

A long-term evaluation of fruiting phenology: importance of climate change

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Abstract: Within the last decade the study of phenology has taken on new importance because of its contribution to climate-change research. However, phenology data sets spanning many years are rare in the tropics, making it difficult to evaluate possible responses of tropical communities to climate change. Here we use two data sets (1970–1983 and 1990–2002) to describe the fruiting patterns of the tropical tree community in Kibale National Park, Uganda. To address variation in spatial patterns, we describe fruiting over 2–3 y among four sites each separated by 12–15 km. Presently, the Kibale region is receiving *c.* 300 mm more rain than it did at the start of the century, droughts are less frequent, the onset of the rainy season is earlier, and the average maximum monthly temperature is 3.5 °C hotter than it was 25 y ago. The 1990–2002 phenology data illustrated high temporal variability in the proportion of the populations fruiting. Interannual variation in community-wide fruit availability was also high; however, the proportion of trees that fruited has increased over the past 12+ y. At the species level a variety of patterns were exhibited; however, a number of the most common species currently rarely fruit, and when they do, typically < 4% of the individuals take part in fruiting events. Combining the data set from 1990 to 2002 with that from 1970 to 1983 for specific species again reveals an increase in the proportion of trees fruiting between 1990 and 2002; however, the proportion of the populations fruiting decreased during the earlier period. When one examines particular species over this whole period a variety of patterns are evident. For example, *Pouteria altissima* exhibited a relatively regular pattern of fruiting during the 1970s; however, it rarely fruited in the 1990s. Contrasting phenological patterns at four sites revealed that at the community level the fruiting patterns of only one of the six pair-wise site combinations were correlated. Relationships between rainfall and fruiting were variable among sites. Contrasting changes in fruiting patterns over the 30 y with differences among the four sites varying in rainfall, suggests that the changes observed in fruiting may be due to climate change. Responses to this climate change are likely complex and will vary among species. However, for some species, current conditions appear unsuitable for fruiting.

Key Words: climate change, flowering, fruiting, Kibale National Park, phenology, seasonality, seed dispersal, tropical trees, Uganda

INTRODUCTION

A variety of factors have been proposed to drive phenological patterns of tropical rain forests. These factors include: abiotic characters such as rainfall, day length, irradiance and temperature (Ashton *et al.* 1988, Newbery *et al.* 1998, Opler *et al.* 1976, van Schaik 1986, van Schaik *et al.* 1993); mode of seed dispersal (Charles-Dominique *et al.* 1981, Smythe 1970, Wheelwright

1985); activity of pollinators or seed dispersers (Frankie *et al.* 1974, Rathke & Lacey 1985, Snow 1965); variation in germination conditions (Frankie *et al.* 1974, Janzen 1967); life history traits (Davies & Ashton 1999, Newstrom *et al.* 1994a); and relative abundance of the trees themselves (van Schaik *et al.* 1993). For example, it is thought that fruit ripening may occur at a time when conditions for dispersal are optimal. Wind-dispersed seeds may ripen during the dry season when winds are stronger and leaves are often absent, allowing for greater dispersal distance (Newstrom *et al.* 1994a). In contrast, peak fruiting periods for some animal-dispersed

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fleshy-fruited species occur during the rainy season, perhaps as a result of increased moisture levels necessary for fruit production (Lieberman 1982, Rathke & Lacey 1985). Fruiting can be directly responsive to climatic conditions (e.g. fleshy fruits are produced when the water needed to produce them is abundant), or fruiting can be triggered by climatic changes which act as cues (Tutin & Fernandez 1993).

Regardless of the mechanism driving fruiting, climatic patterns are likely to be critical in setting the timing of fruiting events. Given this dependence, and the current endangered status of tropical forests and the animals dependent on them for fruit, current projections of climate change are alarming. The earth's climate has warmed by approximately 0.6 °C over the past 100 y, with two main periods of warming (1910–1945 and 1976–present), and the 1990s are the warmest decade on record (Walther *et al.* 2002).

Within the last decade the scientific community has begun to quantify ecological responses to recent climate change and has realized that some communities experience marked changes with slight shifts in temperature or growing-season length (Spark & Menzel 2002, van Vliet & Schwartz 2002, Walther *et al.* 2002). For example, the average first flowering date of 385 British plant species has advanced by 4.5 d over the past decade compared with the previous four decades (Fitter & Fitter 2002). Such changes can modify the composition of communities. Stachowicz *et al.* (2002) demonstrated that increased ocean surface temperatures gave an introduced sea squirt an earlier start after settlement than the native species and thus facilitated a shift in dominance in a sessile marine invertebrate community. Potential impacts of global climate change, such as these, stress the importance of understanding the determinants of phenological patterns to predict responses of specific communities to global climate change (van Vliet & Schwartz 2002). Only with such an understanding can appropriate management practices be initiated to help preserve vulnerable communities. While long-term phenological records are available for some regions (e.g. Europe, Menzel 2000), such data are lacking for many regions, particularly the tropics.

The objective of this study was to describe the temporal fruiting patterns of the tropical tree community in Kibale National Park, Uganda in relation to climate patterns using two data sets (1970–1983 and 1990–2002). In addition, we describe spatial variation in phenological patterns over 2–3 y through the examination of phenological records collected from four sites each separated by 12–15 km. By contrasting the same site across many years or adjacent sites over a few years, we can minimize the effect of many of the proposed mechanisms suggested to influence the timing of fruiting, facilitating the evaluation of the effect of climate. For

example, the disperser community (Chapman *et al.* 2000) and wind patterns are similar among years and sites. Having a spatially and temporally extensive data set allows us to verify whether patterns documented at one site or at one time have general applicability.

METHODS

Study sites

Kibale National Park (766 km²) is located in western Uganda (0 13'–0 41'N, 30 19'–30 32'E) near the foothills of the Ruwenzori Mountains (Chapman *et al.* 1997, Skorupa 1988, Struhsaker 1975, 1997). The park consists of mature, mid-altitude, moist, semi-deciduous and evergreen forest (57%), grassland (15%), woodland (4%), lakes and wetlands (2%), colonizing forest (19%) and plantations of exotic trees (1%; Chapman & Lambert 2000). Mean annual rainfall in the region is 1749 mm (1990–2001, or 1547 mm from 1903–2001); mean daily minimum temperature is 14.9 °C; and mean daily maximum temperature is 20.2 °C (1990–2001). There are distinct wet and dry seasons that are bimodal in distribution. May–August and December–February tend to be drier than other months (Chapman *et al.* 1999a).

This study was conducted at four sites within Kibale. For the temporal study, two long-term phenological data sets come from Kanyawara; the site established by TS in 1970. For the spatial study, to examine how consistent patterns were across space, and to evaluate whether environmental correlates shown to be predictive at one site applied to others, we contrasted phenological patterns at Kanyawara with three other sites that are each 12–15 km apart (Sebatoli, Dura River and Mainaro; Chapman *et al.* 1997). Within Kibale, there is a gradual elevational gradient from north to south, which corresponds to a north to south increase in temperature, decrease in rainfall, and changes in forest composition (Howard 1991, Struhsaker 1997; Table 1). Kibale received National Park status in 1993. Prior to 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing a sustained production of hardwood timber (Chapman & Chapman 1997, Osmaston 1959, Struhsaker 1997).

The most northern site, Sebatoli, is considered *Parinari* forest by foresters because the spreading crown of *Parinari excelsa* can be distinguished on aerial photographs (tree species names follow Hamilton 1991). The canopy is dominated by trees such as *Parinari excelsa*, *Carapa grandiflora*, *Olea capensis* (formerly *O. welwitschii*), *Pouteria altissima* (formerly *Aningeria altissima*), *Strombosia scheffleri* and *Newtonia buchananii* (Osmaston 1959). The Sebatoli forest was commercially logged in the late 1960s. We were unable to obtain information on the level of

Table 1. The density of the 20 most abundant tree species at any of the four sites in Kibale National Park, Uganda (individuals per ha of trees > 10 cm DBH). % of the total sample is the percentage of the total number of trees that is included in the sample of the 20 most abundant tree species.

Species (Family)	Kanyawara	Dura River	Mainaro	Sebatoli
Annonaceae				
<i>Uvariopsis congensis</i>	60.4	60.0	43.8	–
Ulmaceae				
<i>Celtis durandii</i>	47.1	63.8	33.8	2.5
Leguminosae				
<i>Baphiopsis parviflora</i>	–	–	116.3	–
Apocynaceae				
<i>Funtumia latifolia</i>	33.8	43.8	2.5	25.0
Bignoniaceae				
<i>Markhamia lutea</i>	50.0	8.8	1.3	38.8
Sapotaceae				
<i>Chrysophyllum</i> spp.	2.6	47.5	21.2	8.8
Moraceae				
<i>Trilepisium madagascariense</i>	50.0	22.5	–	–
Leguminosae				
<i>Cynometra alexandri</i>	–	–	63.8	–
Sapotaceae				
<i>Bequaertiodendron oblancoelatum</i>	–	57.5	–	–
Olacaceae				
<i>Strombosia scheffleri</i>	12.5	2.5	–	36.3
Ebenaceae				
<i>Diospyros abyssinica</i>	40.0	1.3	1.3	2.5
Euphorbiaceae				
<i>Croton megalocarpus</i>	0.8	–	1.3	41.3
Apocynaceae				
<i>Tabernaemontana</i> spp.	4.6	8.8	–	28.8
Sterculiaceae				
<i>Leptonychia mildbraedii</i>	35.4	–	–	–
Ulmaceae				
<i>Celtis mildbraedii</i>	–	–	32.5	–
Leguminosae				
<i>Newtonia buchananii</i>	–	3.8	–	26.3
Sapotaceae				
<i>Pouteria altissima</i>	1.7	2.5	–	23.8
Apocynaceae				
<i>Pleiocarpa pycnantha</i>	1.3	13.8	2.5	6.3
Ulmaceae				
<i>Chaetacme aristata</i>	17.1	3.8	1.3	–
Monimiaceae				
<i>Xymalos monospora</i>	8.8	–	–	10.0
% of total sample	25.0%	24.2%	41.4%	30.0%
Annual Rainfall (mm)	1749	1500	1394	1491
Elevation (m)	1500	1250	1200	1500

extraction. However, detailed quantification of stand structure suggests that the level of extraction was similar to or slightly lower than an area just to the south, K-15 forestry compartment (adjacent to the Kanyawara site, Chapman & Chapman, unpubl. data), in which the harvest averaged $21 \text{ m}^3 \text{ ha}^{-1}$ or *c.* $7.4 \text{ stems ha}^{-1}$ (Skorupa 1988, Struhsaker 1997). Incidental damage in the K-15 forestry compartment was high, and it is estimated that approximately 50% of all trees were destroyed by logging and incidental damage (Chapman & Chapman 1997, Skorupa 1988).

We monitored the phenology of trees at Kanyawara, also considered a *Parinari* forest, between 1970 and

1983 and since 1990. This area has three forestry compartments. K-15 is a 360-ha section of forest that experienced heavy selective felling in 1968 and 1969 (harvest described above). Just to the south, is the K-14 forestry compartment, a 405-ha forest block that experienced low-intensity selective felling from May through December 1969 (averaging $14 \text{ m}^3 \text{ ha}^{-1}$ or $5.1 \text{ stems ha}^{-1}$). Approximately 25% of all trees in compartment K-14 were destroyed by logging and incidental damage (Skorupa 1988, Struhsaker 1997). K-30 is a 300-ha area that has not been commercially harvested; however, prior to 1970, a few large stems ($0.03\text{--}0.04 \text{ trees ha}^{-1}$) were removed by pitsawyers. This

extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa 1988, Struhsaker 1997).

At the Dura River, the forest is no longer considered a *Parinari* forest, as *P. excelsa* and the tree species associated with it are relatively rare. *Pterygota mildbraedii*, *Cola gigantea*, *Piptadeniastrum africanum* and *Chrysophyllum albidum* are the dominant canopy species (Kingston 1967). Further south at Mainaro, the forest is dominated by *Cynometra alexandri* and affiliated species (Kingston 1967). At both the Dura River and Mainaro sites, a few timber trees have been extracted by pitsawyers (c. 0.1 trees ha⁻¹), but this activity has had little impact on the forest. Detailed enumeration of the tree communities in these areas is provided by Chapman *et al.* (1997).

Climate data

Rainfall data were available between 1903 and 1971 from the Government of Uganda meteorological records for the town of Fort Portal (approximately 20 km east of Kanyawara), between 1972 to 1989 from TS (Kanyawara), and from 1990 to present from CAC and LJC (Kanyawara). Temperature data were available from NASA (http://www.giss.nasa.gov/cgi-bin/update/name_or_map.py) from 1905 to 1948 for Fort Portal, from 1976 to 1989 from TS (Kanyawara), and from 1990 to present from CAC and LJC (Kanyawara).

Temporal phenological monitoring

Here we analyse a 12-y data set (1990–2002) involving all trees in phenology plots collected by CAC, LJC and field assistants, and then for specific species, we compare these results to a 13-y data set (1970–1983) collected by TTS and colleagues. We were unable to collect the phenology data between 1984 and 1989 because early in this period was a time of political unrest in Uganda and 1988 marked the end of the period where TTS was able to collect long-term data (Struhsaker 1997). In the 1990–2002 data set three different monitoring systems were used. First, twenty-six 200 × 10-m plots were established at random locations along the existing trail system at Kanyawara in January 1990 producing a sampling area of 5.2 ha (12 plots in K-30, nine plots in K-14, five plots in K-15; Chapman *et al.* 1999b). All trees with a diameter at breast height (DBH) of ≥ 10 cm and within 5 m of the trail were tagged with aluminium tags and their DBH was recorded. A total of 2096 (67 species) trees were tagged. Phenological data for all trees in these plots were recorded monthly between January 1990 and April 1996. During that time 72% of the trees flowered. Some of those individuals that did not flower were small and probably immature. Subsequently, from May 1996

to May 1998 we randomly selected six of these 26 plots to continue monitoring. Additionally, 591 trees were monitored each month in an area of 1.2 ha. Finally, since May 1998 (until May 2002 analysed here) we evaluated phenological patterns using a trail system that monitored 300 individuals from 33 species (average number of individuals per species = 8.8, range = 2–12). It should be noted that community level patterns documented could be influenced not only by the species included in the analysis, but also by the relative sample sizes of each species. Analyses are presented to evaluate this.

For each monitored tree, we visually examined the crown to determine the presence of different leaf stages (i.e., leaf buds, young leaves and mature leaves), flowers, and unripe and ripe fruit. We evaluated the relative abundance of fruit on a scale of 0–4, which proved to be extremely consistent between observers (Chapman *et al.* 1994, Struhsaker 1975, 1997). Determining when a fruit is ripe is sometimes difficult since for some species there is no colour change associated with ripening (e.g. *Monodora myristica*). As a result, for each fleshy-fruited species we defined fruit as ripe when they were first eaten by frugivores after they had reached full size. For wind-dispersed species, we considered a tree to have mature fruit, when dehiscent fruits opened and seeds could be found under the parent's canopy.

We analysed overall patterns of fruit availability, considering (1) all species that produce fruits and (2) the 10 most abundant species. The 10 most abundant species and their densities are the following: *Uvariopsis congensis* (60.4 trees ha⁻¹), *Markhamia lutea* (formerly *M. platycalyx*, 50.0 trees ha⁻¹), *Trilepisium madagascariense* (formerly *Bosqueia phoberos*, 50.0 trees ha⁻¹), *Celtis durandii* (47.1 trees ha⁻¹), *Diospyros abyssinica* (40.0 trees ha⁻¹), *Funtumia latifolia* (33.8 trees ha⁻¹), *Chaetacme aristata* (17.1 trees ha⁻¹), *Strombosia scheffleri* (12.5 trees ha⁻¹), *Pancovia turbinata* (10.8 trees ha⁻¹), and *Dombeya kirkii* (formerly *Dombeya mukole* 9.2 trees ha⁻¹).

The second data set involves the monitoring of 90 trees of 12 species at Kanyawara from 1970 to 1983. All trees were adults and at least 10 m tall. Each month the relative abundance of the various phytophases were evaluated. The species considered were *Celtis durandii* (n = 10), *Celtis africana* (n = 5), *Lovoa swynnertonii* (n = 5), *Markhamia lutea* (n = 11), *Teclea nobilis* (n = 5), *Diospyros abyssinica* (n = 10), *Pouteria altissima* (n = 6), *Symphonia globulifera* (n = 5), *Funtumia latifolia* (n = 10), *Parinari excelsa* (n = 10), *Strombosia scheffleri* (n = 10) and *Uvariopsis congensis* (n = 5). *Lovoa swynnertonii* and *S. globulifera* were not considered when making comparisons to the 1990–2002 data, since in that data set these species were not well represented.

To determine phenological patterns at the different sites, plots (200 × 10 m) were constructed at each site, 26 plots at Kanyawara (same as was used for the

long-term data) and four each at Dura River, Mainaro and Sebatoli. At the Mainaro, Dura River and Sebatoli sites there were no pre-existing trails, and plots were established perpendicular to each other at 50–100-m intervals. This regime produced a total sampling area of 7.6 ha (5.2 ha at Kanyawara, and 0.8 ha each at Dura River, Mainaro and Sebatoli). Each tree >10 cm DBH within 5 m of each side of a central trail was individually marked with a numbered aluminium tag and measured (DBH). This produced a sample of 3049 trees (2096 trees at Kanyawara, 338 trees at Dura River, 293 trees at Mainaro and 322 at Sebatoli). Phenology of these trees was recorded once a month (as previously described) at Dura, Mainaro and Kanyawara between June 1995 and June 1998. At Sebatoli these data were collected between June 1996 and June 1998. Rebel activity prevented us from sampling at Mainaro in February and April of 1997. We analysed overall patterns of fruit availability, considering (1) all species that produce fruits and (2) the five most abundant species across all sites (*Celtis durandii*, *Funtumia latifolia*, *Strombosia scheffleri*, *Tabernaemontana* spp. and *Uvariopsis congensis*; there were two species of *Tabernaemontana*, *holstii* and *odoratissima*, which were only distinguishable by examining flower morphology. The existence of the second species was only discovered late into the study and it was not possible to re-identify each individual as many did not flower. However, it is thought that the vast majority of the population was *holstii*).

Analyses

It is difficult to portray phenological data (Newstrom *et al.* 1994a, b) and while many statistical approaches (e.g. spectral analysis, Chapman *et al.* 1999b) offer useful means of detecting cycles, they do not illustrate the intensity of fruiting events throughout the cycle. As a result, we rely on graphical representations to illustrate the intensity of cyclic patterns of phenological events.

To detect climatic predictors of phenological events, we relate the proportion of the population fruiting in a given month to climatic variables (rainfall, and average maximum, and minimum temperature) for that month and for each previous month from 1 mo to 11 mo prior. We report all fruiting species and the ten most abundant species (excluding *Markhamia lutea* from graphical presentations since it consistently fruited poorly). In addition, we evaluate climatic predictors for classes of species (i.e., wind dispersed, fleshy fruits, forest and gap species). Categorization of plants by disperser type follows Zanne (1998), while the categorization of habitat preference follows Katende *et al.* (1995), Hamilton (1991), Eggeling & Dale (1951), and Zanne (2003). This analysis should be considered a simple exploration of the data, as we do not

adjust the probability level that we accept as significant to account for multiple comparisons (see Perneger 1999 for a discussion of why Bonferroni adjustments are unnecessary).

It is possible that a change in the percentage of individuals bearing fruit will not reflect actual changes in the abundance of fruit. For example, fewer trees could bear the same amount or more or less fruit than when a greater percentage of the sample trees were fruiting. We considered this issue for those species that were adequately sampled by all methods (*Celtis africana*, *Celtis durandii*, *Diospyros abyssinica*, *Funtumia latifolia*, *Parinari excelsa*, *Pouteria altissima*, *Strombosia scheffleri*, *Teclea nobilis* and *Uvariopsis congensis*; *Markhamia lutea* was excluded since it rarely fruited). When monitoring trees each month, the relative abundance of fruit was evaluated on scale of 0–4. For each of the species considered, we calculated the mean annual fruiting score, and subsequently we evaluated whether this score varied as a function of year. This was not done at the community level since it was not clear how to compare a rank for a fruit such as *Monodora myristica* which is 16 cm in diameter vs *Celtis durandii*, which is less than 0.5 cm in diameter (Balcomb & Chapman 2003). We also evaluated whether a fruiting score that incorporated the intensity of fruiting (the proportion of individuals in the population that were fruiting multiplied by the average fruiting score) was correlated with the changes in the percentage of individuals bearing fruit.

In the majority of analyses, we compare the percentages of individuals bearing fruit each month over time. However, it is possible that the fruiting schedules may have changed. For example, if we documented a decline in the percentage of individuals fruiting each month, it is possible that there was no decline, but rather that the same number of individuals are fruiting, but that they are fruiting over a longer period. To evaluate this possibility, we determined the percentage of the population that fruited in each year for the nine species evaluated in the previous analysis. Only those years where a complete year was sampled using the same system was used in this analysis. When there were appreciable differences in mean values, variation was evaluated using the coefficient of variation (CV; Sokal & Rohlf 1981). We used the CV to evaluate interannual variation in monthly fruit production.

RESULTS

Climate change

Rainfall data collected since 1903 indicate that the region is becoming moister (Figure 1); year and annual rainfall are positively correlated ($r = 0.415$, $P < 0.001$;

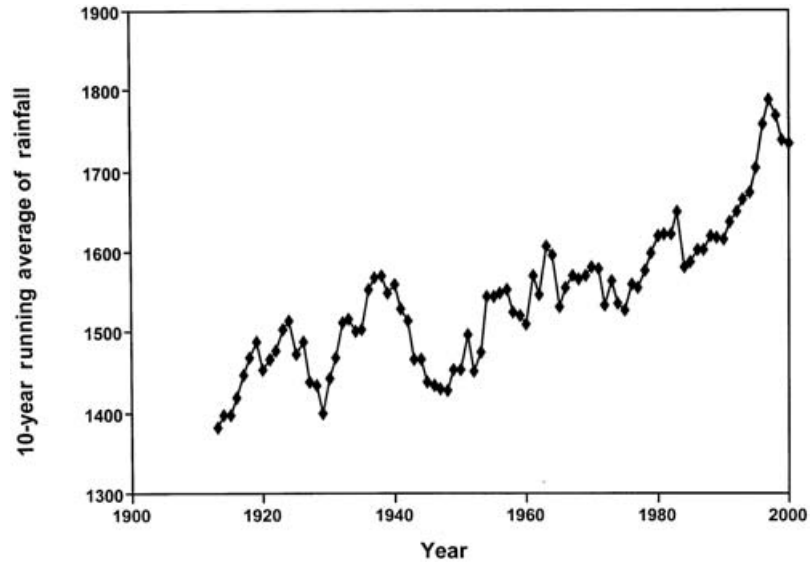


Figure 1. The 10-y running average of the annual rainfall in the area of Kibale National Park, Uganda.

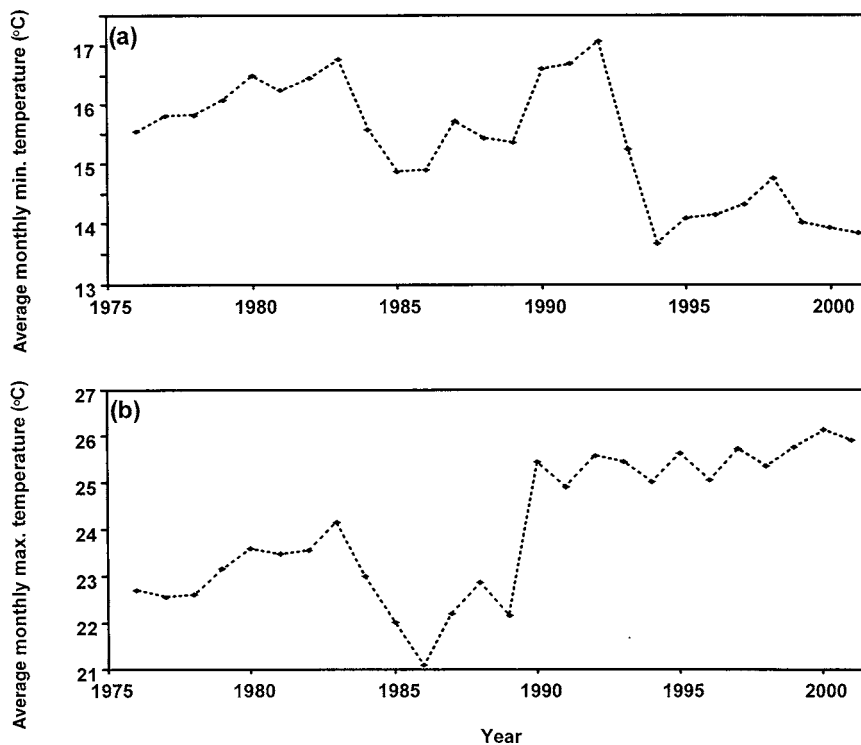


Figure 2. The average annual monthly (a) minimum and (b) maximum temperature ($^{\circ}\text{C}$) measured at Kibale National Park, Uganda, since 1975.

see also Struhsaker 1997). If a drought year is considered one with <1300 mm of rain a year, then there has also been a decline in the number of drought years per decade ($r_{sp} = 0.850$, $P = 0.002$). In addition, we have recorded an increase in the maximum mean monthly temperature since CAC and LJC started recording it in 1990 at Kanyawara ($r = 0.767$, $P < 0.001$). This trend is supported by data collected since 1975 ($r = 0.767$,

$P < 0.001$; Figure 2). By contrast, the average monthly minimum temperature has decreased over that same period ($r = 0.652$, $P < 0.001$, 1990–2002; $r = -0.784$, $P = 0.003$, 1975–2002; Figure 2). Examining temperature data available from 1905 to the present (the average of the minimum and maximum daily temperatures) suggests an increase in temperature; however, the trend was not significant ($r = 0.161$, $P = 0.204$). This analysis

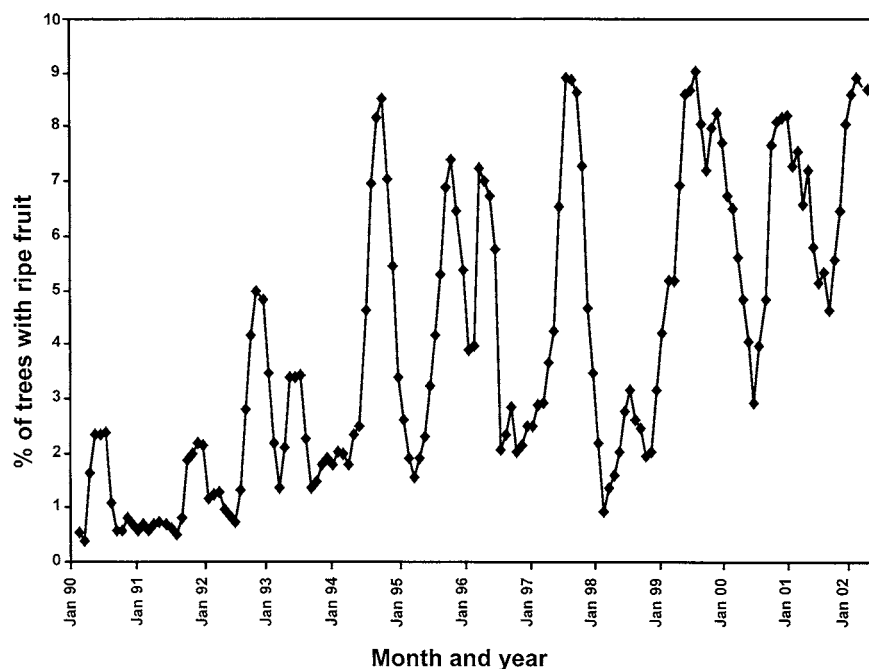


Figure 3. The 4-mo running average of the percentage of trees bearing ripe fruit in Kibale National Park, Uganda, between 1990 and 2002.

averaged maximum and minimum temperatures, and if these parameters are changing in opposite directions as is indicated in Figure 2, the fact that we document no significant change in the averaged values is not surprising.

Temporal phenological patterns: 1990–2002

On average, 3.97% of monitored trees bore ripe fruit each month between 1990 and 2002. However, temporal variability in fruit availability was high (Figure 3). Interannual variation in fruit availability was also high (Table 2). In 1990, an average of 1.09% of trees bore ripe fruit each month; while in 1999, an average 6.67% of the trees bore ripe fruit each month.

The proportion of trees fruiting has increased over the past 12 y (Figure 3; $r = 0.557$, $P < 0.001$). This relationship holds for two of the three methods used to assess phenological patterns (January 1990 – April 1996: $r = 0.506$, $P < 0.001$, May 1996 – May 1998: $r = -0.133$, $P = 0.526$, June 1998 to May 2002: $r = 0.398$, $P = 0.005$). In addition, over the 12 y, there was a consistent decline in the annual coefficient of variability, suggesting decreased seasonal variation (Table 2; $r = -0.921$, $P < 0.001$).

There was no difference in the proportion of fruiting trees ($t = 0.192$, $P = 0.848$) between wet- and dry-season months. Species that had seeds adapted for dispersal by wind did not fruit more in the dry season than in the wet season ($t = 0.80$, $P = 0.424$). However, there was a

Table 2. Interannual variation in fruit production (proportion (%) of trees monitored each month bearing ripe fruit) in Kibale National Park, Uganda. No. 1% and no. < 2% are the number of months in a year where there are less than 1% and 2% of the trees monitored with ripe fruit. Within the year, the months with the lowest (Lowest) and highest (Highest) proportion of trees with ripe fruit are also presented.

Year	Mean	CV	no. < 1%	no. < 2%	Lowest	Highest
1990	1.17	1.49	9	10	1.14	6.11
1991	1.09	1.16	9	11	0.29	4.87
1992	2.06	1.03	6	9	0.44	6.62
1993	2.35	0.89	4	7	0.54	6.30
1994	4.35	0.82	0	4	1.17	10.55
1995	3.93	0.65	1	3	0.98	8.92
1996	4.49	0.91	0	2	1.10	15.93
1997	5.13	0.70	1	3	0.18	11.36
1998	2.22	0.73	4	5	0.37	5.50
1999	6.67	0.48	0	1	1.40	12.28
2000	6.14	0.51	0	1	1.17	13.06
2001	5.93	0.33	0	0	3.47	9.34

tendency for fleshy-fruited species to fruit more in the wet season than the dry season ($t = 1.72$, $P = 0.088$).

Since gap species tend to be shorter lived, one might expect that a greater proportion of gap species would be fruiting at any time compared with forest species and that gap species would have a less variable pattern of fruit production. We found a tendency for gap species to have a greater proportion of their population fruiting (2.93%) compared with forest species (2.01%, $t = 1.69$, $P = 0.092$). However, there was little difference in the variation in their fruiting patterns (CV: gap = 1.85, forest = 1.96).

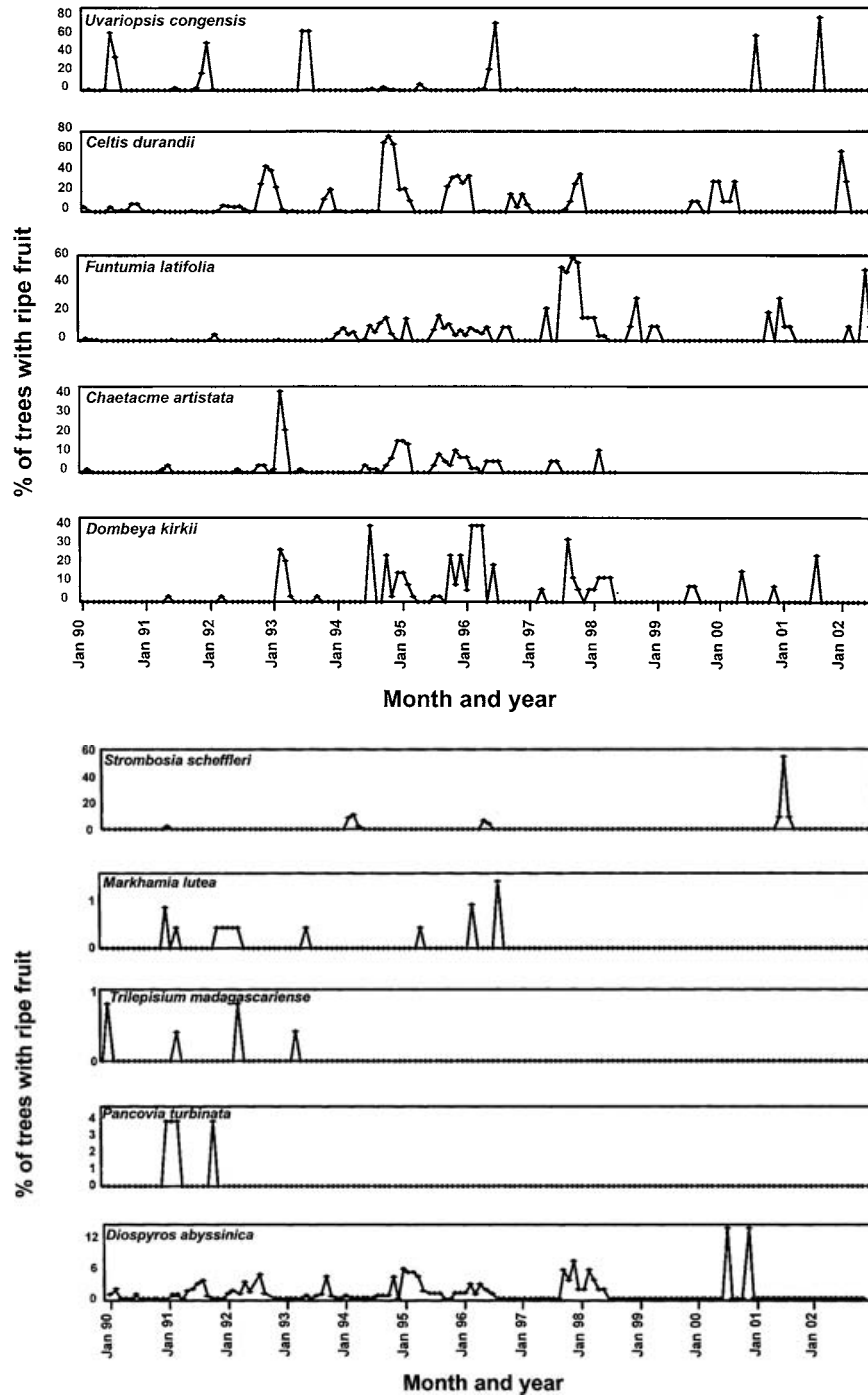


Figure 4. The percentage of trees bearing ripe fruit for the 10 most common species in Kibale National Park, Uganda over a 12-y period (*Uvariopsis congensis* 60.4 tree ha⁻¹, *Celtis durandii* 47.1 tree ha⁻¹, *Funtumia latifolia* 33.8 tree ha⁻¹, *Chaetacme aristata* 17.1 tree ha⁻¹, *Dombeya kirkii* 9.2 tree ha⁻¹, *Strombosia scheffleri* 12.5 tree ha⁻¹, *Markhamia lutea* 50.0 tree ha⁻¹, *Trilepisium madagascariense* 50.0 tree ha⁻¹, *Pancovia turbinata* 10.8 tree ha⁻¹ and *Diospyros abyssinica* 40.0 tree ha⁻¹).

To have a robust sample, fruiting patterns at the species level were examined only for the 10 most abundant tree species. These species showed a diversity of fruiting patterns over the 12 y (Figure 4). *Uvariopsis congensis* exhibited a fairly regular pattern of fruiting, where c. 60%

of the population fruited synchronously typically in June or July (although over 50% of the population did fruit in December 1991). Despite this synchronized pattern, there were often a number of years between fruiting events. For example, *U. congensis* fruited in June 1996, but did not

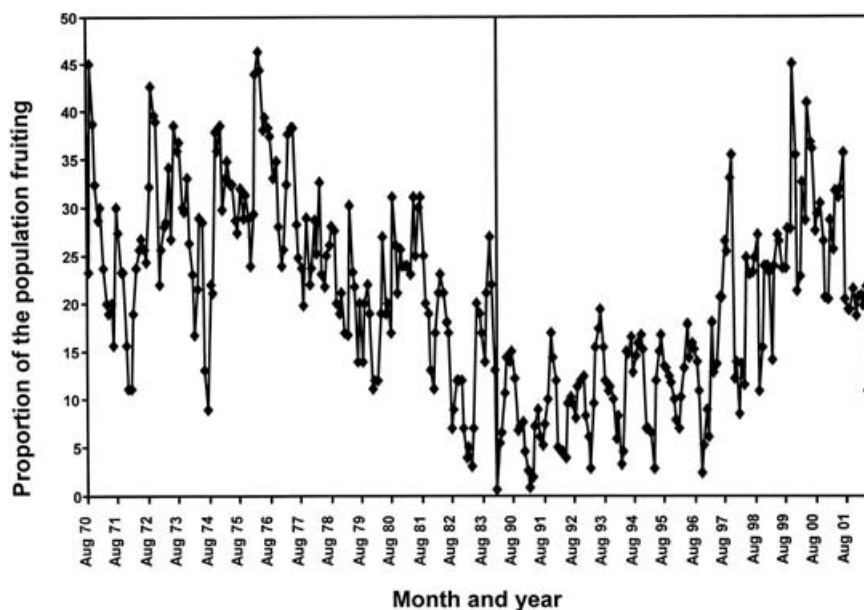


Figure 5. The proportion of the population fruiting between 1970 and 1984 and 1990 and 2002 in Kibale National Park, Uganda. This includes the following species: *Pouteria altissima*, *Celtis africana*, *Celtis durandii*, *Diospyros abyssinica*, *Funtumia latifolia*, *Parinari excelsa*, *Strombosia scheffleri*, *Teclea nobilis* and *Uvariopsis congensis*.

fruit again until July 2000. While *Celtis durandii* had very poor fruiting seasons in 1990 and 1991, subsequently greater than 30% of the trees fruited each year, typically in the October to December period, although it did not fruit in the fall of 2000. A large proportion of the *Strombosia scheffleri* population only fruited once during the entire 12 y. *Funtumia latifolia*, *Chaetacme aristata*, and *Dombeya kirkii* had irregular fruiting patterns; however, they all seemed to fruit poorly in the first 3 y of the study. As a group, *Ficus* spp. had an irregular fruiting schedule (the sample size was not adequate to evaluate each species separately). Less than 4% of the population of *Markhamia lutea*, *Trilepisium madagascariense* and *Pancovia turbinata* fruited in any year. While there were many trees of these species monitored, only a few ever fruited, and these fruiting events tended to be in the first few years of the study.

Considering these 10 species, the proportion of individuals in the population that fruited was strongly correlated to the index that included the rank abundance of fruit in each tree (average $r_{sp} = 0.870$, $P < 0.001$ in all cases). In general, there was a high degree of concordance between these two fruiting scores; however, there were particular months when this was not evident.

Temporal phenological patterns: 1970–2002

Combining the data set from 1990–2002 with that from 1970–1983 reveals that fruiting trends have been changing (Figure 5). For this comparison we included only those species that were sampled in both time

periods ($n \geq 5$ individuals, 10 species). Considering only these species, we observed a significant increase in the proportion of trees fruiting between 1990 and 2002 ($r = 0.725$, $P < 0.001$); however, the proportion of the individuals fruiting in a population decreased during the earlier period ($r = -0.458$, $P < 0.001$).

When one examines particular species a variety of patterns are evident (Figure 6). For example, while *Pouteria altissima* exhibited a relatively regular pattern of fruiting during the 1970s (but the typical fruit score was 1), it rarely fruited and never more than 10% of the population fruited in any year in the 1990s. The proportion of the population fruiting declined between these two periods ($t = 7.46$, $P < 0.001$). With these comparisons we must keep in mind that the methods used to monitor the populations were not identical. In the early period six trees were monitored with the average DBH of 164 cm (Struhsaker 1997), while in the later period 11 trees were monitored with the average DBH of 75 cm. If only those trees over 100 cm DBH are considered in the later data set, the frequency of fruit production still appears to have declined ($t = 6.58$, $P < 0.001$). Similar declines were seen in *Celtis africana* ($t = 6.55$, $P < 0.001$), *Funtumia latifolia* ($t = 8.24$, $P < 0.001$), *Parinari excelsa* ($t = 11.37$, $P < 0.001$), *Strombosia scheffleri* ($t = 3.73$, $P < 0.001$) and *Teclea nobilis* ($t = 3.654$, $P < 0.001$). However, late in the 1990s, the fruiting of *C. africana* and *F. latifolia* increased dramatically. *Markhamia lutea* had poor fruit production in all periods (Struhsaker 1978).

In evaluating the possibility that a change in the percentage of individuals bearing fruit will not reflect

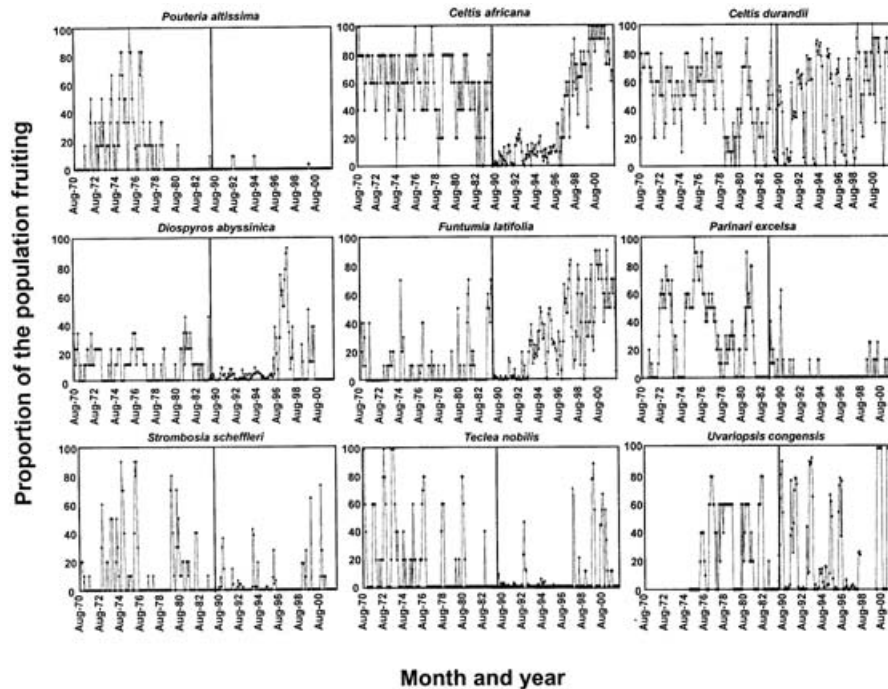


Figure 6. For specific species, the proportion of individuals in the population fruiting between 1970 and 1984 and 1990 and 2002 in Kibale National Park, Uganda.

actual changes in the abundance of fruit, we compared the mean annual fruiting scores collected during the 1970–1983 period and the 1990–2002 period. For four of the nine species considered the mean score was significantly higher in the first period compared with the second ($P < 0.007$ or less). While it is possible that this reflects a change in the intensity of fruiting, it is just as possible that it reflects differences in how the observers in the different periods ranked fruit abundance [there was a high level of inter-observer reliability among observers within a period (Chapman *et al.* 1994, Struhsaker 1975, 1997), but we could not address reliability between periods]. There is no way to evaluate between-period consistency since it was 5 y between the time when the first set of observations stopped and the second began and during that time it was possible that how TTS ranked abundance might have changed. Thus, we evaluate changes in the mean annual fruiting score within each period separately. During the 1970–1983 period, the mean annual fruiting score did not change consistently over time (the lowest probability value when a correlation was made for each species separately was $P > 0.171$), with the exception of *Celtis africana*, which exhibited a significant decline in annual fruiting score over the 13 y ($r = -0.710$, $P = 0.007$). Between 1990 and 2002 the mean annual fruiting score did not change consistently over time for any species ($P > 0.278$), except *Funtumia latifolia*, which showed a decline in annual fruiting score ($r = -0.588$, $P = 0.044$).

To evaluate the possibility that the fruiting schedule had changed, we determined the percentage of individuals of each species that fruited in each year and contrasted these patterns with the same analysis comparing months. In general, the patterns that the two analyses produced were very similar. However, the increased fruiting activity for *Funtumia latifolia* seen between 1995 and 2002 in the monthly analysis was not as evident when the number of individuals that fruited each year was plotted over time.

Environmental correlates

Climatic factors have frequently been proposed to drive phenological patterns of tropical rain forest trees; however, climatic variables covary. Categorizing the six wettest months in a year as the wet season and the six driest months as the dry season, between 1990 and 2002 the dry season had higher average temperatures (25.9°C) than the wet season (25.1°C ; $t = 3.77$, $P < 0.001$), but there were no differences among seasons in the average minimum temperature (dry: 14.84°C , wet: 14.89°C , $t = 0.168$, $P = 0.867$). Correspondingly, the mean monthly maximum temperature was negatively related to the monthly rainfall ($r = -0.354$, $P < 0.001$), while monthly rainfall and minimum temperatures were not related ($r = -0.051$, $P = 0.540$).

The proportion of fleshy-fruited and gap species fruiting tended to be positively correlated with the rainfall in

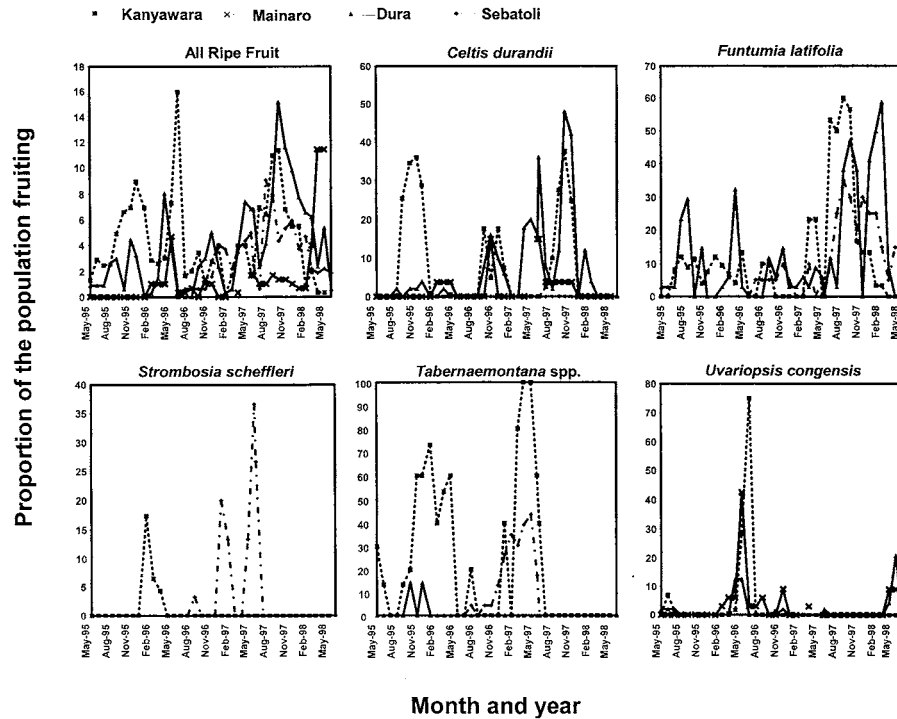


Figure 7. Fruiting phenology for all species and select species at four sites in Kibale National Park, Uganda that are each separated by 12–15 km along a north-south axis.

the months just preceding (data not presented). A similar pattern was observed for *Celtis durandii*. *Uvariopsis congensis* (the most abundant forest species) and all forest species were positively correlated with the rainfall 9 mo prior to the observation period. Possibly, the rainfall in the prior rainy season triggers abundant fruiting of *U. congensis*. The proportions of fleshy-fruited and gap species that fruited in a given month were negatively correlated with the maximum temperature in the 4 mo prior and positively correlated to the maximum temperature 8, 9 and 10 mo prior. Similar patterns were seen for *Celtis durandii* and *Chaetacme aristata*.

Patterns with mean monthly minimum temperature tended to be more consistent than for mean monthly maximum temperature, or rainfall (data not presented). While there was considerable variation among species and groups of species, four general patterns emerged: (1) the proportion of individuals in the population fruiting was negatively correlated with minimum temperature in the preceding 1–11 mo (all species, wind-dispersed species, *Funtumia latifolia*, *Dombeya kirkii*); (2) the proportion of the population fruiting was negatively related to the minimum monthly temperature that month and at 4 mo prior, then for 5–8 mo prior, the relationships were negative but non-significant, and by 9–11 mo prior the proportion of a population fruiting was negatively related to minimum monthly temperature (fleshy-fruited species gap species and *Celtis durandii*); (3) the proportion

of the population fruiting was positively related to mean minimum monthly temperature (this should be viewed with caution since only *Trilepisium madagascariense*, and *Pancovia turbinata* exhibited this pattern and only a small proportion of population of these species fruited and they only fruited in the first couple of years of observation); (4) for *Uvariopsis congensis*, fruiting was correlated with minimum temperature 2, 3 and 4 mo prior.

Spatial phenological patterns

Monthly rainfall was correlated among the three northern sites (Sebato and Kanyawara $r = 0.920$, $P < 0.001$, Sebato and Dura $r = 0.708$, $P < 0.001$, Kanyawara and Dura $r = 0.810$, $P < 0.001$), but not between these sites and the most southern site Mainaro ($P > 0.30$ in all cases).

For only one of six pair-wise site combinations was the proportions of the populations (all species) fruiting correlated, and these sites were not adjacent to one another (Sebato and Dura $r = 0.561$, $P = 0.004$; Figure 7). The lack of concordance among sites in this analysis will partially be caused by differences in forest composition. However, if we just consider common species that regularly fruited at each site, it is possible to address whether there is concordance at the species level. *Celtis durandii* was not found at Sebato, but the proportion

of the population fruiting was related amongst two of the three site combinations (Kanyawara and Dura $r = 0.354$, $P = 0.031$; Dura and Mainaro $r = 0.514$, $P = 0.002$; Kanyawara and Mainaro $r = -0.71$, $P = 0.684$). *Funtumia latifolia* was not found at Mainaro, but the proportion of the population fruiting was related amongst two of the three site combinations and marginally related between the other site combination (Sebatoli and Kanyawara $r = 0.604$, $P = 0.002$; Sebatoli and Dura $r = 0.595$, $P = 0.002$; Kanyawara and Dura $r = 0.290$, $P = 0.082$). *Tabernaemontana* spp. were not found at Mainaro, and the proportion of the population that fruited was related only between Sebatoli and Kanyawara ($r = 0.803$, $P < 0.001$; other sites $P > 0.40$). Lastly, *Uvariopsis congensis* was not found at Sebatoli, and the proportion of the population that fruited at Kanyawara was not related to that at Dura ($r = 0.101$, $P = 0.553$), it was marginally related to that at Mainaro ($r = 0.327$, $P = 0.055$), and Dura and Mainaro were related ($r = 0.596$, $P < 0.001$).

Using this data set we can also examine whether the different populations are responding in the same fashion to climatic conditions. The only climatic factor measured at all sites was rainfall. The proportion of the population of *Celtis durandii* trees that fruited in a given month was not related to rainfall that month at Kanyawara ($r = 0.321$, $P = 0.110$), but was related to rainfall at Dura ($r = 0.501$, $P = 0.013$) and Mainaro ($r = 0.536$, $P = 0.033$). The fruiting pattern of *Funtumia latifolia*, *Tabernaemontana* spp. and *Uvariopsis congensis* were not related to rainfall at any of the sites that month or any prior month up to 11 mo ($P > 0.10$).

DISCUSSION

Phenology data sets that span many years are rare in the tropics (but see Wright *et al.* 1999). This limits our ability to evaluate the magnitude of interannual variation in fruit production and to identify long-term patterns. Our results from Kibale indicate that there is not only considerable interannual variation in fruit production, but that fruit production may consistently change over long periods. In Kibale fruit production declined from 1970 to 1983 and increased between 1990 and 2002. A number of species exhibited large decreases in the proportion of the population that fruited, and others exhibited changes in the abundance of fruit that were produced each time they fruited. For example, *Parinari excelsa* fruited consistently in the 1970s, but has rarely fruited in the 1990s. The Kanyawara region of Kibale is considered a *Parinari* forest by foresters (Kingston 1967, Osmaston 1959), thus it is interesting that little regeneration is occurring. Between 1970 and 1983, the amount of fruit on *Celtis africana* trees declined. Findings, such as this, highlight the importance

of not just considering the presence or absence of fruit, but also considering its abundance.

These changes in the proportion of the individuals in a population fruiting and in the abundance of fruit produced may be linked to climate change. Rainfall data collected since 1903 indicate that the region has become moister and droughts have been less frequent. There has also been an increase in maximum mean monthly temperature and a decrease in minimum mean monthly temperature. The pattern of fruiting of *Trilepisium madagascariense* suggests that climate change is the responsible agent. At Kanyawara, this species fruited at a low level in the first few years of monitoring that began in 1990; however, it has not fruited since 1993. It is possible that the drier climatic conditions found in the early half of the century were more favourable for these species for flower or fruit production. The Dura River site is approximately 15 km south of Kanyawara and has less rainfall (1500 mm). At this site, a large proportion of the *Trilepisium madagascariense* population has repeatedly fruited in recent years (Chapman *et al.* 2002, C. A. Chapman & L. J. Chapman unpubl. data), suggesting that drier conditions may promote fruiting.

At Kanyawara, we had previously reported that minimum temperature in the previous dry season is correlated with the number of trees that fruit (Chapman *et al.* 1999b, see also Struhsaker 1997). Tutin & Fernandez (1993) documented a similar pattern (mean minimum temperature in the dry season and the size of fruit crop in the subsequent season) for eight tree species in Lopé Reserve, Gabon, and suggested that this pattern was mediated by flower production. At Kibale, the time between flower set and fruit production is often highly variable which would suggest that this pattern is not entirely mediated by flower production, but rather by some factor that directly influences fruit production. It may be that minimum temperature is simply acting as a cue to synchronize a segment of the community (Janzen 1974). Alternatively, periods with low night-time temperatures tend to be those with little insulating cloud cover and high levels of irradiance. Thus, it may be that the beginning of the dry season is a time when energy becomes readily available to trees, permitting the build up of assimilates needed for fruiting. Seasonal peaks of irradiance have been documented to coincide with peaks of flower production (Wright & van Schaik 1994). Our analysis suggests that minimum temperature may be an important factor influencing the proportion of the population that fruits. However, it does not appear that minimum temperature is operating as a cue, rather the pattern of correlations between the proportion of the population fruiting and minimum temperature suggests cooler conditions in any month promote fruiting. Since periods with low night-time temperatures tend to be those with little insulating cloud cover

and high levels of irradiance, it may be that any time that there are conditions with high irradiance it promotes fruiting.

It is also worth considering the possibility that climate change has obscured cues that had existed previously. Presently, the Kibale region is receiving approximately 300 mm more rain than it did at the start of the century, and the average maximum monthly temperature is 3.5 °C hotter and the average minimum monthly temperature is 2.0 °C cooler than they were 25 y ago. If we consider the start of the rainy season as the first day when more than 20 mm of rainfall fell, there is evidence that the rainy season is coming earlier. It is conceivable that these changes have obscured the environmental cues that historically synchronized fruiting or flowering patterns.

Unfortunately, it is relatively rare that long-term data are available from tropical forest systems. Given this and the fact that tropical forest systems are being rapidly transformed, it seems useful to speculate on the conservation implications of our findings. First, we documented that fruit production is highly variable among years and periods of fruit scarcity occur on a superannual basis. Thus, a study in any single year will be unlikely to provide the needed insights to understand relationships between frugivore abundance and fruit availability (see also Newbery *et al.* 1998). The fact that we found that sites that were separated by only a few kilometres exhibited different fruiting patterns, suggests that protecting large continuous blocks of forests may help animals with the ability to range widely during periods of fruit scarcity. Finally, our data build on the findings of Struhsaker (1997) and indicate that the climate of the Kibale region is changing. Whether this represents consistent long-term changes associated with global warming, or short-term fluctuations is not known. Regardless, the plant phenological patterns and the animals dependent on these plants are experiencing changes.

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LITERATURE CITED

- ASHTON, P. S., GIVINISH, T. J. & APPANAH, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132:44–66.
- BALCOMB, S. R. & CHAPMAN, C. A. 2003. Bridging the seed dispersal gap: consequences of seed deposition for seedling recruitment in primate-tree interactions. *Ecological Monographs* 73:625–642.
- CHAPMAN, C. A. & CHAPMAN, L. J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29:396–412.
- CHAPMAN, C. A. & LAMBERT, J. E. 2000. Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *American Journal of Primatology* 50:169–186.
- CHAPMAN, C. A., WRANGHAM, R. & CHAPMAN, L. J. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26:160–171.
- CHAPMAN, C. A., CHAPMAN, L. J., WRANGHAM, R., ISABIRYE-BASUTA, G. & BEN-DAVID, K. 1997. Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology* 35:287–302.
- CHAPMAN, C. A., WRANGHAM, R. W., CHAPMAN, L. J., KENNARD, D. K. & ZANNE, A. E. 1999b. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* 15:189–211.
- CHAPMAN, C. A., BALCOMB, S. R., GILLESPIE, T., SKORUPA, J. & STRUHSAKER, T. T. 2000. Long-term effects of logging on African primate communities: a 28 year comparison from Kibale National Park, Uganda. *Conservation Biology* 14:207–217.
- CHAPMAN, C. A., CHAPMAN, L. J., BJORN DAL, K. A. & ONDERDONK, D. A. 2002. Application of protein to fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology* 23:283–310.
- CHAPMAN, L. J., CHAPMAN, C. A., BRAZEAU, D., MCGLAUGHLIN, B. & JORDAN, M. 1999a. Papyrus swamps and faunal diversification: geographical variation among populations of the African cyprinid *Barbus neumayeri*. *Journal of Fish Biology* 54:310–327.
- CHARLES-DOMINIQUE, P., ATRAMENTOWICZ, M., CHARLES-DOMINIQUE, C., GERARD, H., HLADIK, A., HLADIK, C. M. & PREVOST, M. F. 1981. Les mammifères frugivores arboricoles nocturne d'une forêt guyanaise: interrelations plantes-animaux. *Revue d'Ecologie (Terre et Vie)* 35:341–436.
- DAVIES, S. J. & ASHTON, P. S. 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. *American Journal of Botany* 86:1786–1795.
- EGGELING, W. J. & DALE, I. R. 1951. *The indigenous trees of the Uganda Protectorate*. The Government of Uganda Printers, Entebbe, Uganda. 491 pp.
- FITTER, A. H. & FITTER, R. S. R. 2002. Rapid changes in flowering time in British plants. *Science* 296:1689–1692.

- FRANKIE, G. W., BAKER, H. G. & OPLER, P. A. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62:881–919.
- HAMILTON, A. C. 1991. *Uganda forest trees*. Makerere University Printery, Kampala, Uganda, 280 pp.
- HOWARD, P. C. 1991. *Nature conservation in Uganda's tropical forest reserves*. IUCN, Gland, 313 pp.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* 21:620–637.
- JANZEN, D. H. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69–103.
- KATENDE, A. B., BIRNIE, A. & TENGNÄS, B. 1995. *Useful trees and shrubs for Uganda: identification, propagation, and management for agricultural and pastoral communities*. Regional Soil Consultants Unit, Nairobi, Kenya, 710 pp.
- KINGSTON, B. 1967. *Working plan for the Kibale and Itwara Central Forest Reserves*. Ugandan Forest Department, Government of Uganda Printer, Entebbe, Uganda, 143 pp.
- LIEBERMAN, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology* 70:791–806.
- MENZEL, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *International Journal of Biometeorology* 44:76–81.
- NEWBERY, D. M., SONGWE, N. C. & CHUYONG, G. B. 1998. Phenology and dynamics of an African rainforest at Korup, Cameroon. Pp. 267–308 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds). *Dynamics of tropical communities*. Blackwell, Oxford.
- NEWSTROM, L. E., FRANKIE, G. W., BAKER, H. G. & COLWELL, R. 1994a. Diversity of long-term flowering patterns. Pp. 142–160 in McDade, L. A., Bawa, K. S., Hespeneheide, H. A. & Hartshorn, G. S. (eds). *La Selva: Ecology and natural history of a Neotropical rain forest*. The University of Chicago Press, Chicago.
- NEWSTROM, L. E., FRANKIE, G. W. & BAKER, H. G. 1994b. A new classification for plant phenology based on flowering patterns in lowland tropical rainforest trees at La Selva, Costa Rica. *Biotropica* 26:141–159.
- OPLER, P. A., FRANKIE, G. W. & BAKER, H. G. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography* 3:231–236.
- OSMASTON, H. A. 1959. *Working plan for the Kibale and Itwara Forests*. Uganda Forest Department, Government of Uganda Printer, Entebbe, Uganda, 162 pp.
- PERNEGER, T. V. 1999. What's wrong with Bonferroni adjustments. *British Medical Journal* 316:1236–1238.
- RATHKE, B. & LACEY, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179–214.
- SKORUPA, J. 1988. *The effect of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda*. Ph.D. Dissertation, University of California, Davis, USA.
- SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104:25–35.
- SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forest. *Oikos* 15:274–281.
- SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman and Company, San Francisco, 859 pp.
- SPARK, T. H. & MENZEL, A. 2002. Observed changes in seasons: an overview. *International Journal of Climatology* 22:1715–1725.
- STACHOWICZ, J. J., TERWIN, J. R., WHITLATCH, R. B. & OSMAN, R. W. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Science, USA* 99:15497–15500.
- STRUHSAKER, T. T. 1975. *The red colobus monkey*. University of Chicago Press, Chicago, 311 pp.
- STRUHSAKER, T. T. 1978. Interrelations of red colobus monkeys and rain-forest trees in the Kibale Forest, Uganda. Pp. 397–422 in Montgomery, G. G. (ed). *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, DC.
- STRUHSAKER, T. T. 1997. *Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation*. University Presses of Florida, Gainesville, 434 pp.
- TUTIN, C. E. G. & FERNANDEZ, M. 1993. Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. *Journal of Tropical Ecology* 9:241–248.
- VAN SCHAIK, C. P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology* 2:327–347.
- VAN SCHAIK, C. P., TERBORGH, J. W. & WRIGHT, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- VAN VLIET, A. J. H. & SCHWARTZ, M. D. 2002. Phenology and climate: the timing of life cycle events as indicators of climate variability and change. *International Journal of Climatology* 22:1713–1714.
- WALTHER, G. R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J. M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- WHEELWRIGHT, N. T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44:465–477.
- WRIGHT, S. J. & VAN SCHAIK, C. P. 1994. Light and the phenology of tropical trees. *American Naturalist* 143:192–199.
- WRIGHT, S. J., CARRASCO, C., CALDERON, O. & PATTON, S. 1999. The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1647.
- ZANNE, A. E. 1998. *Expediting indigenous tree regeneration in African grasslands: plantations and the effects of distance and isolation from seed sources*. M.Sc. thesis, Univ. of Florida, Gainesville, FL.
- ZANNE, A. E. 2003. *Adaptations to heterogeneous habitats: life-history characters of trees and shrubs*. Ph.D. dissertation, Univ. of Florida, Gainesville, Florida.