

Phenology of forest trees favoured by elephants in the Kakum Conservation Area, Ghana

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Abstract

The reproductive and foliage status of forest trees that are important elephant fruit sources were monitored from July 2001 to June 2002 at the Kakum Conservation Area, Ghana. Phenological events were variable among and within species. Generally, drought conditions triggered leaf shedding while rains induced leaf flushing. Also, rainfall in the wet season was related to the amount of fruits available for elephants in the dry season. However, the best climatic predictor of fruiting was minimum temperature.

Résumé

Le statut de la reproduction et du feuillage des arbres de forêt qui sont d'importantes sources de fruits pour les éléphants a été suivi de juillet 2001 à juin 2002 dans l'Aire de Conservation de Kakum, au Ghana. Les changements phénologiques étaient variables au sein des espèces et entre les espèces. En général, la sécheresse déclenchait la chute des feuilles, et la pluie entraînait l'apparition de nouvelles feuilles. On a aussi trouvé que la quantité de pluie tombée en saison des pluies était liée à l'abondance des fruits disponibles pour les éléphants en saison sèche. Cependant, le meilleur indice climatique de la production des fruits est la température minimale.

Introduction

Most tropical rainforest trees produce fruits that are consumed by forest elephants, which also disperse their seeds (Alexandre 1978; Short 1983; Lieberman et al. 1987; Chapman et al. 1992; Feer 1995). The large number and the diversity of viable seeds in elephant dung piles show the importance of fruits in the diet of forest elephants (Wing and Buss 1970; Alexandre 1978; Short 1981; Merz 1981; Martin 1982; White et al. 1993; White 1994; Theuerkauf et al. 2000; Muoria et al. 2001; Danquah and Oppong 2006) and the significance of elephants as seed dispersal agents (Alexandre 1978; Short 1981; Lieberman et al. 1987; White et al. 1993; Muoria et al. 2001; Waithaka 2001; Blake 2002).

The availability throughout the year of fruits and leaves on which elephants feed is of great importance.

However, there is great variability in tree phenology, which to some extent is influenced by environmental factors like temperature, rainfall, humidity and length of daylight (Longman and Jenik 1974). Hence it is expected that elephant population and reproductive capacity will respond to the phenological patterns of the fruit trees they forage (Struhsaker 1998).

Predicting the effects of climatic elements on forest tree phenology may provide insights into the impact of future climate changes on food (fruits and leaves) availability and diversity for elephants. These predictions are possible by establishing relationships between weather patterns and tree phenology (Inouye et al. 2003). Hence, the current study sought to investigate climatic factors that govern fruit tree phenology in the Kakum Conservation Area of Ghana, which is likely to form the basis for developing good elephant management options.

Materials and methods

Study area

The Kakum Conservation Area (KCA) is located in southern Ghana and comprises Kakum National Park and the adjacent Assin Attandanso Reserve (fig. 1). It encompasses an irregular block of forest measuring 366 km², consisting mainly of *Celtis zenkeri* and *Triplochiton scleroxylon* moist semi-deciduous vegetation (Hall and Swaine 1976), which is transitional to the more typical rainforest *Lophira alata*–*Triplochiton scleroxylon* association in the southern part of the Kakum Reserve (Dudley et al. 1992).

Climatic variables

Mean monthly rainfall collected from seven strategically placed rain gauges around KCA indicated a bimodal distribution with peaks occurring in March–July and September–November, and a dry season between December and February. There is a short dry spell in August.

KCA does not have records for maximum and minimum air temperatures and relative humidity. However, there is some similarity in climatic conditions between KCA and a nearby meteorological station at Asuansi, 18 km east south-east of the park headquarters (Barnes et al. 2003). Therefore data on maximum and minimum air temperatures and relative humidity for Asuansi were used to establish the relationships among weather elements and phenological events in KCA.

Phenological events

KCA was broadly classified into 10 sections: Abrafo (park headquarters), Mfuom, Antwikwaa, Afiaso, Aboabo, Adiembra, Ahomaho, Briscoe 1, Briscoe 2 and Asomdwee (fig. 1). Four sections—Abrafo, Antwikwaa, Briscoe 2 and Ahomaho—were randomly selected and a non-linear phenology

strip transect approximately 3.4 km long and 10 m wide was constructed within each section.

Strip transects were constructed by linking major (frequently used) elephant trails with patrol trails to minimize damage to vegetation when cutting new transects. All trees (> 10 cm diameter at breast height) that are important elephant fruit sources (Merz 1981; Short 1981; Theuerkauf et al. 2000; White et al. 1993) were marked within strip transects.

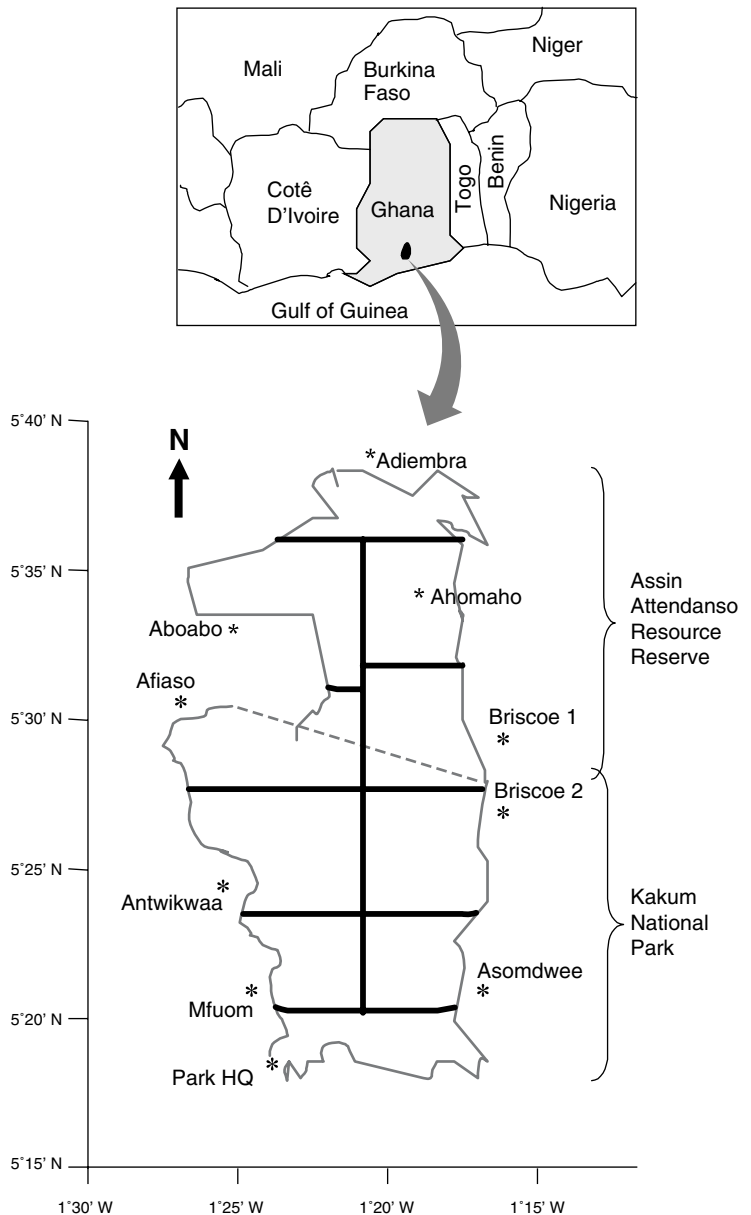


Figure 1. The Kakum Conservation Area showing the 10 camp-beat demarcations.

During the study period (July 2001 to June 2002), all phenology strip transects were synchronously monitored at two-week sampling intervals and the reproductive (flowering and fruiting) and foliage status (flushing, full crown, dropping of leaves, leafless) were noted on all marked trees. Observations were made with 8 x 30 binoculars.

The coefficient of dispersion (CD) (standard deviation, arising from the (mean estimates of the trees sampled) / mean monthly number of trees showing a phenological event over the entire study)) was used to represent the synchrony of fruiting and flowering events (Chapman et al. 1999). When the CD is > 1, the pattern is synchronized, that is fruiting and flowering events occur in the same period; when > 1, the pattern is uniform; and equal to 1 when the pattern is random.

Fruit availability and diversity study

During each sampling period, fruits available to elephants was assessed by counting the number of freshly fallen fruits from marked trees along the phenology strip transects (Chapman et al. 1994). Fruit availability was expressed as number of fallen fruits per square kilometre. Fruit diversity was also expressed as the number of species with fallen fruits per square kilometre.

Climatic predictors of phenological events

The association between climatic elements and phenological events was determined by relating the number of trees fruiting, flowering and leaf flushing or leaf dropping in a given month to climatic variables such as mean rainfall, minimum and maximum air temperatures, and relative humidity. These analyses compared the occurrence of phenological events for a given month with climatic variables for the same month and with each preceding month up to seven months (lagged climatic variables; Chapman et al. 1999).

Results

Phenological events

Nineteen tree species were marked and their phenology monitored (table 1). Flowering was not observed on *Desplatsia* sp. Flowering and fruiting in *Panda* sp. was staggered over the period of study. However, *Parinari* and *Ficus* species flowered and fruited only four months within the period. Fruiting (mean = 40.917, SD = 14.419, CD = 0.35) and flowering (mean = 10.417, SD = 7.997, CD = 0.77) were uniform (CD < 1.0) when values were pooled for all species.

Table 1. Phenological events of tree species for each month at Kakum Conservation Area

Species	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
<i>Aningeria robusta</i> (n = 4)	OX	X	X	X	X	X	-	-	+	+	-	O
<i>Antiaris africana</i> (n = 11)	-	+	O+	OX+	X	X	X	X	X	-	-	-
<i>Antrocaryon micraster</i> (n = 3)	OX	X	X	X	X	X	-	+	+	-	-	O
<i>Desplatsia dewevrei</i> (n = 6)	X	X	X	X	-	-	-	-	-	-	X	X
<i>Ficus capensis</i> (n = 5)	-	-	-	-	-	-	O+	OX+	X	X	X	-
<i>Klainedoxa gabonensis</i> (n = 4)	X	X	X	X	X	X	-	-	-	O+	X+	X
<i>Mammea africana</i> (n = 3)	X	X	X	X	X	X	-	-	O	O	O	OX
<i>Microdermis puberla</i> (n = 6)	O	O	OX	X	X	X	X	X+	+	-	-	O
<i>Milicia excelsa</i> (n = 7)	-	-	-	-	+	O+	OX	X	X	X	X	X
<i>Musanga cercropoides</i> (n = 4)	X	X	X	X		+	O+	O	X	X	X	X
<i>Myrianthus arboreus</i> (n = 8)	X	X	X	X	X	-	-	-	+	O+	OX	X
<i>Ongokea gore</i> (n = 5)	OX	X	X	X	X	X	-	-	-	O	O	OX
<i>Panda oleosa</i> (n = 11)	X	X	OX	OX	X	X	X	X	O	O	OX	X
<i>Parinari excelsa</i> (n = 2)	-	-	O	X	X	X	X	-	-	-	+	+
<i>Ricnodendron heudelotii</i> (n = 8)	X	X	X	X	-	-	+	+	+	O	OX	X
<i>Strombosia glaucescens</i> (n = 3)	X	X	X	X	X	X	+	+	+	-	O	O
<i>Strychnos aculeata</i> (n = 4)	-	-	-	O	OX	X	X	X	X	X	X	X
<i>Tieghemella hecklii</i> (n = 9)	O	OX	X	X	X	X	-	-	-	-	+	+
<i>Treculia africana</i> (n = 6)	-	O	O	O	OX	OX	X	X	X	OX	OX	X

x = presence of fruits, o = presence of flowers, + = exchange of leaves, n = sample size

However, fruiting (63%) and flowering (94%) were synchronous ($CD > 1.0$) when the values were analysed for each species (table 2).

Fruit availability was significantly related ($r^2 = 0.902$, $P < 0.05$) to fruit diversity (fig. 2). Fruit diversity increased with fruit availability and was more rapid when fruit density exceeded the threshold of 15,000 fruits per square kilometre.

Climatic predictors of phenological events

Phenological events varied among tree species (table 3). Leaf flushing was occasional with fewer tree species experiencing foliage fluxes (flushing, shedding leaves, becoming leafless) than reproductive changes (flowering and fruiting). Fruiting was the most common phenological event while leaf loss was rare.

Rainfall

The majority (68%) of the tree species were deciduous; 32% remained evergreen. The highest leaf shed-

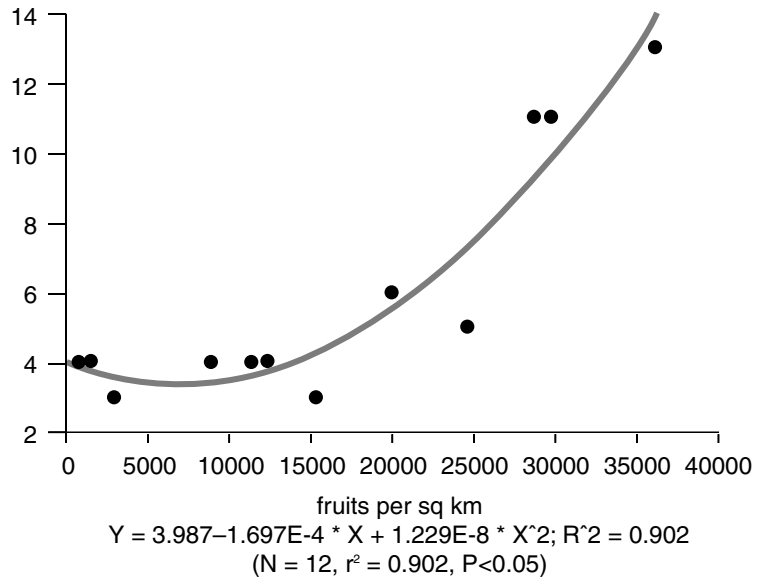


Figure 2. The relationship between fruit availability and fruit diversity in the Kakum Conservation Area.

Table 2. Pattern of fruiting and flowering in tree species based on the coefficient of dispersion (CD) (standard deviation (SD) / mean number of trees in each month)

Species	Fruiting				Flowering			
	Mean no. of trees	SD	CD	Pattern	Mean no. of trees	SD	CD	Pattern
<i>Aningeria robusta</i>	1.167	1.403	1.20	synchronized	0.500	0.798	1.6	synchronized
<i>Antiaris africana</i>	3.333	4.334	1.30	synchronized	1.167	2.725	2.3	synchronized
<i>Antrocaryon micraster</i>	1.750	1.765	1.01	synchronized	0.417	0.900	2.2	synchronized
<i>Desplatsia dewevrei</i>	2.833	2.980	1.05	synchronized	0.000	0.000	0.0	not observed
<i>Ficus capensis</i>	0.583	0.900	1.54	synchronized	0.167	0.389	2.3	synchronized
<i>Klainedoxa gabonensis</i>	0.667	0.492	0.74	uniform	0.083	0.289	3.5	synchronized
<i>Mammea africana</i>	0.917	0.996	1.09	synchronized	0.500	0.798	1.6	synchronized
<i>Microdermis puberla</i>	2.500	2.939	1.18	synchronized	1.000	1.907	1.9	synchronized
<i>Milicia excelsa</i>	1.833	2.250	1.23	synchronized	0.500	1.446	2.9	synchronized
<i>Musanga cercropoides</i>	0.667	0.492	0.74	uniform	0.167	0.389	2.3	synchronized
<i>Myrianthus arboreus</i>	4.000	3.838	0.96	uniform	0.667	2.309	3.5	synchronized
<i>Ongokea gore</i>	1.583	1.443	0.91	uniform	0.667	1.155	1.7	synchronized
<i>Panda oleosa</i>	8.250	4.202	0.51	uniform	1.333	3.200	2.4	synchronized
<i>Parinari excelsa</i>	0.333	0.492	1.48	synchronized	0.083	0.269	3.2	synchronized
<i>Ricinodendron heudelotii</i>	3.333	3.525	1.06	synchronized	1.000	1.954	2.0	synchronized
<i>Strombosia glaucescens</i>	0.500	0.522	1.04	synchronized	0.167	0.389	2.3	synchronized
<i>Strychnos aculeata</i>	1.750	1.357	0.78	uniform	0.500	1.243	2.5	synchronized
<i>Tieghemella hecklii</i>	2.583	3.370	1.30	synchronized	0.917	2.234	2.4	synchronized
<i>Treulia africana</i>	3.000	2.374	0.79	uniform	0.833	1.193	1.4	synchronized

Table 3. Mean climatic variables and phenological events of tree species in each month for the period July 2001 to June 2002

Season/ month	Rainfall (mm)	Max temp (° C)	Min temp (° C)	Rel hum (%)	Leaf flush- ing	Leaf shed- ding	Leaf- less	Flower- ing	Fruit- ing	No. fruits/ km ²
<i>Major season</i>										
Mar	69.86	31.9	24.2	82.4	26	10	10	4	19	16,412
Apr	129.36	32.6	24.5	83.0	9	2	2	31	18	12,301
May	141.56	32.4	24.3	82.2	2	1	0	14	27	1,522
June	262.64	29.5	23.5	85.6	0	0	1	9	46	860
July	70.72	28.7	22.6	87.4	1	0	0	15	42	2,875
<i>Short dry spell</i>										
Aug	24.10	27.9	22.5	87.6	0	0	0	11	49	8,934
<i>Minor season</i>										
Sep	89.20	29.4	22.9	85.8	0	7	7	12	58	19,941
Oct	153.54	31.7	23.5	83.0	7	0	0	14	57	36,169
Nov	106.93	30.8	23.6	85.2	0	5	0	4	54	29,699
<i>Dry season</i>										
Dec	32.23	32.0	23.9	84.0	5	1	6	6	53	28,610
Jan	19.76	29.6	22.5	86.2	1	11	2	3	38	24,581
Feb	53.49	31.9	24.1	83.2	2	10	18	2	30	11,434
Total					53	47	46	125	491	

ding occurred in January, leaf flushing in March and flowering in April (table 3).

Fruiting was highest in the minor wet season (table 3) and correlated ($r = 0.764$, $P < 0.05$) highly with mean rainfall in the previous three months of the major wet season (table 4). Similarly, fruit availability was high in October and during the dry season and also showed a high correlation with rainfall in the last four ($r = 0.857$, $P < 0.01$) and five ($r = 0.867$, $P < 0.01$) months prior to October. However, rainfall was inversely correlated ($r = -0.811$, $P < 0.01$) to leaf shedding.

Temperature

Leaf flushing occurred at the onset of the major wet season and showed a positive correlation ($r = 0.714$, $P < 0.05$) with mean maximum temperature during the same month (table 5).

Fruit production was inversely correlated to mean maximum temperature (fruiting, $r = -0.762$, $P < 0.05$; fruit availability, $r = -0.739$, $P < 0.05$ (table 5) and mean minimum temperature (fruiting, $r = -0.877$, $P < 0.05$; fruit availability, $r = -0.781$, $P < 0.05$) (table 6) that occurred three months prior to the month the estimate was recorded.

Table 4. Correlation of lagged rainfall with phenological events in the Kakum Conservation Area

Event	Rainfall (mm)							
	<i>n</i>	<i>n</i> - 1	<i>n</i> - 2	<i>n</i> - 3	<i>n</i> - 4	<i>n</i> - 5	<i>n</i> - 6	<i>n</i> - 7
Leaf flushing	-0.114	-0.489	-0.539	-0.525	-0.150	0.325	0.582	0.154
Leaf shedding	-0.811**	-0.632*	-0.504	-0.061	0.193	0.372	0.214	0.382
Leafless	-0.712*	0.585	0.265	0.200	0.080	0.291	0.109	0.076
Flowering	0.523	0.365	0.312	-0.039	-0.418	-0.277	-0.014	-0.337
Fruiting	0.112	0.301	0.566	0.764*	0.601	0.322	-0.070	-0.273
Fruit availability	-0.301	-0.280	-0.119	0.245	0.857**	0.867**	0.601	0.147

* $P < 0.05$; ** $P < 0.01$; *n*, month in which phenological event occurred

Relative humidity

The climatic element of relative humidity had a low correlation with phenological events but there was a solitary inverse correlation between leaf flushing and relative humidity during the time of data collection. Fruit availability also showed an inverse correlation with relative humidity two and three months prior to the period the estimate was recorded (table 7).

Discussion

The data were collected over a one-year period, and it is likely that fluctuations over longer periods cannot be adequately described (Martin 1982). However, the results presented provide an insight into what might be expected on average over the long term and also serve as a baseline on which future elephant management strategies could be based.

Table 5. Correlation of lagged mean maximum temperature with phenological events in the Kakum Conservation Area

Event	Mean maximum temperature (° C)							
	<i>n</i>	<i>n</i> - 1	<i>n</i> - 2	<i>n</i> - 3	<i>n</i> - 4	<i>n</i> - 5	<i>n</i> - 6	<i>n</i> - 7
Leaf flushing	0.714*	0.261	-0.038	-0.043	-0.279	-0.037	-0.372	-0.370
Leaf shedding	0.366	0.145	-0.127	-0.243	-0.243	-0.426	-0.599	-0.370
Leafless	0.295	-0.071	0.045	-0.095	0.036	-0.346	-0.686*	-0.491
Flowering	0.069	-0.100	0.026	0.058	0.429	0.582	0.453	0.216
Fruiting	-0.504	-0.543	-0.511	-0.762*	-0.109	0.259	0.602	0.504
Fruit availability	0.161	-0.207	-0.680*	-0.739*	-0.581	-0.151	0.161	0.357

* $P < 0.05$; *n*, month in which phenological event occurred

Table 6. Correlation of lagged mean minimum temperature versus phenological events in the Kakum Conservation Area

Events	Mean minimum temperature (° C)							
	<i>n</i>	<i>n</i> - 1	<i>n</i> - 2	<i>n</i> - 3	<i>n</i> - 4	<i>n</i> - 5	<i>n</i> - 6	<i>n</i> - 7
Leaf flushing	0.549	0.041	-0.129	-0.278	-0.483	-0.020	-0.326	-0.199
Leaf shedding	0.021	-0.030	-0.396	-0.502	-0.334	-0.447	-0.371	-0.286
Leafless	-0.084	-0.215	-0.098	-0.381	-0.104	-0.340	-0.454	-0.317
Flowering	0.332	0.137	0.384	0.150	0.316	0.574	0.243	0.216
Fruiting	-0.606	-0.469	-0.235	-0.877**	0.250	0.457	0.581	0.580
Fruit availability	-0.214	-0.357	-0.677*	-0.781*	-0.288	0.134	0.358	0.473

* $P < 0.05$; ** $P < 0.01$; *n*, month in which phenological event occurred

Table 7. Correlation of lagged relative humidity and phenological events in the Kakum Conservation Area

Event	Relative humidity (%)							
	<i>n</i>	<i>n</i> - 1	<i>n</i> - 2	<i>n</i> - 3	<i>n</i> - 4	<i>n</i> - 5	<i>n</i> - 6	<i>n</i> - 7
Leaf flushing	-0.685*	-0.285	0.066	0.330	0.333	-0.125	0.283	0.064
Leaf shedding	-0.204	0.123	0.276	0.258	0.117	0.357	0.284	0.420
Leafless	-0.299	0.139	0.191	0.131	-0.175	0.295	0.380	0.440
Flowering	-0.014	-0.138	-0.259	0.090	-0.225	-0.498	-0.417	-0.369
Fruiting	0.272	0.444	0.428	0.242	-0.060	-0.225	-0.525	-0.592
Fruit availability	-0.233	0.201	0.656*	0.709*	0.435	-0.063	-0.315	-0.382

* $P < 0.05$; *n*, month in which phenological event occurred

Phenological events

Temporal variations in the production of flowers, fruits and young leaves were complex, making it difficult to generalize. Similarly, combining data for all tree species for the entire study period masked important variations in phenological episodes.

Time of leaf fall and leaf flush was often not well defined, hence foliage fluxes were rather tricky to record reliably. Therefore, small and brightly coloured leaves, which appeared as new leaves, may have been several months old (Lieberman 1982) and might have introduced errors in the estimates. Also, the enormous variability in fruiting regime made it difficult to judge reproductive events accurately, bearing in mind that the observer in most cases had to judge from a distance of more than 25 m through an understorey that allowed only a partial view of the tree crown.

It is presumed that the flowering and fruiting data are incomplete, especially for species with small, inconspicuous flowers or fruits. Fruiting in *Panda oleosa* was staggered and is likely to provide a longer source of fruit supply for elephants as compared with other tree species that were more season specific. Richards (1998) also noted that species with staggered fruiting seasons provide a year-round food supply for unspecialized frugivores and seedeaters such as elephants.

The pooled data showed uniformity in reproductive regimes for tree species. However, intraspecific fruiting or flowering synchrony was prevalent, where many individuals of the same species produce flowers or fruits over a relatively short time over large areas. Temporal variations in the production of flowers and fruits by different tree species may result in varying density, diversity and distribution of fruits available to elephants in any particular season. In the dry season, for instance, a threshold fruit density of about 15,000 fruits/km² is attained, beyond which fruit diversity increases significantly with availability. However, the long wet season experiences periods of low fruit diversity and availability, far below the threshold fruit density. When fruit density falls below the threshold, elephants may possibly use a different feeding strategy to compensate for the lack of fruits and may depend much more on supplementary food, including cultivated crop species (Danquah and Oppong 2006). The timing and abundance of fruiting tree species may play an important role in predicting the distribution and movement of elephants in particular seasons.

Climatic predictors of phenological events

RAINFALL

Periods of low rainfall resulted in leaf shedding; thus leafless periods occurred in the dry season. Leaf flushing occurred in the major wet season since the young growing leaves require a lot of water for their development (Struhsaker 1998). The availability of fresh browse (leaves) within reach of elephants may supplement their feed in the major wet season at KCA when fruit availability drops and reduce their incursion into nearby crop farms—and thus ease human–elephant conflict. Danquah and Oppong (2006) reported an increased amount of leaf fragments in elephant dung piles for the same season at KCA.

Not all trees of the same species produced new leaves in each flush period. In the major wet season, for instance, all *Myrianthus* species developed new leaves, while only about 70% of *Tieghemella* species had leaves. Also, leaf flushing was sometimes not simultaneous on adjacent trees of the same species, as in the case of *Antiaris africana*. Rainfall undoubtedly is important in determining the leaf-flush behaviour in KCA, particularly the length and severity of the dry season (Richards 1998).

Rainfall also significantly influenced fruiting, as young growing fruits required a lot of water for their development (Lieberman 1982). The reproductive events showed that most tree species relied on the rains in the major wet season (March–July) to reproduce. Fruit availability was highest in October (four months after the peak rainy season) and influenced positively the amount of fruits available to elephants several months into the dry season.

TEMPERATURE

Leaf flushing was influenced by the mean maximum temperature. Nonetheless, this observation is more likely to be linked to rainfall since the two variables are necessary for plant growth and development.

The association between flowering and temperature during this study was not dependable although Tutin and Fernandez (1993) found that flower initiation was stimulated by low temperature at Lope Reserve in central Gabon. Fruit production was especially negatively correlated to minimum temperature. Hence, confirming the reports of Tutin and Fernandez (1993) and Chapman et al. (1999) that the number of

trees that fruit in a fruiting season may be influenced by low temperature. With data from a single year's investigation it is difficult to be conclusive, but the potential importance of this finding is enormous for elephant management, as a small rise in minimum temperatures resulting from global warming may result in the inability of certain tree species to fruit, therefore reducing the quantity of feed (Tutin and Fernandez 1993) available to elephants.

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