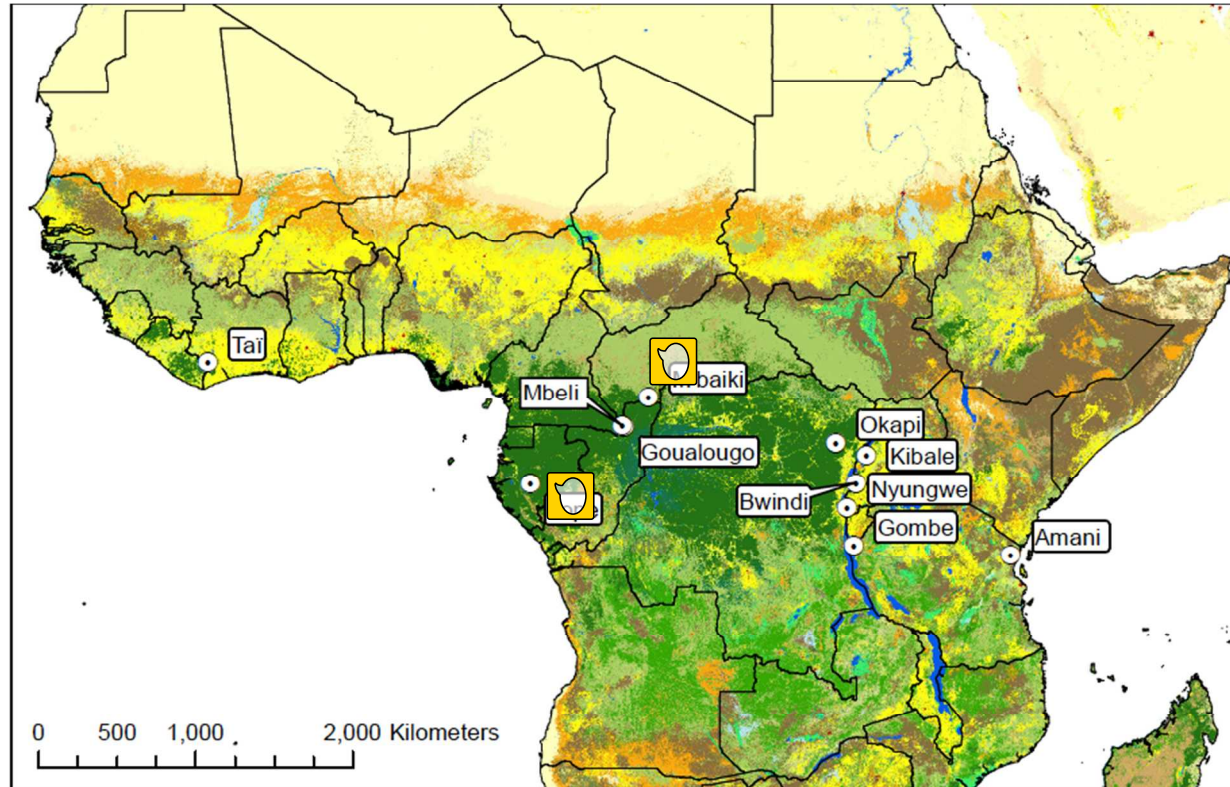
740

741 **FIGURES**

742

743 **FIGURE 1.**

744



745

746

747

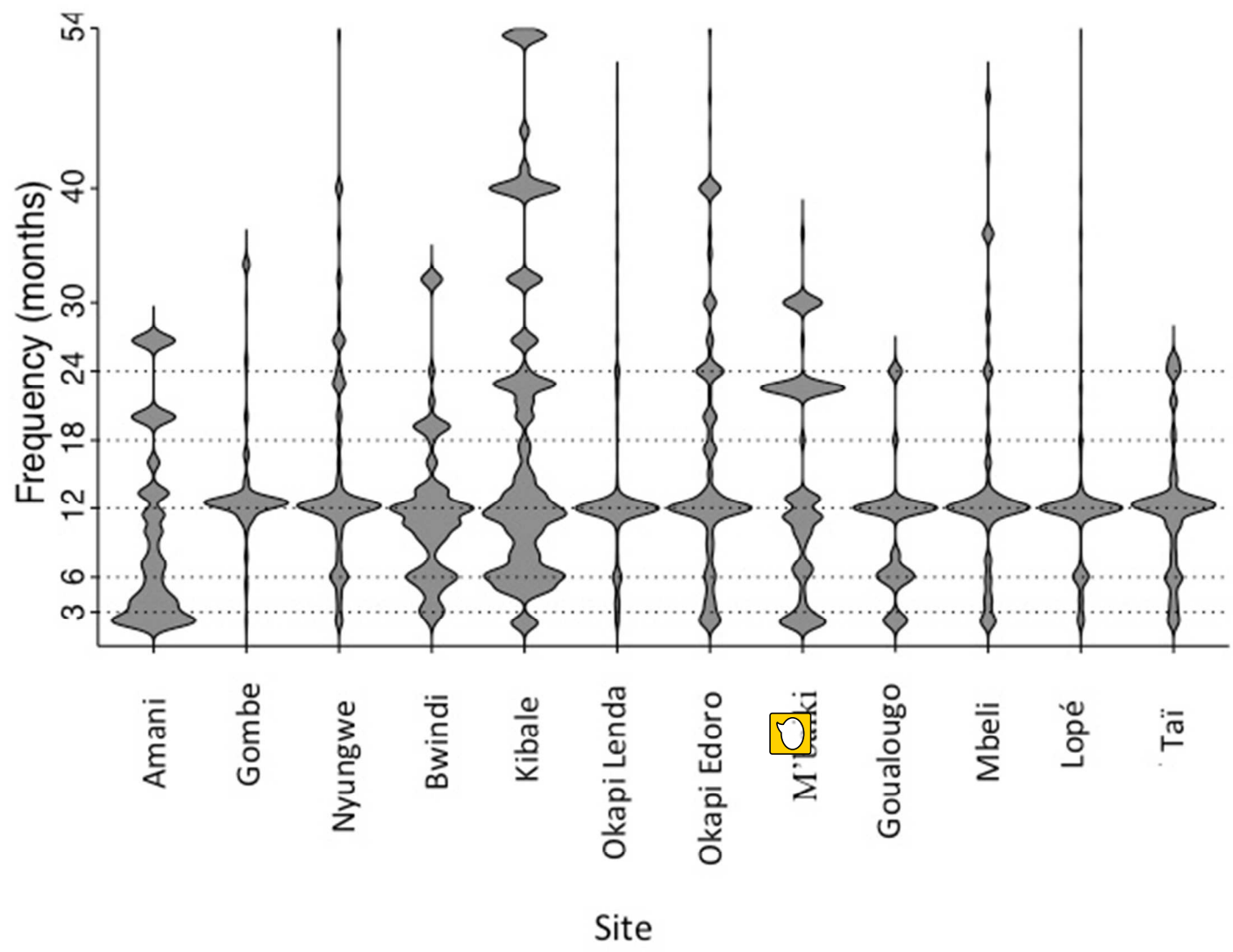
748

749

750

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

751 **FIGURE 2.**



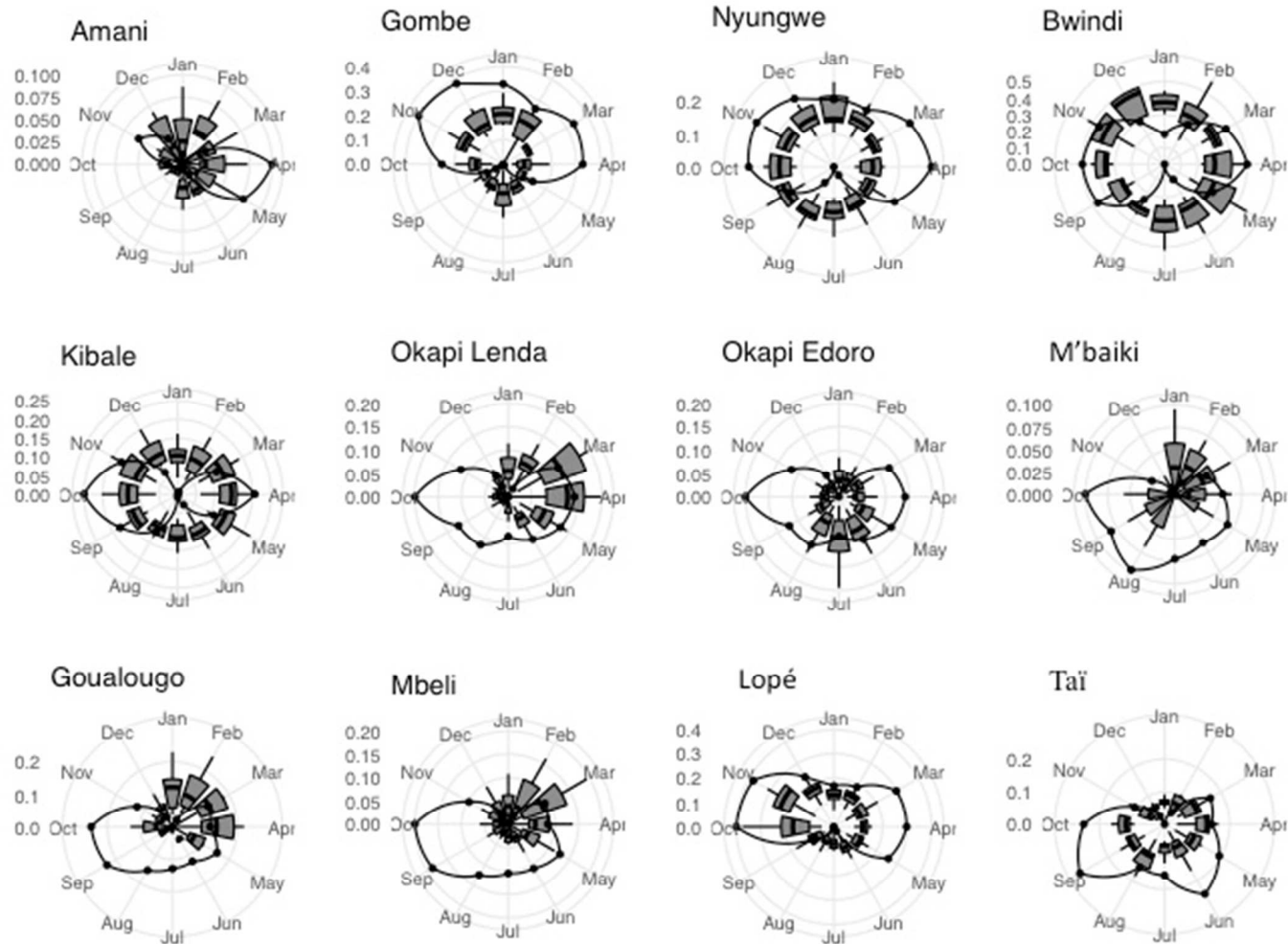
752

Adamescu *et al.*

Annual reproduction in African tropical trees

753 **FIGURE 3.**

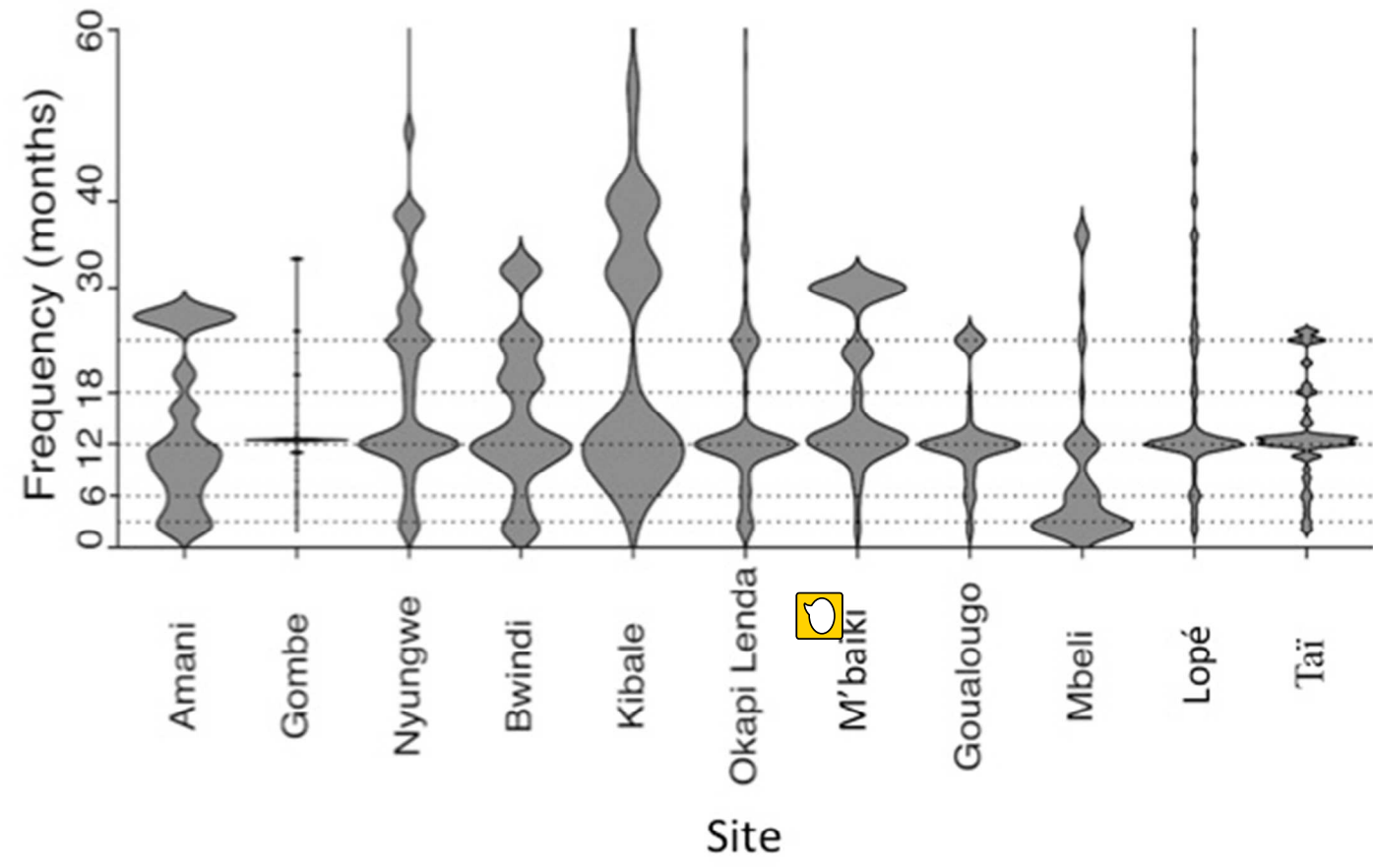
754



755

756

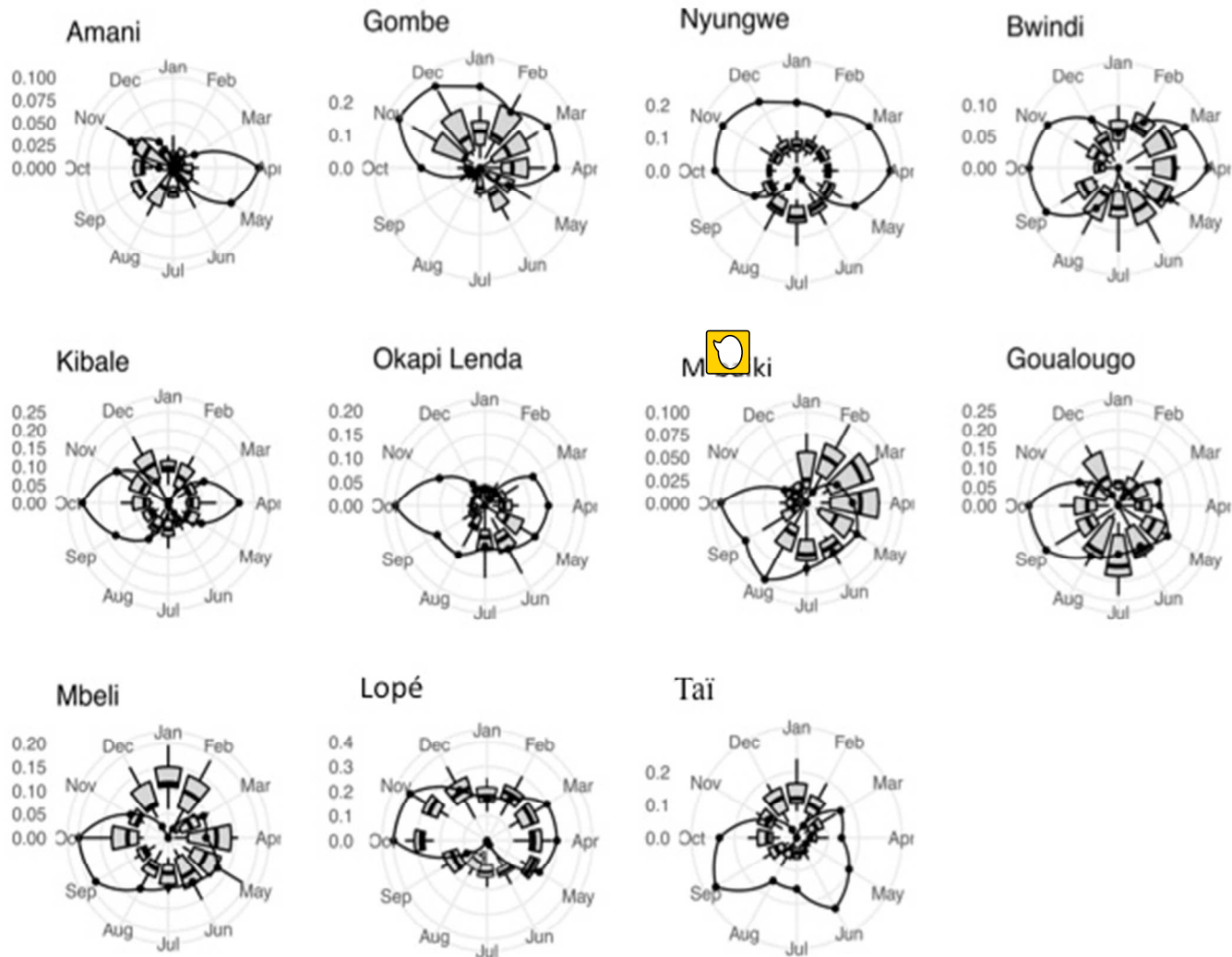
FIGURE 4.



757

758

FIGURE 5.



759

Supplementary Material A

Table 1. Species characteristics

Species	Site	Family	Genus	Dioecious	Liana	Dispersal	Pod / Capsule	Fleshy Fruit	Nut	Winged Seed
Afzelia bella	Tai	Fabaceae	Afzelia	0	0	auto	1	NA	NA	NA
Agelaea paradoxa	Tai	Connaraceae	Agelaea	0	0	zoo	1	1	NA	NA
Alangium chinense	Nyungwe	Alangiaceae	Alangium	0	0	zoo	NA	1	NA	NA
Albizia gummifera	Okapi Lenda	Fabaceae	Albizia	0	0	wind	1	NA	NA	NA
Albizzia grandibracteata	Kibale	Fabaceae	Albizia	0	0	wind	1	NA	NA	NA
Allanblackia stuhlmannii	Amani	Clusiaceae	Allanblackia	1	0	zoo	NA	NA	1	NA
Alsodeiopsis schumannii	Amani	Icacinaceae	Alsodeiopsis	0	0	zoo	NA	1	NA	NA
Alstonia boonei	Okapi Lenda	Apocynaceae	Alstonia	0	0	wind	1	NA	NA	NA
Alstonia boonei	Okapi Lenda	Apocynaceae	Alstonia	0	0	wind	1	NA	NA	NA
Anisophyllea obtusifolia	Amani	Anisophyllaceae	Anisophyllea	1	0	zoo	NA	1	NA	NA
Anonidium mannii	Mbeli	Annonaceae	Anonidium	0	0	zoo	NA	1	NA	NA
Anthonotha macrophylla	Okapi Edo	Fabaceae	Anthonotha	0	0	auto	1	NA	NA	NA
Antidesma vogelianum	Lope	Euphorbiaceae	Antidesma	1	0	zoo	NA	1	NA	NA
Apodytes dimidiata	Okapi Edo	Icacinaceae	Apodytes	0	0	zoo	NA	1	NA	NA
Apodytes dimidiata	Okapi Edo	Icacinaceae	Apodytes	0	0	zoo	NA	1	NA	NA
Aucoumea klaineana	Lope	Burseraceae	Aucoumea	1	0	wind	1	NA	NA	1
Balthasaria schliebenii	Nyungwe	Theaceae	Melchiora	0	0	auto	1	NA	NA	NA
Beilschmiedia rwandensis	Nyungwe	Lauraceae	Beilschmiedia	0	0	zoo	NA	1	NA	NA
Bersama abyssinica	Nyungwe	Meliantaceae	Bersama	0	0	zoo	1	1	NA	NA
Blighia welwitschii	Okapi Edo	Sapindaceae	Blighia	1	0	zoo	1	NA	NA	NA
Blighia welwitschii	Okapi Edo	Sapindaceae	Blighia	1	0	zoo	1	NA	NA	NA

1											
2											
3											
4											
5											
6											
7	Bobgunnia fistuloides	Lope	Fabaceae	Bobgunnia	0	0	zoo	1	NA	NA	NA
8	Bridelia brideliifolia	Nyungwe	Euphorbiaceae	Bridelia	0	0	zoo	NA	1	NA	NA
9	Calpocalyx aubrevillei	Tai	Fabaceae	Calpocalyx	0	0	Ball	1	NA	NA	NA
10	Calpocalyx										
11	brevibracteatus	Tai	Fabaceae	Calpocalyx	0	0	Ball	1	NA	NA	NA
12	Canarium schweinfurthii	Lope	Burseraceae	Canarium	0	0	zoo	NA	1	NA	NA
13	Carapa grandiflora	Nyungwe	Meliaceae	Carapa	0	0	zoo	NA	1	NA	NA
14	Casearia runssorica	Nyungwe	Flacourtiaceae	Casearia	0	0	zoo	NA	1	NA	NA
15	Cassia mannii	Okapi Egoro	Fabaceae	Cassia	0	0	auto	1	NA	NA	NA
16	Cassipourea										
17	ruwenzoriensis	Nyungwe	Rhizophoraceae	Cassipourea	0	0	zoo	1	NA	NA	NA
18	Celtis adolfi-fridericii	Goualougo	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
19	Celtis africana	Amani	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
20	Celtis durandii	Kibale	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
21	Celtis durandii	Kibale	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
22	Celtis durandii	Kibale	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
23	Celtis mildbraedii	Okapi Lenda	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
24	Celtis tessmannii	Lope	Ulmaceae	Celtis	0	0	zoo	NA	1	NA	NA
25	Cephalosphaera										
26	usambarensis	Amani	Myristicaceae	Cephalosphaera	0	0	zoo	NA	1	NA	NA
27	Chaetacme aristata	Kibale	Ulmaceae	Chaetachme	1	0	zoo	NA	1	NA	NA
28	Chionanthus africanus	Nyungwe	Oleaceae	Chionanthus	0	0	zoo	NA	1	NA	NA
29	Chrysophyllum										
30	africanum	Mbaiki	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
31	Chrysophyllum										
32	boukokoense	Mbaiki	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
33	Chrysophyllum										
34	gorungosanum	Nyungwe	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
35	Chrysophyllum										
36	rwandense	Nyungwe	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
37	Chrysophyllum	Tai	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1											
2											
3											
4											
5											
6											
7		subnudum									
8	Chrysophyllum	Lope	Sapotaceae	Chrysophyllum	0	0	zoo	NA	1	NA	NA
9	Cissus dinklagei	Lope	Vitaceae	Cissus	0	1	zoo	NA	1	NA	NA
10	Cleistanthus pierlotti	Okapi Egoro	Euphorbiaceae	Cleistanthus	0	0	auto	1	NA	NA	NA
11	Cola lateritia	Okapi Lenda	Sterculiaceae	Cola	0	0	zoo	1	NA	NA	NA
12	Cola lizae	Lope	Sterculiaceae	Cola	0	0	zoo	1	NA	NA	NA
13	Comiphyton gabonense	Okapi Egoro	Anisophyllaceae	Comiphyton	0	1	zoo	NA	1	NA	NA
14	Coula edulis	Tai	Olacaceae	Coula	0	0	zoo	NA	1	NA	NA
15	Croton haumanianus	Okapi Egoro	Euphorbiaceae	Croton	0	0	zoo	NA	1	NA	NA
16	Croton macrostachyus	Bwindi	Euphorbiaceae	Croton	0	0	zoo	1	NA	NA	NA
17	Cynometra alexandri	Okapi Egoro	Fabaceae	Cynometra	0	0	auto	1	NA	NA	NA
18	Cynometra alexandri	Okapi Egoro	Fabaceae	Cynometra	0	0	auto	1	NA	NA	NA
19	Dacryodes buettneri	Lope	Burseraceae	Dacryodes	1	0	zoo	1	NA	NA	NA
20	Dacryodes klaineana	Tai	Burseraceae	Dacryodes	1	0	zoo	1	NA	NA	NA
21	Daniellia thurifera	Tai	Fabaceae	Daniellia	0	0	auto	1	NA	NA	NA
22	Detarium macrocarpum	Mbeli	Fabaceae	Detarium	0	0	zoo	NA	1	NA	NA
23	Dialium aubrevillei	Tai	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
24	Dialium corbisieri	Okapi Egoro	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
25	Dialium lopense	Lope	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
26	Dialium pentandrum	Okapi Egoro	Fabaceae	Dialium	0	0	zoo	1	NA	NA	NA
27	Dictyophleba lucida	Gombe	Apocynaceae	Dictyophleba	0	0	zoo	NA	1	NA	NA
28	Diospyros dendo	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
29	Diospyros ivoriensis	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
30	Diospyros polystemon	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
31	Diospyros sanza-minika	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
32	Diospyros soubreana	Tai	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
33	Diospyros zenkeri	Lope	Ebenaceae	Diospyros	1	0	zoo	NA	1	NA	NA
34											
35											
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1											
2											
3											
4											
5											
6											
7	Diplorhynchus										
8	condylocarpon	Gombe	Apocynaceae	Diplorhynchus	0	0	zoo	1	NA	NA	NA
9	Dombeya goetzenii	Nyungwe	Sterculiaceae	Dombeya	0	0	auto	1	NA	NA	NA
10	Dombeya mukou	Kibale	Sterculiaceae	Dombeya	0	0	auto	1	NA	NA	NA
11	Drypetes gerrardii	Bwindi	Euphorbiaceae	Drypetes	1	0	zoo	NA	1	NA	NA
12	Duboscia macrocarpa	Mbeli	Tiliaceae	Duboscia	1	0	zoo	1	NA	NA	NA
13	Duboscia macrocarpa	Mbeli	Tiliaceae	Duboscia	1	0	zoo	1	NA	NA	NA
14	Duguetia staudtii	Tai	Annonaceae	Duguetia	1	0	zoo	1	NA	NA	NA
15	Duguetia staudtii	Tai	Annonaceae	Duguetia	1	0	zoo	1	NA	NA	NA
16	Elaeis guineensis	Gombe	Arecaceae	Elaeis	0	0	zoo	NA	1	1	NA
17	Entandrophragma										
18	angolense	Tai	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	NA
19	Entandrophragma										
20	cylindricum	Mbaiki	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	1
21	Entandrophragma										
22	excelsum	Nyungwe	Meliaceae	Entandrophragma	0	0	wind	1	NA	NA	1
23	Erythrophleum										
24	suaveolens	Okapi Lenda	Fabaceae	Erythrophleum	0	0	auto	1	NA	NA	NA
25	Erythrophleum										
26	suaveolens	Okapi Lenda	Fabaceae	Erythrophleum	0	0	auto	1	NA	NA	NA
27	Erythroxyllum manni	Tai	Erythroxylaceae	Erythroxyllum	0	0	zoo	NA	1	NA	NA
28	Eucalyptus	Kibale	Myrtaceae	Eucalyptus	0	0	NA	NA	NA	NA	NA
29	Ficalhoa laurifolia	Nyungwe	Theaceae	Ficalhoa	0	0	auto	1	NA	NA	NA
30	Ficus lutea	Okapi Edo	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
31	Ficus oreodryadum	Nyungwe	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
32	Ficus sansibarica	Tai	Moraceae	Ficus	0	0	zoo	NA	1	NA	NA
33	Funtumia latifolia	Kibale	Apocynaceae	Funtumia	0	0	wind	1	NA	NA	1
34	Galiniera coffeoides	Nyungwe	Rubiaceae	Galiniera	0	0	zoo	NA	1	NA	NA
35	Ganophyllum giganteum	Lope	Sapindaceae	Ganophyllum	1	0	zoo	NA	1	NA	NA
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1											
2											
3											
4											
5											
6											
7	Garcinia huillensis	Gombe	Clusiaceae	Garcinia	0	0	zoo	NA	1	NA	NA
8	Gilbertiodendron										
9	dewevrei	Okapi Lenda	Fabaceae	Gilbertiodendron	0	0	auto	1	NA	NA	NA
10	Gilbertiodendron										
11	splendidum	Tai	Fabaceae	Gilbertiodendron	0	0	auto	1	NA	NA	NA
12	Greenwayodendron										
13	suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	NA	NA	NA
14	Greenwayodendron										
15	suaveolens	Lope	Annonaceae	Polyalthia	0	0	zoo	1	NA	NA	NA
16	Grewia oligoneura	Mbeli	Tiliaceae	Grewia	0	0	zoo	NA	1	NA	NA
17	Hallea stipulosa	Okapi Edo	Rubiaceae	Hallea	0	0	auto	1	NA	NA	NA
18	Harungana										
19	madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
20	Harungana										
21	madagascariensis	Gombe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
22	Harungana montana	Nyungwe	Hypericaceae	Harungana	0	0	zoo	NA	1	NA	NA
23	Heisteria parvifolia	Lope	Olacaceae	Heisteria	0	0	zoo	NA	1	NA	NA
24	Heritiera utilis	Tai	Sterculiaceae	Tarrietia	1	0	wind	NA	NA	NA	1
25	Ilex mitis	Nyungwe	Aquifoliaceae	Ilex	1	0	zoo	NA	1	NA	NA
26	Irvingia excelsa	Mbeli	Irvingiaceae	Irvingia	0	0	zoo	NA	1	NA	NA
27	Irvingia gabonensis	Lope	Irvingiaceae	Irvingia	0	0	zoo	NA	NA	NA	NA
28	Irvingia grandifolia	Lope	Irvingiaceae	Irvingia	0	0	zoo	NA	NA	NA	NA
29	Irvingia wombolu	Okapi Edo	Irvingiaceae	Irvingia	0	0	zoo	NA	1	NA	NA
30	Ixora burundensis	Nyungwe	Rubiaceae	Ixora	0	0	zoo	NA	1	NA	NA
31	Julbernardia seretii	Okapi Edo	Fabaceae	Julbernardia	0	0	auto	1	NA	NA	NA
32	Klainedoxa gabonensis	Lope	Irvingiaceae	Klainedoxa	0	0	zoo	NA	1	NA	NA
33	Macaranga capensis	Amani	Euphorbiaceae	Macaranga	1	0	zoo	1	NA	NA	NA
34	Macaranga										
35	kilimandscharica	Nyungwe	Euphorbiaceae	Macaranga	1	0	zoo	1	NA	NA	NA
36	Macaranga	Okapi Edo	Euphorbiaceae	Macaranga	1	0	auto	1	NA	NA	NA
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47

schweinfurthii

Maesa lanceolata	Nyungwe	Myrsinaceae	Maesa	0	0	zoo	NA	1	NA	NA
Maesopsis eminii	Amani	Rhamnaceae	Maesopsis	0	0	zoo	NA	1	NA	NA
Maesopsis eminii	Amani	Rhamnaceae	Maesopsis	0	0	zoo	NA	1	NA	NA
Magnistipula butayei	Nyungwe	Chrysobalanaceae	Magnistipula	0	0	zoo	1	NA	NA	NA
Magnistipula butayei	Nyungwe	Chrysobalanaceae	Magnistipula	0	0	zoo	1	NA	NA	NA
Manilkara zenkeri	Okapi Edoro	Sapotaceae	Manilkara	0	0	zoo	NA	1	NA	NA
Maranthes goetzeniana	Amani	Chrysobalanaceae	Maranthes	0	0	zoo	NA	1	NA	NA
Margaritaria discoidea	Okapi Lenda	Euphorbiaceae	Margaritaria	1	0	zoo	NA	1	NA	NA
Massularia acuminata	Lope	Rubiaceae	Massularia	0	0	zoo	NA	1	NA	NA
Maytenus acuminata	Nyungwe	Celastraceae	Gymnosporia	0	0	zoo	1	NA	NA	NA
Memecylon lateriflorum	Tai	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Memecylon polyanthemos	Tai	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Memecylon walikalense	Nyungwe	Melastomataceae	Memecylon	0	0	zoo	NA	1	NA	NA
Mesogyne insignis	Amani	Moraceae	Mesogyne	0	0	zoo	NA	1	NA	NA
Milicia excelsa	Lope	Moraceae	Milicia	0	0	zoo	NA	1	NA	NA
Milletia dura	Kibale	Fabaceae	Milletia	0	0	auto	1	NA	NA	NA
Milletia dura	Kibale	Fabaceae	Milletia	0	0	auto	1	NA	NA	NA
Monanthes congoensis	Lope	Annonaceae	Monanthes	0	0	zoo	NA	1	NA	NA
Monanthes poggei	Gombe	Annonaceae	Monanthes	0	0	zoo	NA	1	NA	NA
Musanga cecropioides	Okapi Lenda	Moraceae	Musanga	0	0	zoo	NA	1	NA	NA
Myrianthus arboreus	Lope	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Myrianthus holstii	Amani	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Myrianthus holstii	Amani	Moraceae	Myrianthus	1	0	zoo	NA	1	NA	NA
Nauclea diderrichii	Okapi Edoro	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA

1											
2											
3											
4											
5											
6											
7	Nauclea xanthoxylon	Tai	Rubiaceae	Nauclea	0	0	zoo	NA	1	NA	NA
8	Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
9	Neoboutonia macrocalyx	Nyungwe	Euphorbiaceae	Neoboutonia	1	0	zoo	1	NA	NA	NA
10	Newtonia buchananii	Nyungwe	Mimosaceae	Newtonia	0	0	wind	1	NA	NA	NA
11	Ochna afzelii	Nyungwe	Ochnaceae	Ochna	0	0	zoo	NA	1	NA	NA
12	Ocotea usambarensis	Nyungwe	Lauraceae	Ocotea	0	0	zoo	NA	1	NA	NA
13	Odyendea zimmermannii	Amani	Simaroubaceae	Quassia	0	0	zoo	NA	1	NA	NA
14	Olea capensis	Bwindi	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
15	Olea welwitschii	Kibale	Oleaceae	Olea	0	0	zoo	NA	1	NA	NA
16	Olinia rochetiana	Nyungwe	Oliniaceae	Olinia	0	0	zoo	NA	1	NA	NA
17	Ongokea gore	Lope	Olacaceae	Ongokea	0	0	zoo	NA	1	NA	NA
18	Panda oleosa	Lope	Pandaceae	Panda	0	0	zoo	NA	1	NA	NA
19	Parinari capensis	Gombe	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
20	Parinari excelsa	Okapi Egoro	Chrysobalanaceae	Parinari	0	0	zoo	NA	1	NA	NA
21	Parkia bicolor	Lope	Fabaceae	Parkia	0	0	zoo	1	NA	NA	NA
22	Pentaclethra macrophylla	Lope	Fabaceae	Pentaclethra	0	0	auto	1	NA	NA	NA
23	Pentadesma butyracea	Tai	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
24	Pentadesma reyndersii	Nyungwe	Clusiaceae	Pentadesma	0	0	zoo	NA	1	NA	NA
25	Podocarpus latifolius	Nyungwe	Podocarpaceae	Podocarpus	0	0	zoo	NA	1	NA	NA
26	Polyathia suaveolens	Amani	Annonaceae	Polyathia	0	0	zoo	NA	1	NA	NA
27	Polyscias fulva	Nyungwe	Araliaceae	Polyscias	0	0	zoo	NA	1	NA	NA
28	Porterandia cladantha	Lope	Rubiaceae	Aorantho	0	0	zoo	NA	1	NA	NA
29	Pouteria altissima	Mbaiki	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
30	Pouteria aningeri	Tai	Sapotaceae	Pouteria	0	0	zoo	NA	1	NA	NA
31	Prunus africana	Nyungwe	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
32	Prunus africanum	Kibale	Rosaceae	Prunus	0	0	zoo	NA	1	NA	NA
33	Pseudospondias	Lope	Anacardiaceae	Pseudospondias	1	0	zoo	NA	1	NA	NA
34											
35											
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1											
2											
3											
4											
5											
6											
7	microcarpa										
8	Pseudospondias										
9	microcarpa	Lope	Anacardiaceae	Pseudospondias	1	0	zoo	NA	1	NA	NA
10	Psidium guineense	Lope	Myrtaceae	Psidium	0	0	zoo	NA	1	NA	NA
11	Psychotria mahonii	Nyungwe	Rubiaceae	Psychotria	0	0	zoo	NA	1	NA	NA
12	Psychotria vogeliana	Lope	Rubiaceae	Psychotria	0	0	zoo	NA	1	NA	NA
13	Pterocarpus soyauxii	Lope	Fabaceae	Pterocarpus	0	0	wind	1	NA	NA	NA
14	Pterocarpus tinctorius	Gombe	Fabaceae	Pterocarpus	0	0	wind	1	NA	NA	NA
15	Pycnanthus angolensis	Tai	Myristicaceae	Pycnanthus	0	0	zoo	NA	1	NA	NA
16	Pycnanthus angolensis	Tai	Myristicaceae	Pycnanthus	0	0	zoo	NA	1	NA	NA
17	Rapanea melanophloeos	Nyungwe	Myrsinaceae	Rapanea	0	0	zoo	NA	1	NA	NA
18	Rawsonia lucida	Amani	Flacourtiaceae	Rawsonia	0	0	zoo	NA	1	NA	NA
19	Ricinodendron heudelotii	Okapi Lenda	Euphorbiaceae	Ricinodendron	0	0	zoo	NA	1	NA	NA
20	Ricinodendron heudelotii	Okapi Lenda	Euphorbiaceae	Ricinodendron	0	0	zoo	NA	1	NA	NA
21	Rytiginia kigeziensis	Nyungwe	Rubiaceae	Rytiginia	0	0	zoo	NA	1	NA	NA
22	Saba comorensis	Gombe	Apocynaceae	Saba	0	1	zoo	NA	1	NA	NA
23	Sacoglottis gabonensis	Tai	Humiraceae	Sacoglottis	0	0	zoo	NA	1	NA	NA
24	Santiria trimera	Lope	Burseraceae	Santiria	0	0	zoo	NA	1	NA	NA
25	Sarcocephalus pobeguini	Okapi Lenda	Rubiaceae	Sarcocephalus	0	0	zoo	NA	1	NA	NA
26	Schefflera goetzenii	Nyungwe	Araliaceae	Schefflera	0	0	zoo	NA	1	NA	NA
27	Scottelia klaineana	Tai	Flacourtiaceae	Scottellia	0	0	zoo	NA	1	NA	NA
28	Scytopetalum tieghemii	Tai	Scytopetalaceae	Scytopetalum	0	0	zoo	NA	1	NA	NA
29	Sorindeia madagascariensis	Amani	Anacardiaceae	Sorindeia	0	0	zoo	NA	1	NA	NA
30	Staudtia kamerunensis var. gabonensis	Lope	Myristicaceae	Staudtia	0	0	zoo	NA	1	NA	NA
31	Sterculia oblonga	Tai	Sterculiaceae	Eribroma	0	0	zoo	1	NA	NA	NA
32											
33											
34											
35											
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

1											
2											
3											
4											
5											
6											
7	Strombosia pustulata	Tai	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
8	Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
9	Strombosia scheffleri	Kibale	Olacaceae	Strombosia	0	0	zoo	NA	1	NA	NA
10	Strombosiaopsiopsis tetrandra	Okapi Edo	Olacaceae	Strombosiaopsiopsis	0	0	zoo	NA	1	NA	NA
11	Symphonia globulifera	Nyungwe	Clusiaceae	Symphonia	0	0	zoo	NA	1	NA	NA
12	Synsepalum afzelii	Tai	Sapotaceae	Synsepalum	0	0	zoo	NA	1	NA	NA
13	Syzygium cordatum	Bwindi	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA
14	Syzygium guineense	Nyungwe	Myrtaceae	Syzygium	0	0	zoo	NA	1	NA	NA
15	Tabernaemontana penduliflora	Mbeli	Apocynaceae	Tabernaemontana	0	0	zoo	NA	1	NA	NA
16	Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA
17	Tetrapleura tetraptera	Lope	Fabaceae	Tetrapleura	0	0	zoo	1	NA	NA	NA
18	Thomandersia laurifolia	Mbeli	Acanthaceae	Thomandersia	0	0	auto	1	NA	NA	NA
19	Trichoscypha acuminata	Mbeli	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA
20	Trichoscypha arborea	Tai	Anacardiaceae	Trichoscypha	0	0	zoo	NA	1	NA	NA
21	Triplochiton scleroxylon	Mbaiki	Malvaceae	Triplochiton	0	0	wind	NA	NA	NA	1
22	Uapaca corbisieri	Tai	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA
23	Uapaca guineensis	Okapi Edo	Euphorbiaceae	Uapaca	1	0	zoo	NA	1	NA	NA
24	Uvariastrum pierreanum	Lope	Annonaceae	Uvariastrum	0	0	zoo	NA	1	NA	NA
25	Vitex doniana	Mbeli	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA
26	Vitex fischeri	Gombe	Verbenaceae	Vitex	0	0	zoo	NA	1	NA	NA
27	Xylia evansii	Tai	Fabaceae	Xylia	0	0	auto	1	NA	NA	NA
28	Xylophia aethiopica	Lope	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA
29	Xylophia hypolampra	Lope	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA
30	Xylophia quintasii	Tai	Annonaceae	Xylophia	0	0	zoo	NA	1	NA	NA
31	Zanha golungensis	Tai	Sapindaceae	Zanha	1	0	zoo	NA	1	NA	NA
32	Zanthoxylum gillettii	Okapi Lenda	Rutaceae	Zanthoxylum	1	0	zoo	NA	1	NA	NA
33											
34											
35											
36											
37											
38											
39											
40											
41											
42											
43											
44											
45											
46											
47											

- NA = not applicable
- 1 = applicable
- 0 = absent

For Peer Review Only

Responses to Edito's comments

We thank the editor and reviewers for their particularly thorough reviews and suggestions for improving the manuscript. We have attempted to address all these issues and believe the manuscript is considerably improved as a consequence. To conveniently document the changes we have made in response to specific comments, we summarise the key comments, changes we have made and an example of the line numbers where we have made changes relevant to this in the table below – though we note that the manuscript has been extensively redrafted so changes are present throughout. We hope you will agree that our changes have improved the manuscript and look forward to hearing from you in due course.

First of all, the writing still needs to be polished. I have done my best for signalling a few grammar errors or typos, but I guess that authors would need to use a professional linguistic editorial service.

The manuscript has been checked by at least 3 UK faculty staff with native English. We believe the English now to be error-free and apologise if there are any remaining typos.

Second, I would still recommend some rewriting of the discussion section. Try to avoid repetition of ideas regarding the common annual patterns (e.g. L308-311, 330-331, L331-333, L347-348, L409-410 say virtually the same) or the lack of quality weather data in Africa (repeated in L344-346 and 421-422). By contrast, some deeper discussion of differences among sites would be interesting and this is still lacking (despite the interesting pattern from west to east), with more site-specific description (Referee #3 signalled this too in the previous review).

We have added a few sentences to discuss the lack of clear geographic patterning in fruiting season (wet vs dry) or seasonality or aseasonality in flowering or fruiting, and to clarify that the west to east patterning in cycle profile remains only a weak effect. We feel that further discussion of patterning across sites may be an over-interpretation of our data thus far, but we have made recommendations for addressing this need.

Lines 308-311 state “Using Fourier based analysis we effectively estimated flowering patterns for 5446 individual trees of 196 species and fruiting patterns for 4595 trees of 191 species across 12 and 11 sites, respectively, both at the site level and among tropical forests spanning from western to eastern Africa.

We think this is necessary information to recall our main dataset for the reader.

Lines 331-333 were repetitive of lines 330-331 and have been removed.

Lines 347-348 considered the likelihood of cycles being driven by an annual environmental cue, which is a different subject from the original statement of results.

1
2
3 However, our broader revisions to the discussion mean that these lines have been
4 deleted.

5
6 Lines 409-410 do repeat the major conclusion, but we believe this is standard practice
7 within a conclusions section.
8

9
10 Lines 421-422 are a recommendation for future data collection to address the lacunae
11 mentioned in lines 344-346 and thus do not really repeat the earlier statement.
12

13
14 We have revised the whole discussion section and reduced repetition throughout.
15

16
17 Third, there is a major misunderstanding regarding the interpretation of the Rayleigh
18 test: when the distribution is uniform or multimodal, you cannot technically say that
19 there is any kind of seasonality, as the test is not correctly applied in those cases.
20

21
22 Therefore, sentence in L385-387 is not correct, as Kibale had a uniform flowering
23 seasonality. When the distribution is bimodal, you can apply the Rayleigh test
24 dividing the circle and calculating two angular means. I would also include in the
25 circular graphs an arrow with the value of the r vector, signalling the seasonality
26 intensity (only for unimodal distributions).
27

28 I removed the mean angles as they are likely to be meaningless and did not
29 correspond well to the data.
30

31
32 Fourth, I thank authors for including the supplementary material with a final list of
33 selected species per site (and their most important traits such as dispersal mode, etc).
34 However, the table heading of the table is missing, and it is not cited in the text. The
35 other supplementary information including intra-specific variation of cycles within
36 species should be edited (titles, x axis including years, etc) before publication but I
37 guess that might be finally removed, as it is even not cited in the text.
38

39
40 I have made the suggested correction and cited in text.
41

42
43 In addition to all these points, the format of Biotropica is not followed at many parts
44 of the paper (use of small caps for the first sentence and reference list, for instance,
45 table titles in capitals, subheadings in small caps, etc), so the manuscript needs to be
46 revised following these guidelines. Very importantly, the entire list of references
47 needs major review, as numerous small mistakes are present, such as lacking journal
48 and pages, etc.
49

50
51 The formatting has been corrected throughout.
52

53
54 As I signalled before, the data share statement needs to include the DOI of the WCS
55 portal website. Sites with embargo need to be noted in detail, and also, the length of
56
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

the embargo and the contact email for discussing the potential access to information.
Editors of Biotropica will give you more assistance regarding this.
[We have modified the statement and eagerly await into from Biotropica's editors.](#)

For Peer Review Only

1
2
3
4 Minor comments:

5 L72. Include “the” before “most common”.

6 Done
7

8
9 L76. Put “cycle” in plural.

10 This suggestion is not grammatically correct in English; it should stay as ‘cycle’.
11 However, the lines 75-79 have been revised in response the next comment and the
12 point is now differently phrased.
13
14

15 L76-77. I find this sentence too vague: which sites had continuous flowering and
16 fruiting?
17

18 We believe that the Introduction should build the general picture. As we have not
19 introduced the reader to our site names, it would be confusing to talk about them in
20 detail in the Introduction. We have revised to include general geographical patterns.
21
22

23 L85-86. Remove “Introduction”. Put the first line in Small Caps.

24 Done. But the guidelines state the first phrase (not entire line) needs to be in small
25 caps.
26

27 L87. I believe that this sentence needs to be in singular (“phenology... is essential”).

28 Corrected
29

30
31 L168. All subheadings need to be in small caps.

32 Done
33
34

35 L170. Here and in other parts of the text, you need to be consistent with the spelling
36 of the site M’Baiki (I believe that this might be the correct spelling). Please,
37 consistently write the name of the site in L183, 275, 476, 477, L681, L691, Tables 1-
38 5, Figs. 1-5.
39

40 Done
41

42 L174-176. Cite Table 3 here (although I believe that it should be condensed with
43 Table 1). In case that you maintain the two tables as separated, you need to inverse
44 numbers for actual Tables 2 and 3.

45 We have maintained the two tables separately, as a merged table seemed too large and
46 confusing. We have checked the Table numbers in their text citations and legends.
47 Table 2 now is referred to in the correct order.
48
49
50

51 L194 & 204. There is a major confusion with the correct citation of publications of
52 Bush et al. Please, be aware that the article published in Methods in Ecology and
53 Evolution is from 2017, whereas the article in Biotropica is from 2018! The same
54 reference is repeated in the final list, in addition.
55

56 Checked and corrected throughout
57
58
59
60

1
2
3
4 L219. Remove “of”.

5 Done
6

7
8 L231. Replace by “time between flowering or fruiting events)

9 Done
10

11 L242. Put the entire name of the dataset (Climate Hazards Group InfraRed
12 Precipitation with Station data) first time of use and the corresponding acronym
13 (CHIRPS) in parenthesis later. I already signalled that the acronym is bad written.

14 Done
15

16
17 L246. Replace by CHIRPS.

18 Done
19

20
21 L254. Include “to” before “identify multi-modality”.

22 Done
23

24
25 L255. Please, see my previous comments about bimodality and the Rayleigh test. In
26 the Kibale case, the Rayleigh could be applied with previous preparation of the data;
27 reduce the angles to one side of the circle and calculate two means (see Morellato et
28 al. 2010 and Zar 1999).

29 See our comments in the table of major responses
30

31
32 L258. The citation of the software used for the circular analyses is lacking (and the
33 package if you were using R).

34 Citation has been added and this section revised in the light of comments on the
35 suitability of the Rayleigh test for multi-modal situations.
36

37
38 L267-271. I think this fits better to the method section.

39 Methods have been revised accordingly and the section moved up.
40

41
42 L277-279. Were those two plots in Okapi the same forest type? This is not specified
43 in Table 1.

44 Now clarified in the table – they are the same forest type.
45

46
47 L295-296. I believe this needs to be included in the methods.

48 The sentence on significance levels has been removed to Methods section.
49

50
51 L315. Lopé is written in smaller font size.

52 Corrected
53
54
55
56
57
58
59
60

1
2
3
4 L320. The authors say here and in other parts of the text (L349-350, 434-435) that
5 sub-annual cycles are the most frequent in South America. I have said in my previous
6 two reviews that I disagree with this statement; it is true that Newstrom et al. (1994)
7 state that subannual life cycles abound for La Selva and supra-annual patterns
8 dominate in Lambir (Sakai 2001), but other Neotropical examples show frequent
9 annual and supra-annual patterns. For instance, Nouragues in French Guiana shows
10 predominantly annual and supra-annual patterns (Norden et al. 2007, Mendoza et al.
11 this issue), and there is evidence of annual variation of fruiting on Barro Colorado
12 Island, where 54% of species showed CV larger than 1 (indicating masting) (Wright
13 et al. 2005). I sincerely believe that life cycles of tropical plants are not well evaluated
14 (even less using Fourier analyses) and would acknowledge some discussion on it (and
15 the inclusion of these references).
16
17
18

19 We agree that the main conclusion from the body of literature available is that the
20 question is as yet under studied. We have included an improved discussion of this
21 point and used the literature suggested. The 54% of species (a small majority)
22 showing masting – a supra-annual strategy- at BCI is in contrast to the predominance
23 of annual cycles in African forests in general although more similar to our eastern
24 sites, which is interesting.
25
26
27

28 L323. And also, evolutionary pressures for flowering and fruiting are different.
29 Acknowledged – we have included a comment on this and a reference to the recent
30 paper showing diverse evolutionary origins of African forests (Slik et al, 2018).
31
32

33 L373-375. The close of the parenthesis is lacking here. In addition, you should
34 include any reference of the statement that wind dispersed seeds fruit during dry
35 season, whereas fleshy fruits tend to appear during the rainy season.
36

37 Done
38

39 L178, 231 & 385. Remove space after and before the “/”.

40 Corrected – we have written out the words in other cases where we had used the /
41
42

43 L401. Put in Italics “et al.” here and elsewhere in the text.

44 Corrected throughout
45

46 L446. Substitute for “vary”.

47 This line has been revised and this word is no longer used.
48
49

50 Acknowledgements: They are exceptionally long, could be condensed and/or
51 summarized? Put always first the complete name of the Institution and the
52 abbreviation in parenthesis later (is written the opposite for M’Baiki site).
53

54 We do not feel it is appropriate to suppress acknowledgements that should be made.
55 As this is an exceptionally long, multi-site comparison of empirical data, there are a
56 lot of people, institutions and funders involved.
57
58
59
60

1
2
3 Reference list: It needs massive review. First, the guidelines of Biotropica are not
4 followed regarding small caps. The following errors have been detected:

5 Arino et al. 2009. The title, journal and pages are lacking.

6
7 [Corrected](#)

8
9 Bush et al. 2016 and 2017 is the same article!

10
11 [2016 deleted](#)

12
13 Hudson & Keatley was published in 2010.

14
15 [Corrected](#)

16
17 Medway 1972. I guess that is “Malaysia” and not “Malaya”.

18
19 [No, Malaya was the name in use at the time](#)

20
21 Morellato et al. 2010. Editors of the book are lacking.

22
23 [Added](#)

24
25 National Weather Service 2010. Remove the “a” of “Nationala”.

26
27 [Done](#)

28
29 Plumtre et al. 2012. Editorial and city are lacking.

30
31 [Added](#)

32
33 Polansky & Boesch 2013. Repeated the same reference at the end.

34
35 [Removed repeat](#)

36
37 Takenoshita et al 2008. Journal name and pages are lacking.

38
39 [Corrected](#)

40
41 Tutin & Fernandez. Put year after author names. Remove the quotation marks.

42
43 [Corrected](#)

44
45 Tables 1 and 3. I suggest condensing both tables 1 and 3, as the rainfall seasonality is
46 part of the description of each site. Taï site is lacking from Table 3.

47
48 [We have added the Taï site to Table 3, however we believe that merging these two
49 tables will result in an overly large and confusing table, thus we have kept them
50 separated.](#)

51
52 Table 2. I still do not understand this table. I think you should also include the actual
53 number of species and individuals used for Fourier analyses after you applied the
54 criteria, instead of only the original dataset (from which you subtracted a substantial
55 part). In addition, the heading of the table needs rewriting (“al” is bad spelled).

56
57 [The original data are in Column 2. The headings are corrected](#)

1
2
3
4 Figures 4 and 5. Please, correct the spelling of all sites (Lopé, M'Baïki, Taï,...). If
5 you do not feel able to do this with R, use any kind of image processing software.
6

7 [Site spellings corrected.](#)
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Peer Review Only