

Fruit and flower phenology at two sites in Kibale National Park, Uganda

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ABSTRACT. Examination of phenological patterns of tropical trees at different temporal and spatial scales can elucidate biotic and abiotic factors that correlate with fruiting, flowering and/or leaf set patterns. In this study, 3793 trees from 104 species in Kibale National Park, Uganda were monitored. The trees were selected from two sites (Kanyawara and Ngogo) separated by 10 km. Trees were monitored monthly to document community-wide and population-level fruiting and flowering patterns for a maximum of 76 mo. Analysis of two sites over a number of years permitted examination of generalities of patterns found on smaller spatial and temporal scales. Spectral analysis indicated that community-level flowering and fruiting at Kanyawara exhibited regular annual peaks, although the flowering peaks were of shorter duration. At Ngogo, community-level flowering also displayed regular annual peaks, but fruiting had an irregular pattern with no distinct peaks. The abundance of fruiting trees at Kanyawara was negatively related to the minimum temperature in the previous season (3–7 mo prior). Since fruiting tended to peak when the first wet season of the year was ending and the dry season was beginning, this suggests that the minimum temperature in the previous dry season is important in determining how many individuals fruit. Flowering at Kanyawara peaked immediately after the maximum annual period of high irradiance. Within-species synchronization was evident in the flowering for all species examined at Ngogo and for 64% of those at Kanyawara. Fruiting was synchronous within species for 64% of the species at both sites. Despite this general community-level synchronization, the months of peak fruiting and flowering for some species varied markedly among years. Furthermore, for a number of species the timing of fruiting or flowering events differed between Kanyawara and Ngogo. For some species, trends that were suggested from one year of data were not supported when additional years were considered. Although these two sites are close together, share many of the same species, and experience similar climatic regimes, many phenological patterns were site-dependent.

KEY WORDS: Africa, flowering, fruiting, Kibale National Park, phenology, seasonality, seed dispersal, spectral analysis, tropical trees

INTRODUCTION

Studies of tropical rain forests suggest that phenological patterns of trees are driven by a variety of factors including: abiotic characters such as rainfall, irradiance, and temperature (Ashton *et al.* 1988, Newbery *et al.* 1998, Opler *et al.* 1976, van Schaik 1986, van Schaik *et al.* 1993, Sun *et al.* 1996, Tutin & Fernandez 1993); mode of seed dispersal (Charles-Dominique *et al.* 1981, Smythe 1970, Snow 1965, 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); canopy position (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. Some evidence suggests that wind-dispersed seeds may ripen during the dry season when tradewinds are stronger and leaves are often absent, allowing for greater wind dispersal (e.g., Newstrom *et al.* 1994a). In contrast, some animal-dispersed fleshy-fruited species have their peak fruiting period during the rainy season, perhaps due to increased moisture levels necessary for fruit production (Lieberman 1982, Rathke & Lacey 1985). Phenological studies of temperate forests and tropical dry forests often detect clearly defined seasonal patterns associated with marked changes in rainfall and temperature (Hilty 1980, Lieberman 1982). However, some studies have suggested that phenological patterns of tropical lowland rain forests are not as well defined (Putz 1979). The more continuous high temperatures and moisture that typify lowland rain forests foster growth all year long (Richards 1996). The phenological patterns that result are diverse and the environmental cues influencing the patterns remain generally obscure (van Schaik 1986).

An understanding of the phenological patterns in different geographical regions and of factors underlying these patterns is important for a number of reasons. First, frugivores are the dominant group of vertebrates in most tropical forests (Emmons *et al.* 1983, Fleming *et al.* 1987, Gautier-Hion *et al.* 1985, Terborgh 1986), and regional differences in their abundance may be caused by differences in food availability (Terborgh & van Schaik 1987). Second, an understanding of phenological patterns and factors underlying these patterns will assist conservation scientists in predicting consequences of perturbations such as atypical climatic events (Foster 1982b) or global warming (Tutin & Fernandez 1993, Tutin & White *in press*). Third, phenological patterns are linked to many processes governing forest function and structure including: population biology of pollinators, dispersers, seed predators, and herbivores, interspecific competition among trees, and processes of primary production (Newstrom *et al.* 1994a, Smythe 1970, van Schaik *et al.* 1993). Thus, an understanding of what governs phenological process is valuable in understanding forest function and structure and in providing the basis for developing management options. For example, during timber harvesting, maintenance of trees

producing fruit in periods of habitat-wide fruit scarcity could increase the carrying capacity of the post-harvest area for frugivores (White 1994), or logging could be initiated after the period of peak seed set to facilitate regeneration.

In this study, we examine flowering and fruiting patterns for up to 76 mo for 3793 trees from 104 species at two sites in Kibale National Park, Uganda. We use spectral analysis (Fourier analysis) to detect cycles in fruiting and flowering at the two sites. We quantify community- and population-level phenology and compare phenological cycles of emergent and mid-storey species, and common and rare species. We have attempted to overcome some shortcomings that have limited some previous studies in three ways. First, each month we monitored a large number of trees at each location. Second, the study was conducted over a 6-y period, thus it is possible to assess the generality of patterns observed in any one year by comparing years. Finally, by contrasting two sites within one region we can provide an initial examination of the generality of the patterns obtained from one site.

METHODS

Study sites

Kibale National Park (766 km²) is located in western Uganda, just east of the Ruwenzori Mountains (0° 13'–0° 41'N and 30° 19'–30° 32'E). The moist evergreen forest is transitional between lowland rain forest and montane forest (Chapman & Chapman 1997; Skorupa 1988; Struhsaker 1975, 1997). Kibale is comprised of mature forest, swamp, grassland, plantation and secondary forest (Butynski 1990).

We analysed phenological patterns from two relatively undisturbed sites within the park (Kanyawara (K-30) and Ngogo). Kanyawara is located at an elevation of 1500 m and receives a mean annual rainfall of 1700 mm (1984–1996). Mean daily minimum temperature is 15.5 °C, and mean daily maximum temperature is 23.7 °C (1990–1996; Chapman & Chapman 1997). Ngogo is located at an elevation of 1350 m and receives a mean annual rainfall of 1500 mm (1977–1984). Mean daily minimum temperature is 16.7 °C, and mean daily maximum temperature is 24.2 °C (1977–1984; Butynski 1990). Both study areas consist of a series of moderately undulating valleys with an average slope of 8.7° at Kanyawara and 6.0° at Ngogo. Within each site there are elevational changes from hill tops to valley bottoms that are often as large as 150–200 m (measured with a Paulin Micro Surveying Altimeter). It rains on an average of 166 d per year (Kingston 1967), but the pattern of rainfall is bimodal in distribution. May–August and December–February tend to be drier than other months, with the May–August dry period of longer duration than the second dry season. On average, the first rains of the year (March–April) are less severe than the September–November rains. Despite these bimodal trends, there is great year-to-year variation in the magnitude, onset, and duration of wet and dry seasons (Figure 1).

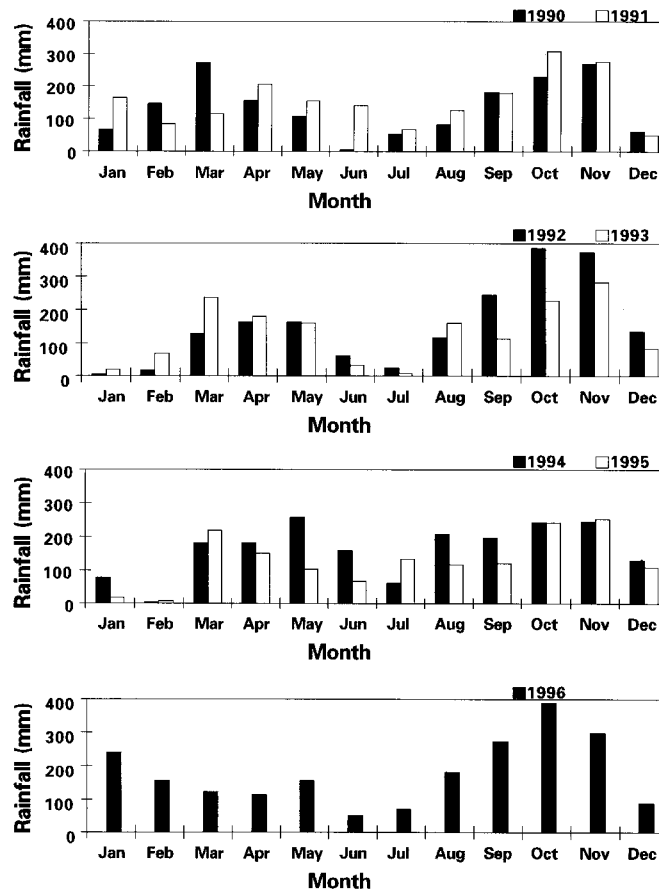


Figure 1. Rainfall data from the Kanyawara site, Kibale National Park, Uganda for 1990–1996.

Foresters have classified Kanyawara as a *Parinari* forest, distinguished on photo-aspect maps by large spreading crowns of *Parinari excelsa* (Kingston 1967, Skorupa 1988). The presence of *P. excelsa* and the subdominants found near Kanyawara (*Aningeria altissima*, *Olea capensis*, *Newtonia buchananii* and *Chrysophyllum gorungosanum*) are thought to indicate a climax forest between 1370 m and 1525 m (Osmaston 1959). Ngogo, at 1350, has some features of lower elevation forest. *P. excelsa* is still present, but the forest is very mixed with *Chrysophyllum* spp. and *Celtis* spp. being common. These two forests, although located only 10 km apart, show differences in species composition (Chapman *et al.* 1997). Of all species found at either site ($n = 104$) only 52% were found at both sites. If rare species (< 1 individual ha^{-1}) are excluded, the two sites share 72% of the species.

Data collection

Twelve 200-m \times 10-m transects were established randomly along the existing trail system at Kanyawara in January 1990, producing a total sampling area of

2.4 ha. Twenty-four 200-m \times 10-m transects were established randomly along the existing trail system at Ngogo in May 1990 producing a sampling area of 4.8 ha. At both sites, all trees with a diameter at breast height (DBH) $>$ 10 cm and within 5 m of the trail were tagged and the DBH recorded. A total of 1171 trees (67 species) at Kanyawara and 2622 trees (92 species) at Ngogo were tagged (Table 1). Phenological data for all trees along the transects were recorded monthly between January 1990 and April 1996 at Kanyawara and between May 1990 and April 1996 at Ngogo (between August 1995 and February 1996 data could not be collected at Ngogo). During that time 72% of the trees at Kanyawara and 76% of the trees at Ngogo flowered. The majority of those individuals that did not flower were small individuals and were probably immature. When monitoring the transects each month, each tree containing flowers and ripe or unripe fruit was noted. Ripe and unripe fruit were combined into one category due to the difficulty in determining the ripeness of some fruits that do not change colour. Data were collected by Ugandan field assistants, the first author, and North American volunteers. The accuracy of assessing phenological status by these different individuals was repeatedly assessed throughout the study.

Analysis

It is difficult to portray phenological data graphically (Newstrom *et al.* 1994a,b) and while many statistical approaches (e.g., spectral analysis) offer useful means of detecting cycles, they do not illustrate the intensity of fruiting or flowering events throughout the cycle. With this limitation in mind, we rely on spectral analysis to portray general cycles and use graphical representations of important aspects of the data (e.g., community level fruiting and flowering and specific species) to illustrate the intensity of cyclic patterns of phenological events.

To detect climatic predictors of phenological events, we relate the number of individuals fruiting or flowering in a given month to climatic variables (rainfall, average maximum temperature, average minimum temperature, and irradiance) for that month and for each previous month from 1 to 11 mo prior). We report all contrasts for community level analyses. For individual species, we document the climatic variable that was most strongly correlated with the number of individuals fruiting and flowering. This analysis of climatic predictors of phenology patterns should be considered as a simple exploration of the data for several reasons including the fact that we do not adjust the probability level that we accept as statistically significant to take into account the fact that we are conducting multiple comparisons.

The coefficient of dispersion (CD; standard deviation/mean for monthly number of trees participating in a phenological event over the entire study) was used to represent the synchrony of fruiting and flowering events (Sokal & Rohlf 1981). The value of the CD is greater than one when the distribution pattern is clumped (fruiting or flowering events occur in one period), less than one when the pattern is uniform, and equal to one when the pattern is random.

Table 1. Tree density (individuals ha⁻¹) and tree height category of the trees for which phenology was monitored in Kibale National Park, Uganda: C, canopy; E, emergent; M, midstorey.

Species	Density		Height category
	Kanyawara	Ngogo	
Anacardiaceae			
<i>Pseudospondias microcarpa</i>	1.7	1.3	C
Annonaceae			
<i>Monodora myristica</i>	0.4	0.4	C
<i>Uvariopsis congensis</i>	60.4	100.6	M
Apocynaceae			
<i>Funtumia latifolia</i>	33.8	36.3	C
<i>Pleiocarpa pycnantha</i>	1.3	1.3	M
<i>Rauwolfia oxyphylla</i>	—	2.1	M
<i>Tabernaemontana</i> sp.	4.6	34.4	M
Araliaceae			
<i>Polyscias fulva</i>	0.8	0.2	C
Balanitaceae			
<i>Balanites wilsoniana</i>	1.7	1.7	E
Bignoniaceae			
<i>Kigelia moosa</i>	3.3	0.8	M
<i>Markhamia lutea</i>	50.0	24.8	C
<i>Spathodea campanulata</i>	0.8	2.3	M
Boraginaceae			
<i>Cordia millenii</i>	0.4	0.2	E
Canellaceae			
<i>Warbugia ugandensis</i>	—	1.3	E
Capparidaceae			
<i>Euaenia eminens</i>	—	0.2	M
<i>Maerua duchesnei</i>	1.3	0.4	M
Celastraceae			
<i>Cassine buchananii</i>	0.4	2.7	E
Celtidaceae			
<i>Celtis africana</i>	4.2	1.0	C
<i>Celtis durandii</i>	47.1	57.5	C
<i>Celtis mildbraedii</i>	—	0.2	E
Chrysobalanaceae			
<i>Parinari excelsa</i>	2.9	0.2	E
Ebenaceae			
<i>Diospyros abyssinica</i>	40.0	69.0	C
Euphorbiaceae			
<i>Croton</i> sp.	0.8	0.4	C
<i>Macaranga scheiwinfurthii</i>	—	0.4	M
<i>Margaritaria discoide</i>	—	2.1	C
<i>Neoboutonia</i> sp.	1.3	7.9	M
<i>Sapium ellipticum</i>	—	0.6	C
<i>Thecacoris lucida</i>	1.3	—	M
Fabaceae			
<i>Albizia grandibracteata</i>	1.3	—	C
<i>Millettia dura</i>	3.3	7.7	M
<i>Newtonia buchananii</i>	—	0.2	E
<i>Piptadeniastrum africanum</i>	—	1.9	E
Flacourtiaceae			
<i>Casearia</i> sp.	1.3	0.2	E
<i>Dasylepis</i> sp.	1.3	7.9	M
<i>Lindackeria</i> sp.	—	1.3	M
<i>Oncoba</i> sp.	—	0.4	M
Guttiferae			
<i>Symphonia globulifera</i>	0.4	—	E
Icacinaceae			
<i>Apodytes dimidiata</i>	0.8	—	C

Table 1. *cont.*

Species	Density		Height category
	Kanyawara	Ngogo	
Lauraceae			
<i>Beilshmiadia ugandensis</i>	0.4	—	C
Loganiaceae			
<i>Strychnos mitis</i>	7.5	0.2	E
Malvaceae			
<i>Dombeya kirkii</i>	9.2	3.1	M
<i>Leptonychia mildbraedii</i>	35.4	2.5	M
<i>Pterygota mildbraedii</i>	—	10.8	E
Meliaceae			
<i>Entandrophragma angolense</i>	—	0.2	E
<i>Lovoa seynnertonii</i>	0.8	4.4	E
<i>Turraea</i> sp.	—	1.5	M
<i>Turraeanthus africanus</i>	—	0.4	M
Melanthaceae			
<i>Bersama abyssinica</i>	0.4	—	M
Monimiaceae			
<i>Xymalos monospora</i>	8.8	2.3	M
Moraceae			
<i>Antiaris toxicaria</i>	0.4	—	E
<i>Bosqueia phoberos</i>	50.0	5.6	C
<i>Ficus conraui</i>	0.4	0.2	C
<i>Ficus cyathistipula</i>	—	1.0	M
<i>Ficus exasperata</i>	3.8	0.4	C
<i>Ficus mucoso</i>	—	0.6	E
<i>Ficus natalensis</i>	0.4	0.6	M
<i>Ficus ovata</i>	—	0.2	M
<i>Ficus sansibarica</i>	1.7	2.1	E
<i>Ficus saussureana</i>	—	0.6	E
<i>Ficus trichopoda</i>	—	0.4	C
<i>Morus lactea</i>	—	0.2	E
<i>Myrianthus arboreus</i>	2.1	—	M
<i>Treculia africana</i>	—	0.2	C
Olacaceae			
<i>Strombosia scheffleri</i>	12.5	3.1	C
<i>Linociera johnsonii</i>	5.4	7.5	M
<i>Olea capensis</i>	3.3	3.1	E
<i>Schrebera arborea</i>	—	1.5	E
Rhizophoraceae			
<i>Cassipourea ruwensorensis</i>	7.1	5.0	M
Rosaceae			
<i>Prunus africana</i>	—	3.0	E
Rubiaceae			
<i>Coffea eugenoides</i>	0.4	—	M
<i>Craterispermum laurinum</i>	1.7	—	M
<i>Dictyandra arborescens</i>	0.4	12.1	M
<i>Euclinia longiflora</i>	0.8	—	M
<i>Mitragyna rubrostipulata</i>	—	0.4	M
<i>Oxyanthus latifolia</i>	—	0.4	M
<i>Psychotria</i> sp.	—	0.2	M
<i>Rothmannia urcelliformis</i>	1.3	5.2	M
<i>Tarenna pavettoides</i>	—	4.4	M
<i>Vangueria apiculata</i>	—	0.2	M
Rutaceae			
<i>Fagaropsis angolensis</i>	2.5	0.6	C
<i>Tectea nobilis</i>	17.1	3.8	C
<i>Zanthoxylum leprieurii</i>	0.8	0.2	M

Table 1. *cont.*

Species	Density		Height category
	Kanyawara	Ngogo	
Sapindaceae			
<i>Aphania senegalensis</i>	1.7	4.6	M
<i>Blighia</i> sp.	0.8	1.0	M
<i>Pancovia turbinata</i>	10.8	0.2	M
Sapotaceae			
<i>Aningeria altissima</i>	1.7	—	E
<i>Chrysophyllum</i> sp.	2.6	64.6	E
<i>Mimusops bagshawei</i>	3.3	3.1	E
Simaroubaceae			
<i>Harrisonia abyssinica</i>	—	2.5	M
Ulmaceae			
<i>Chaetacme aristata</i>	17.1	4.8	M
Verbenaceae			
<i>Premna angolensis</i>	4.6	4.4	C
<i>Vitex amboniensis</i>	—	0.2	M
Violaceae			
<i>Rinorea oblongifolia</i>	—	0.2	M

The significance of the departure of the CD from random was calculated using the index of dispersion (Southwood 1978).

Spectral analysis (Fourier analysis) is a type of analysis of variance used to detect cycles of various frequencies in time series (Platt & Denman 1975). This is accomplished by comparing the variation in the time series about the mean to sine functions of different frequencies. The result is a periodogram which displays the least-squares fit of each frequency to the time series. Each data set analysed was 64 mo long, spanning from May 1990 to August 1995 (64 mo is the longest possible wavelength that can be analysed by spectral analysis with this data set). Because data were not collected from August 1995 to February 1996 at Ngogo, we only had 63 mo of continuous data. To analyse the Ngogo data, we used the July 1995 data again for August 1995 to give us 64 continuous months.

Using spectral analysis we analysed community-level fruiting and flowering patterns (all trees along the transects >10 cm DBH), population-level fruiting and flowering patterns of the most abundant tree species at each site (all species along the transects with > 40 individuals at one site and > 10 individuals at the other site), fruiting and flowering patterns of emergent and mid-storey trees, and fruiting and flowering patterns of common and rare species. For the population-level analysis, 11 species were analysed at Kanyawara. At Ngogo those same 11 species and three other species were considered (Table 1).

We defined emergent trees as all species that reach average heights of > 30 m. Mid-storey species were defined as species that reach average heights of < 25 m (Table 1). Common species were defined as those with 40 or more individuals recorded in the transects. Rare species were those with four or fewer individuals in the transects.

From graphs of the number of individuals fruiting or flowering versus months and periodograms of least-squares fit versus wave frequency in months, the monthly fruiting and flowering frequencies were determined. The strongest peak in the periodogram was used to define whether the pattern was sub-annual (regular pattern, < 12 mo), annual (regular 12-mo pattern), supra-annual (regular pattern, > 12 mo), irregular (no regular pattern or pattern not detectable in our data set), or continuous (some individuals always fruiting) (modified from Newstrom *et al.* 1994a,b).

RESULTS

Weather patterns

Rainfall in the region exhibited a distinct bimodal pattern, but the onset and duration of particular seasons varied among years (Figure 1). For example, onset of the first dry season in 1991 was later than other years and relatively wet with no month receiving < 66 mm of rain. Monthly rainfall varied from 4 to 388 mm. During the period of study annual rainfall averaged 1783 mm (range 1536 to 2140 mm). Ninety-four years of rainfall data are available for the area of Kibale National Park, Uganda (1902–1996), and the mean annual rainfall for this period is 1537 mm. However, during the current study the range in annual rainfall was 1119 mm to 2140 mm, and the rainfall was within 100 mm of the overall mean in only 33% of the years.

Average minimum and maximum temperatures also varied markedly between months (minimum daily temperature by month average = 15.3 °C, range = 13–18 °C; maximum temperature average = 23.8 °C, range = 21–27 °C) and between years. For example, the average maximum temperature in March 1993 was 21.4 °C, while in March 1994 it was 26.2 °C.

Community-level patterns

At Kanyawara there was an average of 65.6 trees flowering per ha each month (SD = 45.8, CD = 0.67, Figure 2). The density of flowering trees did not exhibit peaks as high as fruiting (range 1.25–82.5 trees flowering/ha each month; Figure 2). The season of peak flowering was variable, but often occurred at the end of the March to April wet season or at the start of the May to August dry season (Figure 2).

At Kanyawara there was an average of 66.7 trees fruiting per ha each month (range 10 to 133 trees fruiting/ha; SD = 27.2, CD = 0.4; Figure 2). The time of peak fruiting was variable, but it often occurred when the first wet season was ending and the dry season was beginning. January to March were often (e.g., February 1995) periods of fruit scarcity (Figure 2).

At Ngogo there was an average of 28.9 trees flowering per ha each month (SD = 24.7, CD = 0.85, Figure 2). This value is less than the average density of flowering trees at Kanyawara. However, the range of flowering individuals

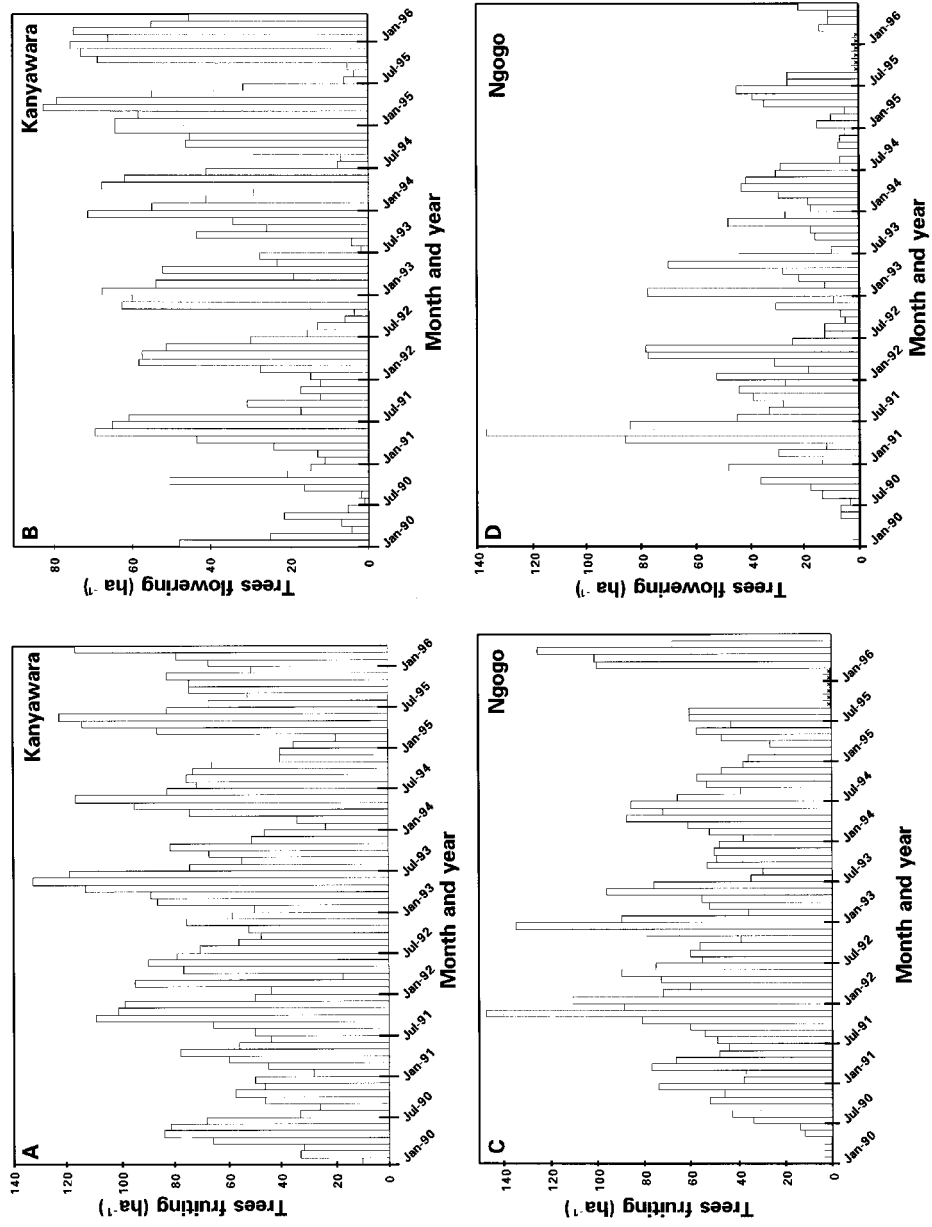


Figure 2a–d. Community wide fruiting and flowering patterns for two sites within Kibale National Park, Uganda (Kanyawara and Ngogo) in 1990–1996 measured as the number of fruiting or flowering individuals on a per ha basis.

ha⁻¹ per month at Ngogo (range between months = 3.3–136.7 flowering individuals ha⁻¹) was much greater than at Kanyawara. At Ngogo, a number of common species flowered synchronously in May 1992 producing a very high density of flowering trees, which did not occur in any of the other years.

The average monthly density of fruiting trees at Ngogo was 60.2 fruiting trees ha⁻¹ (SD = 26.5, range = 146.9–11.3 fruiting trees ha⁻¹, CD = 0.44, Figure 2), which was similar to Kanyawara. However, there was less regularity in the timing of seasonal peaks than at Kanyawara (Figure 2; see also spectral analysis below).

At both sites the number of trees flowering in any given month was lower than the number of trees fruiting (Figure 2). This is unexpected since fruiting is contingent on flowering. However, the duration of flowering is typically short, while trees can bear fruit for a number of months. Furthermore, because of the difficulty in determining the ripeness of fruits of some species that do not change colour, a tree was considered to be fruiting if it was bearing either ripe and/or unripe fruit. For example, *Monodora myristica* trees will often bear fruit for up to 6 mo (S. Balcomb, *pers. comm.*).

Spectral analysis

Spectral analysis indicated that community-level flowering at Kanyawara had a 12-mo periodicity. In contrast, community-level fruiting at Kanyawara was continuous with some individuals fruiting at all times of the year, although 12-mo peaks were evident (Table 2 and Figure 3). Species categorized as common and rare showed synchronized 12-mo flowering peaks at Kanyawara. Common species had a strong 6-mo fruiting peak with weak 12- and 24-mo peaks, while rare species had an irregular fruiting pattern. Mid-storey and emergent species at Kanyawara both had strong 9-mo and weak 6-mo flowering patterns and 24-mo fruiting patterns. Mid-storey species also had a weak 6-mo fruiting pattern. Mid-storey and emergent species were synchronized in their flowering patterns, but their fruiting patterns were offset.

Population-level patterns for fruiting and flowering at Kanyawara varied. Flowering patterns included irregular (two species), sub-annual (two species), annual (four species), and supra-annual (three species). Fruiting patterns included irregular (four species), annual (two species), and supra-annual (five species). *Leptonychia mildbraedii* was the only species that showed the same periodicity for its fruiting and flowering (12-mo). The 10 other species all showed differing patterns. For example, *Celtis durandii* had an irregular flowering pattern, but had 12-mo fruiting peaks.

At Ngogo, community-level flowering and fruiting both tended to be continuous, with individuals of some species flowering or fruiting at all months of the year (Table 2, Figure 3). However, community-level flowering showed a more distinct pattern than fruiting with a 12-mo peak frequency, whereas fruiting appeared to have no consistent pattern. For both fruiting and flowering, common species had a more continuous pattern than rare species, which were

Table 2. Flowering and fruiting patterns for 14 tree species and total tree species, common, rare, emergent and mid-storey species from Kanyawara (first line) and Ngogo (second line) in Kibale National Park, Uganda as suggested by spectral analyses. Emergent trees were defined as all species that reached average heights of > 30 m. Mid-storey species were defined as species that reach average heights of < 25 m. Common species were defined as those with 40 or more individuals recorded in the transects. Rare species were those with four or fewer individuals in the transects. The patterns of fruiting and flowering are categorized as per Newstrom *et al.* (1999a,b). When possible the periodicity between fruiting and flowering peaks is presented. A ‘—’ is given when no clear peak was evident. To examine whether weather patterns affected fruiting or flowering, the number of individuals fruiting or flowering in a given month were correlated with the rainfall, average maximum temperature, average minimum temperature for that month and for each previous month from 1 to 11 mo prior. The climatic variables that were most strongly correlated with fruiting or flowering are reported (e.g., Max Temp 11 indicates that flowering was most strongly correlated with the maximum temperature 11 mo previously).

Species	Kanyawara		Flowering Peak 1 (Peak 2)	Strongest correlation	GD	Fruiting Kanyawara		Peak 1 (Peak 2,3)	Strongest correlation	GD
	Supra-annual	Irregular				Supra-annual	Ngogo			
<i>Bosquetia phoberos</i>	Supra-annual	Irregular	24(12) 3	Irradiance 5	1.24* 2.89*	Irregular	Irregular	—	Max Temp 9	3.91* 1.80*
<i>Celtis darandii</i>	Irregular	Irregular	—	Max Temp 3	1.03	Annual	Annual	12	Irradiance 7	0.73
<i>Chaetacme aristata</i>	Annual	Irregular	12(9)	Irradiance 9	2.24* 1.64* 4.33*	Supra-annual	Supra-annual	24	Max Temp 1	0.91
<i>Chrysophyllum gorungosanum</i>	—	—	—	—	—	—	—	<64	—	1.78*
<i>Tabernaemontana</i> spp.	Sub-annual	Irregular	9(6)	Min Temp 0	2.04* 1.95*	Supra-annual	Supra-annual	36	—	1.09
<i>Diclyandra arborescens</i>	Sub-annual	—	6	—	1.43*	—	—	36	—	0.56
<i>Diospyros abyssinica</i>	Supra-annual	Annual	24 (6) 12	Irradiance 2	1.83* 0.94	Supra-annual	Supra-annual	24	Irradiance 1	0.70
<i>Funtumia latifolia</i>	Supra-annual	Sub-annual	24	—	2.53*	Supra-annual	Supra-annual	36	—	1.19*
<i>Leptonychia mildbraedii</i>	Sub-annual	Annual	6(12) 6	Min Temp 0	0.91	Sub-annual	Sub-annual	24	Max Temp 10	1.23*
<i>Markhamia lutea</i>	Annual	Irregular	12	Rain 5	1.41* 1.34*	Annual	Annual	18(6) 12(6)	Rain 7	1.00
<i>Mimusops bagshawei</i>	Supra-annual	Annual	18(36) 12	Irradiance 2	2.56* 0.93	Supra-annual	Supra-annual	6	Max Temp 10	1.08
<i>Pterygota mildbraedii</i>	Annual	Sub-annual	12	Max Temp 6	1.70* 1.10*	Annual	Supra-annual	36	—	1.05
<i>Tectea nobilis</i>	Sub-annual	Supra-annual	9	—	1.98*	Sub-annual	Supra-annual	18	Rain 11	3.41* 1.99*
<i>Uvariopsis congensis</i>	Annual	Supra-annual	12	Min Temp 8	1.91* 1.37*	Annual	Annual	12(>64)	Max Temp 2	8.71* 1.32*
Total species	Supra-annual	Irregular	36(12) 18	Max Temp 6	2.26* 1.43*	Supra-annual	Supra-annual	—	Max Temp 2	3.03* 2.57*
Canopy species	Annual	Continuous	12	—	2.33*	Annual	Annual	24	Irradiance 10	1.27*
Mid-storey species	Annual	Annual	12(>64) 12(6)	—	0.67 0.85	Continuous	Continuous	>64(6) 12(6)	—	1.54*
Common species	Annual	Irregular	12	—	0.76	Supra-annual	Supra-annual	24	—	0.41
Rare species	Annual	Irregular	12	—	1.28* 0.77	Supra-annual	Supra-annual	36	—	0.87
	Annual	Annual	9(6) >64	—	1.11	Supra-annual	Supra-annual	24(6)	—	0.63
	Annual	Irregular	12	—	0.70	Sub-annual	Sub-annual	6(12,24)	—	0.66
	Annual	Irregular	>64	—	1.04	Continuous	Continuous	>64	—	0.50
	Annual	Irregular	12	—	0.77	Irregular	Irregular	—	—	0.65
	Irregular	—	>64	—	1.67*	Irregular	Irregular	—	—	3.63*

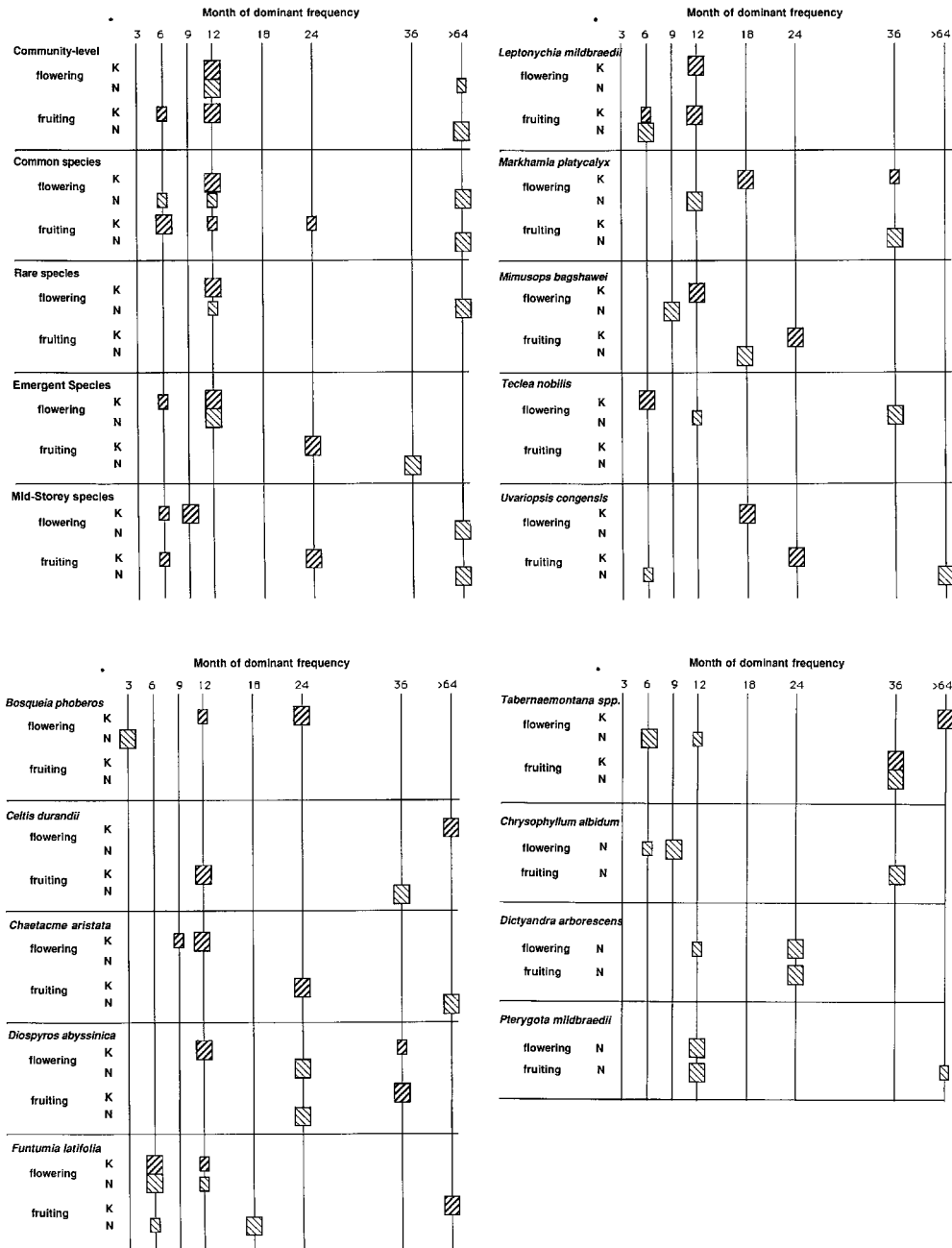


Figure 3. The results of spectral analysis of 64 mo of fruiting and flowering data from two sites in Kibale National Park, Uganda (Kanyawara (K)-upper and Ngogo (N)-lower) for all species, abundance and height classes, and for individual species. The strongest, and if it existed, the second strongest peak in the periodogram produced from the spectral analysis are indicated by the sizes of the boxes for each site.

typified by distinct peaks at irregular intervals. Flowering and fruiting peaks of mid-storey species were somewhat offset from peaks of emergent species, but this was not repeated every year. A variety of population-level flowering patterns were documented at Ngogo including: irregular (five species), sub-annual (four species), supra-annual (three species), and annual (two species). The most common population-level fruiting pattern was supra-annual (eight species), followed by irregular (four species), annual, and sub-annual (one species each). The type of flowering pattern did not always coincide with the type of fruiting pattern for a given species. For example, *Markhamia lutea* had an annual flowering pattern with a 12-mo frequency, as well as a supra-annual fruiting pattern with a 36-mo frequency. However, some species did have flowering and fruiting patterns that shared similar frequencies. For example, *Dictyandra arborescens* and *Diospyros abyssinica* had 24-mo frequencies for both fruiting and flowering patterns.

In general, few species or groups of species (e.g., emergent trees) showed similar peak frequencies between flowering and fruiting (Kanyawara = three out of 12, Ngogo = six out of 14). Further, few species or groups of species showed similar peak frequencies between the two sites (flowering – four, fruiting – seven). Even when peaks at Kanyawara and Ngogo occurred at the same times, the Kanyawara peaks tended to be of similar heights (i.e., similar number of trees flowering or fruiting) and widths (i.e., similar number of months flowering or fruiting) across years, whereas Ngogo peaks varied in height and width. Interestingly, *Uvariopsis congensis* had fruiting peaks at similar times at the two sites, but the peaks at Kanyawara were broader than at Ngogo. Further, some of the species at the two sites had similar peak times, but the number of trees participating in a fruiting event differed greatly between sites. For example, *D. abyssinica* had five individuals out of 96 (5%) participating in a fruiting peak at Kanyawara and 75 out of 331 (23%) individuals fruited at the same time at Ngogo (Figure 4).

General patterns for each species

Synchronization of flowering within species was evident for all species at Ngogo and for 64% of those at Kanyawara (as indicated by a significant departure of the coefficient of dispersion from random; Table 2). Within species synchronization of fruiting was evident for 64% of the species at both sites. To illustrate patterns of synchronization, the fruiting patterns of four species that were relatively abundant are depicted in Figure 4. Despite this synchronization within species, many species did not synchronize fruiting or flowering at specific times of the year. For example, the peak flowering of *Funtumia latifolia* at Kanyawara occurred in November in 1990, July in 1991, December 1992 and January 1993. For a number of species, the timing of fruiting or flowering events differed between Ngogo and Kanyawara. For example, March 1995 had the highest proportion of *Funtumia latifolia* trees flowering at Kanyawara, but few trees of this species flowered at Ngogo. For some species trends that were

suggested from one year of data (e.g., fruiting occurs in the dry season), were not supported when additional years of data were considered (Figure 4).

Phenological correlations with rainfall and temperature

At the community level a number of significant correlations were found between the number of individuals fruiting or flowering in a given month at Kanyawara and climatic variables for that month and for each previous month from 1 mo to 11 mo prior (Figure 5 a,b). Minimum temperature in the previous season (3 to 7 mo prior) was negatively related to the number of fruiting trees. Fruiting tended to peak at the end of the first wet season and at the start of the dry season. This suggests that the minimum temperature in the previous dry season influences how many individuals fruit. We do not have complete climatic data from Ngogo, thus a similar analysis cannot be made.

Two relationships between flowering patterns and climatic variables were evident. First, flowering frequently followed immediately after peak periods of irradiance. Second, the maximum temperature 8–11 mo prior was positively related to the number of flowering trees. Since peak flowering tends to occur at the end of the March to April wet season or at the start of the May to August dry season, this suggests that maximum temperature in the previous May to August dry season is important in determining flowering intensity. At the population level, the best climatic predictor of fruiting and flowering varied among species (Table 2).

DISCUSSION

Conducting this study at two sites over 6 y permitted us to examine spatial and temporal predictability in phenological patterns. Many trends apparent after 1 or 2 y of sampling disappeared when a larger sample of years was analysed. In addition, many trends apparent at one site were not observed at the second site, despite the fact that these sites are only 10 km apart, share many of the same species, and experience similar climatic regimes. Such findings question the generality of conclusions derived from one location and call for further effort to document phenological patterns. There were, however, some patterns that were evident at both sites and were consistent among years. The uniqueness of these patterns can be considered in light of the fact that the Kibale area receives a bimodal pattern of rainfall, whereas many previous published studies of phenological patterns of tropical trees were conducted in areas with only one wet and one dry season.

Phenological studies in tropical dry forests have documented marked seasonality in leafing and flowering which is often believed to be mediated by highly seasonal patterns of rainfall and cloud cover (Lieberman 1982, Opler *et al.* 1980, Rathke & Lacey 1985, van Schaik *et al.* 1993). In contrast to tropical dry forests, plants in tropical wet forests are thought to show less synchronization (Frankie *et al.* 1974, Hilty 1980, Opler *et al.* 1980, Putz 1979). The majority of

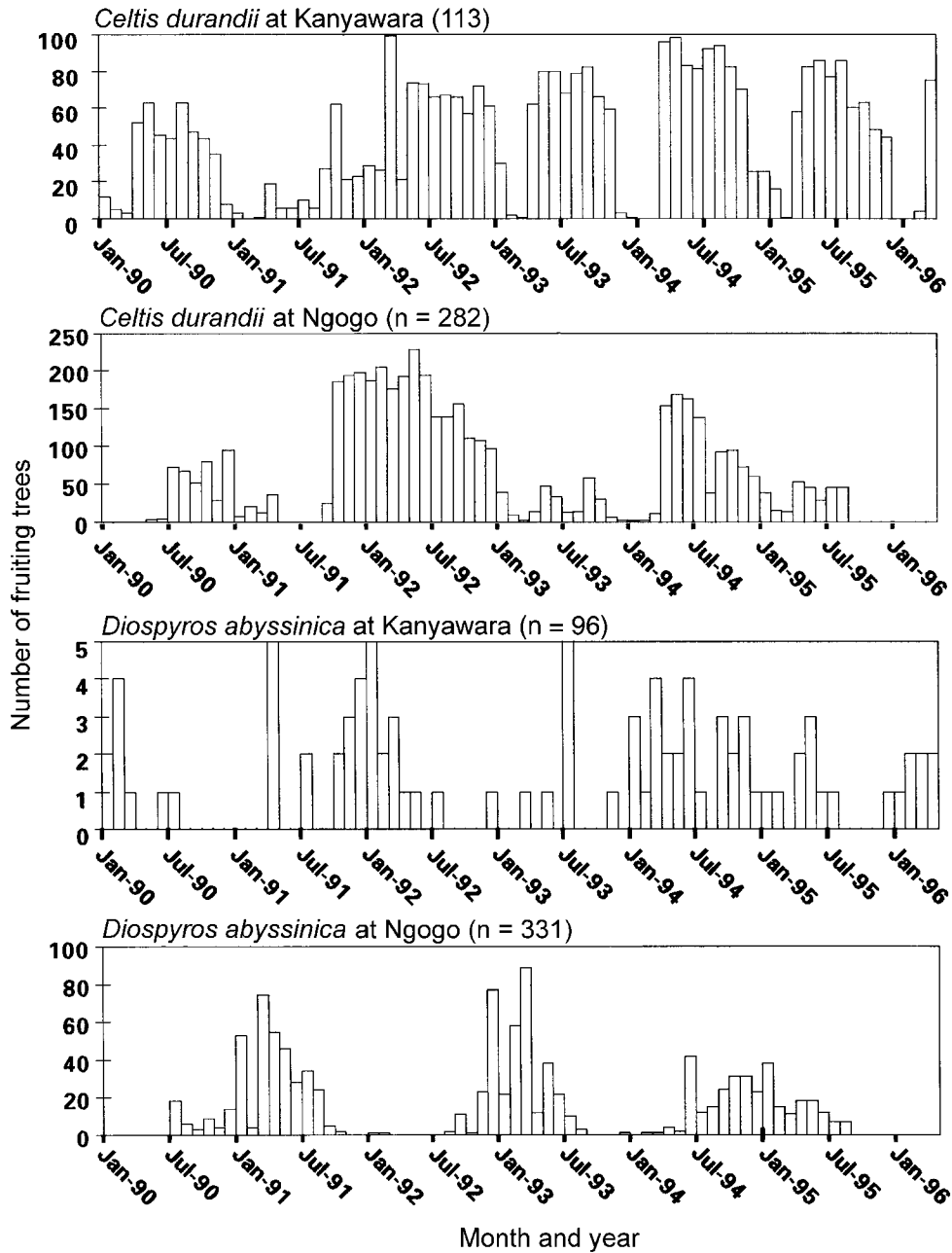


Figure 4. The fruiting pattern of four species chosen to illustrate general patterns and to depict differences between the two sites studied in Kibale National Park, Uganda.

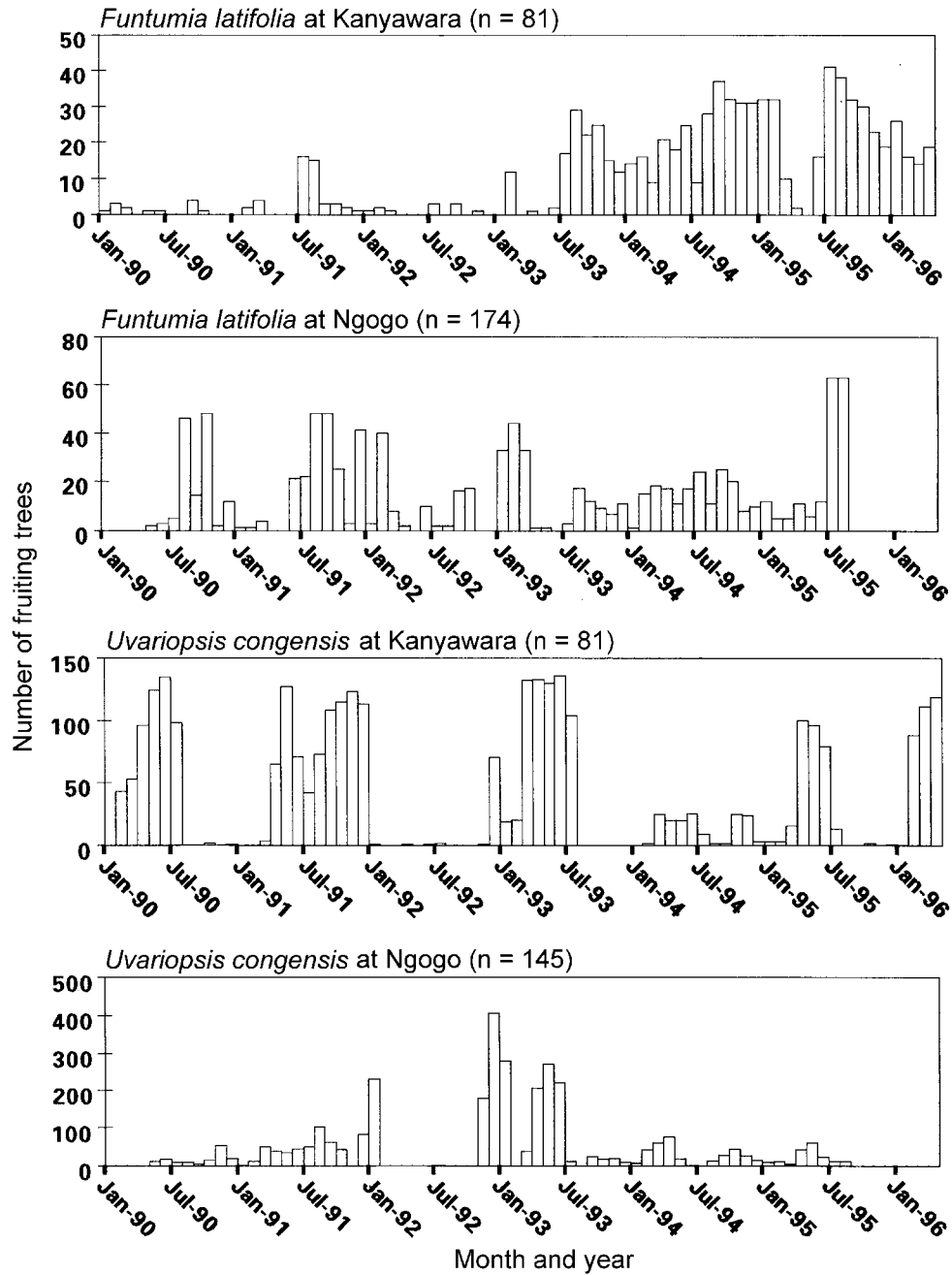


Figure 4—continued

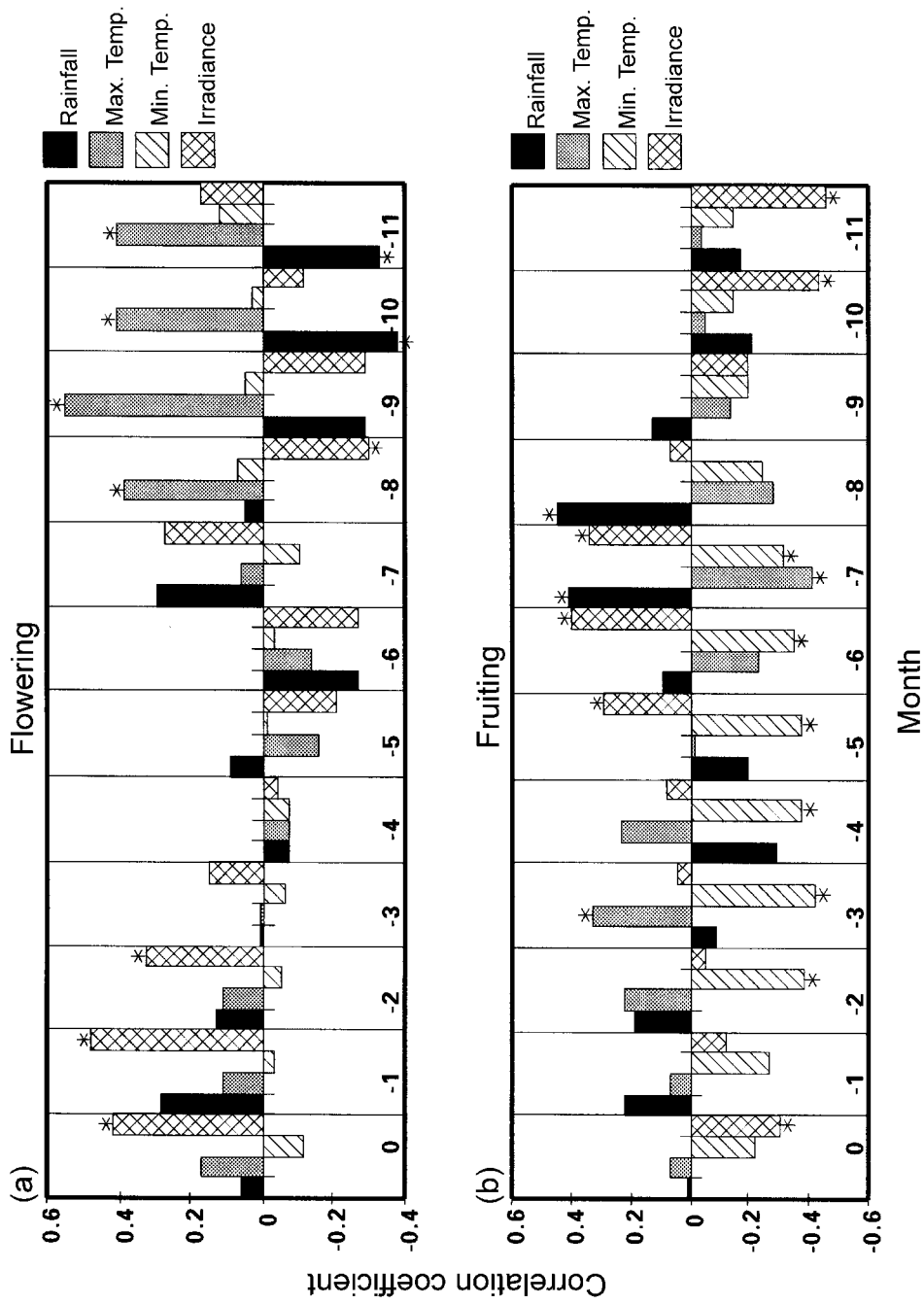


Figure 5. Strength of relationship (r values) between the density of (a) fruiting and (b) flowering trees (number of trees ha^{-1}) at the Kanyawara field site in Kibale National Park, Uganda and rainfall, average maximum and minimum temperatures and irradiance for that month and for each previous month from 1 to 11 months prior. Significant r values ($P < 0.05$) are indicated by *.

studies in either of these forest types have been conducted in areas with one wet season. In areas with two wet seasons per year, the fitness cost of delaying flowering or fruiting to the next appropriate season may be relatively less than it would be in areas with only one wet season.

Researchers are often interested in community-level patterns of fruiting and flowering, since this represents the food supply for frugivores and nectivores, the competitive environment for recruitment of trees, and the basis for viewing the fruiting or flowering of particular species. Community-level fruiting at Kanyawara was variable, but it tended to peak when the first rainy season was ending and dry season was beginning. In contrast, at Ngogo there was little evidence of predictable seasonal cycles in fruiting. Researchers have previously suggested that some animal-dispersed fleshy-fruited species have their peak fruiting period during the rainy season, perhaps due to an increased moisture level necessary for fruit production (Foster 1982a,b; Janzen 1967, Karr 1976, Lieberman 1982, Rathke & Lacey 1985). The fruiting of trees at the end of the first wet season and the start of the dry season at Kanyawara and the absence of a predictable fruiting pattern at Ngogo, may indicate that biannual rainfall reduces water stress to a level much lower than more seasonal habitats where the majority of these previous studies have been conducted (e.g., Costa Rica, Panama, Ghana).

Community-level flowering at both Kanyawara and Ngogo showed 12-mo peaks. The time of the greatest density of flowering trees was variable, but tended to occur when the first rainy season was ending and dry season was beginning. The density of flowering trees at Kanyawara was over twice that of Ngogo. Previous research, concentrated in Central America, has documented large geographical variations in flowering patterns (Borchert 1980, 1996; Newstrom *et al.* 1994b). In some species, lack of moisture in the dry season may inhibit flowering (Borchert 1980, 1986; Reich & Borchert 1984). The fact that many species and individuals are flowering at the start of the dry season in Kanyawara and Ngogo suggests that, as with fruiting, biannual rains may reduce water stress.

At Kanyawara the minimum temperature in the previous dry season is correlated with the number of trees that fruit. 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 within a species is often highly variable which suggests that this pattern is not entirely mediated by flower production, but rather by some factor that directly influences fruit production. Newbery *et al.* (1998) found that the minimum dry season temperature was related to the fruiting of 16 species monitored in Korup National Park, Cameroon. Korup has only one wet season. Temperature has also been demonstrated to correlate with flowering of dipterocarp forests of

Southeast Asia which have various rainfall patterns (Richards 1996, Wycherley 1973). Thus, correlations between minimum temperature and phenological patterns is not limited to locations with biannual rainy seasons. 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 the tree, permitting the build-up the assimilates needed for fruiting.

Flowering at Kanyawara seemed to follow immediately after peak periods of irradiance. This pattern seems common in both weakly seasonal and strongly seasonal forests (Wright & van Schaik 1994). Van Schaik *et al.* (1993) suggest that the young leaves that are abundant when irradiance is at peak levels are most efficient at photosynthesis and at controlling transpirational water loss. At this time, it is energetically most efficient to transfer assimilates directly into growing organs, in this case flowers, rather than storing them for later allocation (van Schaik *et al.* 1993).

Intraspecific synchronization was evident in flowering for all species at Ngogo and for 64% of those at Kanyawara. Fruiting was synchronous for 64% of the species at both sites. Despite this synchronization, many species did not fruit or flower at specific times of the year. And, for a number of species the timing of fruiting or flowering events differed between Ngogo and Kanyawara. For some species, trends suggested from one year of data (e.g., fruiting occurs in the dry season), were not supported when additional years of data were considered. The high level of synchronization, coupled with peak flowering and fruiting occurring during one period of the year, would suggest that either an annual pattern would be commonly seen, or a supra-annual pattern. Trees with a supra-annual pattern of reproduction would tend to skip a fruiting or flowering season. These observations are consistent with the idea that in areas that have two wet seasons, the fitness cost of delaying flowering or fruiting to the next appropriate season is relatively less than it would be in areas with annual rains. Supra-annual patterns of fruiting and flowering were commonly observed for trees in both areas (Ngogo fruiting 57%, flowering 21%; Kanyawara fruiting 42%, flowering 25%). In contrast to the data from Kibale, supra-annual patterns were only observed in 9% of the trees at La Selva, Costa Rica (Newstrom *et al.* 1994a).

At both sites within Kibale the pattern of fruiting and flowering usually differed. In fact at Kanyawara, *Leptonychia mildbraedii* was the only species that showed the same periodicity for fruiting and flowering (12-mo). The 10 other species analysed all showed differing patterns. For example, *Celtis durandii* had an irregular flowering pattern, but had 12-mo fruiting peaks. These two reproductive events, pollination versus seed dispersal, are under different selective pressures. Further, fruiting does not necessarily follow flowering events if pollination fails, or if young fruits are aborted or destroyed. For example, *M. lutea*

had very different flowering and fruiting cycles. This may be attributed to the fact that most flowers are eaten by primates leading to few flowers maturing to fruits (Struhsaker 1978). Finally, fruit maturation can be delayed after pollination and different species can take different times to ripen their fruit according to light and moisture availability. This can lead to different fruiting and flowering periodicities.

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