Factors Influencing Tree Phenology in Taï National Park, Côte d'Ivoire[1]

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ABSTRACT

Entrained phenology patterns of tropical trees are expected to be sensitive to short-term fluctuations in typical rainfall and temperature. We examined 47 mo of data on the flowering, fruiting, and new leaf phenology for 797 trees from 38 species in the Taï National Park, Côte d'Ivoire. We determined the timing of the phenology cycles in relation to seasonal rainfall, temperature, and solar radiation. Regression analysis was used to examine how variations in rainfall and temperature influenced deviations in the peaks and troughs of phenology cycles. We also investigated whether populations that fruit during periods of community-wide fruit scarcity were those populations with relatively long- or short-fruiting duration. Flower, fruit, and leaf-flushing phenophases all exhibited 12-mo cycles. The broad peak in flowering began with the northward zenithal passing in April and ended with the southward zenithal passing in September. Fruiting peaks occurred in the long dry season, and leaf flushing peaked in the long dry season but continued into the wet season. Deviations from phenology cycles were largely attributable to short-term fluctuations in rainfall and/or temperature. Fruiting durations of species were related to the mean diameter at breast height. Species with long- and short-fruiting durations contributed equally to fruit abundance during periods of community-wide fruit scarcity.

RESUME

On s'attend à ce que les modèles phénologiques des arbres tropicaux soient sensibles aux fluctuations à court terme aux précipitations et température typiques. Nous avons examiné 47 mois de données sur la floraison, la fructification, et la phénologie de nouvelles feuilles pour 797 arbres de 38 espèces dans le Parc National de Taï, Côte d'Ivoire. Nous avons déterminé comment les cycles phénologiques ont été orientés par rapport aux changement saisonniers des précipitations, de la température, et du rayonnement solaire. L'analyse de régression a été adoptée pour examiner comment les variations des précipitations et de la température ont influencé les déviations dans les pics et les creux des cycles phénologiques. Nous avons également étudié si les populations qui portent des fruits pendant des périodes de pénurie de fruit à l'échelle communautaire étaient des populations à durée de fructification relativement longue ou courte. Les phénophases de floraison, de fructification et de feuillaison ont toutes montré les cycles de douze mois. Le large pic dans la floraison a commencé avec le passage zénithal du nord en avril et pris fin avec le passage zénithal du sud en septembre. Les pics de fructification se sont produits pendant la longue saison sèche, et le rougissement des feuilles a eu un pic pendant la longue saison sèche mais a continué en saison des pluies. Les déviations des cycles de phénologie étaient en grande partie attribuables aux fluctuations à court terme dans les précipitations et/ou la température. Les durées des fructifications des espèces étaient liées au diamètre moyen à hauteur de poitrine. Les espèce à longue et courte durée fructification ont contribué également à l'abondance de fruit pendant des périodes de pénurie de fruit à l'échelle communautaire.

TROPICAL TREE COMMUNITIES DEMONSTRATE SUBSTANTIAL SEASONALITY in flowering, fruiting, and leaf-flushing events (Terborgh 1986, van Schaik *et al.* 1993, Sun *et al.* 1996, Chapman *et al.* 1999). Most community-wide phenological cycles are expected to follow a 12-mo, or a multiple of 12-mo cycle. However, semiannual (twice per year) peaks in phenophases are possible in the tropics because the sun passes overhead twice each year, influencing insolation rates and weather patterns. Over evolutionary time, biotic and abiotic factors have entrained a cyclic rhythm in plants, which results in flowering, fruiting, and leaf flushing at times that maximize their reproductive success. Phenological patterns may be influenced by the temporal abundance of pollinators, seed dispersers, seed predators, or herbivores (Frankie *et al.* 1974, Rathcke & Lacey 1985, Wheelwright 1985, Aide 1992, Murah & Sukumar 1993,

Curran & Leighton 2000); or by predictable temporal variations in rainfall, temperature, radiation, and photoperiod (Opler *et al.* 1976, Ashton *et al.* 1988, Tutin & Fernandez 1993, Chapman *et al.* 1999, Borchert *et al.* 2002, Rivera *et al.* 2002, Williamson 2002).

Deviations from a typical phenology cycle for a community or population of trees are commonly observed, but are not well understood (Chapman *et al.* 2004). In response to short fluctuations in environmental conditions, plants may vary the start time, intensity, and duration of the phenophase. The intensity of a given phenophase is expected to vary more than the duration or the start time of the phenophase, because the timing of one phenophase will affect that of the other phenophases. For example, if the initiation of flowering is delayed, the timing of fruiting will be offset as well, and may not coincide with optimal fruiting conditions. Consequently, if conditions were not favorable for flowering, it may be more advantageous for a plant to reduce the flowering intensity than to delay flowering until conditions improve. The phenophase

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response of plants may be sensitive to the conditions at the time of the phenophase, or to the conditions in the preceding months (Tutin & Fernandez 1993, Chapman *et al.* 1999).

Phenology cycles and deviations from entrained patterns may be influenced by the potentially interacting effects of radiation, rainfall, and temperature. Flowering and the flushing of new leaves should coincide with high insolation, to take advantage of high photosynthetic activity (Opler *et al.* 1976, van Schaik 1986, van Schaik *et al.* 1993, Wright & van Schaik 1994, Chapman *et al.* 1999). Flowering and leaf flushing may be more sensitive to seasonal rainfall where water is limiting plant production (Borchert 1983, Lieberman & Lieberman 1984, van Schaik *et al.* 1993). High water availability may also enhance fleshy fruit production (Lieberman 1982, Rathcke & Lacey 1985) and germination success (van Schaik *et al.* 1993, Justiniano & Fredericksen 2000). Similarly, temperature may act directly on flowering and fruiting (Tutin & Fernandez 1993, Newbery *et al.* 1998, Chapman *et al.* 1999), or as an environmental cue that induces community-wide phenological events (Ashton *et al.* 1988).

Frugivorous animals depend on the temporal distribution of fruit production; therefore, it is important to understand the attributes of tree species that produce fruits during periods of community-wide fruit scarcity. Evidence from Uganda suggests that fruiting peaks in mid-story and emergent trees may be offset temporally, and consequently, both the groups are essential for providing a continuous food supply for vertebrate frugivores (Chapman *et al.* 1999). The large storage capacity of carbon and water may permit large trees to have long-fruiting durations that extend through the period of community-wide fruit scarcity.

We examined 47 mo of data on the flowering, fruiting, and leaf-flushing phenology for 797 trees from 38 species in the Taï National Park, Côte d'Ivoire. We fitted sine and cosine wave functions to the phenophases to identify cyclic patterns (semiannual, annual, or supra-annual), to examine the timing of the cycles in relation to seasonal variations in rainfall and temperature. We also examined how monthly variations in rainfall and temperature increased or decreased the phenophase peaks and troughs. Environmental fluc-

tuations occurring up to 19 mo prior to the examined phenophase were also considered. Although we did not collect data on solar radiation, we did examine whether the solar zenithal position was associated with the cyclic pattern of the three phenophases. Finally, we investigated whether the mean tree size for each species was related to its mean duration of fruiting events, and whether those species with long-fruiting duration produced fruits during periods of fruit scarcity in the forest.

METHODS

STUDY SITE.—The study site was located on the western border of the Taï National Park in the Ivory Coast (5°52′N, 7°20′W). The Taï forest was the largest remaining tract (4500 km^2) of undisturbed lowland rain forest in West Africa (Boesch & Boesch-Achermann 2000). The study site was situated at *ca* 120 m a.s.l., and was characterized by rolling-hill topography. Range in relief in the study area was *ca* 40 m. Drainage was related to topography, with increased moisture availability on the lower slope from lateral drainage and finer soil texture (Lescure & Boulet 1985, de Rouw 1991).

METEOROLOGICAL DATA.—Rainfall and temperature data were collected from July 1995 to December 1999 (Noë, pers. comm.). Data were collected daily at 0700 h in a forest opening within the Taï forest *ca* 2 km from the study site. Rainfall was collected and measured by a rain gauge. Daily maximum and minimum temperatures were measured by a maximum–minimum thermometer placed in a thermometer shelter. The climate at Taï is characterized by two wet seasons (April–June and September–October) and two dry seasons (July–August and November–March) and mean rainfall of 1893 mm/yr (Fig. 1). The mean minimum and maximum temperatures were 21.7°C and 30.1°C, respectively, and there was substantial monthly and annual variation in rainfall. At Taï, the northward zenithal passing of the sun occurs in early April and the southward zenithal passing is in early September. These two events coincided with two separate wet seasons.
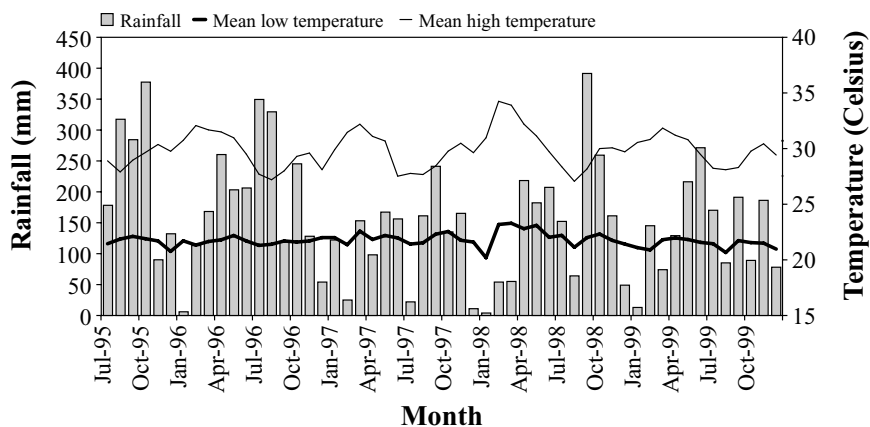

FIGURE 1.   Monthly rainfall, mean minimum and maximum temperatures from Taï National Park for July 1995–December 1999.

PHENOLOGY.—Phenology observation routes (*sensu* Malenky *et al.* 1993) were established along access trails that covered an area of *ca* 12.5 km². We marked and observed, monthly, 797 individual trees from 38 species (Appendix 1). Each species was represented by at least seven individual trees. Because this research was part of a chimpanzee ecology study, all the tree species included in this analysis were chosen because their fruits are consumed by chimpanzees. The majority of species produced fleshy fruits (32 out of 38), while only four species produced dehiscing leguminous pods and two species were wind-dispersed samaras. Trees were selected along the phenology routes if they appeared to be healthy, had a canopy visible to the observer, and were of reproductive size.

During the period between February 1997 and December 2000, we returned to each tree, monthly, and noted the presence or the absence of ripe fruits and/or flowers. Trees were considered to be in either fruit or flower stage if there was more than a nominal amount of fruits/flowers in the canopy. We differentiated between ripe and unripe fruit; unripe fruit was not considered in this analysis. Trees were counted as being in flower mode if they presented either buds or open flowers. Phenology observations began on leaf phenology in February 1998 and continued till December 2000 (35 mo). A tree was considered to be in flushing leaves mode if 25 percent or more of the leaves in the canopy were new leaves. Phenology observations were conducted over a 7-d period in the middle of each month.

To quantify changes in fruit abundance, we calculated an index that incorporated the fruit phenology data with data on the density and basal area of the studied tree species. Separate from the phenology routes, we placed seven long parallel belt transects of 4100 × 10 m in the north–south direction, 500 m apart (see Anderson *et al.* 2002). In addition, multiple short belt transects of 400 × 10 m were put in between each of the long belt transects to increase the sampling area. A total of 47.1 km of transects were sampled, covering an area of 47.1 ha. We measured the density and basal area of all trees with a diameter at breast height (DBH) ≥ 10 cm.

ANALYSIS.—We quantified each of the phenophases for each month of the study as the percentage of species that were flowering, fruiting, or flushing new leaves. A species was considered in a particular phenophase if one or more of the sampled individuals were in the phenophase. This approach gives similar results as those obtained when a species is considered in a phenophase only if at least 25 percent of sampled trees are in the corresponding phenophase (Sun *et al.* 1996).

For fruit phenology, we also calculated a fruit abundance index as an estimate of how much fruit was in the study area in each month. The food abundance index A_m for month m is defined as follows:

$$A_m = \sum_{k=1}^{n} D_k B_k P_{km},$$

where D_k is the density of species k across the study area; B_k is the mean basal area of species k across the study area; and P_{km} is the percentage of observed trees of species k presenting ripe fruits in month m.

To determine the periodicity of the phenophases, we used regression analysis to fit cosine and sine wave functions to the percentage of species in each of the phenophases over time. We used as predictor variables, the cosine and sine wave functions with periodicities of 6, 12, and 24 mo. The sine (X_{sp}) and cosine (X_{cp}) wave functions of period p were calculated as follows:

$$X_{sp} = \mathrm{Sin} \left(\frac{2\pi t}{p} \right)$$

$$X_{cp} = \mathrm{Cos} \left(\frac{2\pi t}{p} \right),$$

where t is the month of the study (ranging from 1 to 47). The sine and cosine functions of a given periodicity (p) were always entered into or removed from regression models as a pair. For example, if the sine function (X_{sp}) was a significant predictor of a particular phenophase, but the cosine function (X_{cp}) was not, then both functions were kept in the model. The reason why both terms are needed is to allow a flexible location of peaks and valleys. A model with a cosine term alone would force the maxima to occur at $t = 0$, $t = p$, $t = 2p$, *etc.*; and minima at $t = p/2$, $t = 3p/2$, *etc.* The effect of using the sine term alone would be similar. By including both terms, the fitted coefficients for the two terms allow the data to determine where the peaks occur. This is often referred to as the "phase."

The best predictive regression model was sought for each phenophase: the percentage of species in flower, fruit, flushing leaves, and fruit abundance. In addition to determining the cyclic nature of the phenophases, the relative predictive capabilities of monthly rainfall and monthly mean minimum and maximum temperatures were also explored. We considered not only the effects of rainfall and temperature on the phenophases in the current month, but also in the preceding months, up to 19 mo before the current month.

In order to determine the months in the preceding 19 mo that were important, we put each of the meteorological variables into blocks of 3 mo. For example, if $t_k =$ current month and $t_{k-1} =$ the preceding month, then the months were put into blocks as follows: t_k, t_{k-1}, t_{k-2}; and t_{k-1}, t_{k-2}, t_{k-3}; and ... t_{k-17}, t_{k-18}, t_{k-19}. The regression analysis was repeated using each time block independently. If a time block was significant ($\alpha = 0.05$), we focused on that time period and expanded and reduced the number of months in the time block, until we were able to determine the months that resulted in the model with the best fit.

Regression analyses were conducted using the Proc GLM procedure of SAS 8 (SAS Institute Inc. 1999). We employed the Durbin–Watson statistic to test for temporal autocorrelation (Chatterjee & Price 1991). If significant autocorrelation was found at the level $\alpha = 0.05$, then an autoregressive order 1 covariance structure (Box *et al.* 1994) was incorporated into the regression model using the Proc Mixed procedure of SAS, and Type III tests of fixed effects were used to determine the significant covariates (Littell *et al.* 1996). For each analysis, all possible interaction effects between independent variables were explored.

The duration of a fruiting event for a given species was measured as the time in months, from the first to the last month fruit

was seen on that species. If two fruiting months were separated by one nonfruiting month, the nonfruiting month was considered as a recording error and counted as a fruiting month. However, if two consecutive nonfruiting months separated two fruiting events, then the second fruiting event was considered independent from the previous one. The mean duration of fruiting events for each species was calculated as the average duration (in months) of all fruiting events for that species over the 47-mo period. *Syzygium owariense* and *Daniellia thurifera* were removed from this analysis as they were never in fruit during this study. Regression analysis was conducted to determine whether there was a relationship between the average size of a tree species, as measured by the mean DBH, and the mean duration of fruiting events.

We determined the peak fruiting months for each species. This was defined as the month(s) in a fruiting event that had the highest percentage of individuals in fruit. For example, if a particular species was in fruit from January through March, and the highest percentage of individuals of that species was in fruit in February, then February would be considered the peak fruiting month for this fruiting event. Most species (31 out of 38) had more than one fruiting event during the study; and for many species, the peak fruiting month was different in their separate fruiting events. If 2 mo in the same fruiting event had the same highest percentage of individuals in fruit, then both months were considered as peak months. Using the data on the peak fruiting months, we compared graphically the timing of peak fruiting events between species with short- and long-fruiting durations. To classify each species as having short- or long-fruiting duration, we examined a histogram of fruiting duration to identify a natural break among species.

RESULTS

The 38 tree species monitored in this study represent 16 percent of the species measured in the transects (47.1 ha). While this is a relatively low percentage of total species, the monitored species are relatively common and represent 55 percent of the stems measured and 54 percent of the total basal area.

The variables that best predicted the percentage of species in flower in a given month were the cosine and sine functions with a periodicity of 12 mo, and the mean minimum temperature in the preceding 4–7 mo (Table 1). An autoregressive order 1 covariance structure was incorporated into this model, as the Durbin–Watson

autocorrelation statistic was significant ($d = 0.932$, $N = 39$ mo, $P < 0.05$). Due to missing meteorological data in the year 2000, the phenology data used in this analysis were restricted to the period between February 1997 and April 2000 (39 mo). When the cosine and sine functions were fitted to the phenology data without the temperature data, the regression line predicted that peak flowering should occur in July (during the short dry season; Fig. 2a). However, the peaks never occurred in July, but rather in April and September. The flowering peaks in April and September coincided with the solar zenith at Taï. The cosine/sine curve encompassed both of these peaks, and consequently predicted that a peak should occur in July. When the mean minimum temperature in the preceding 4–7 mo was added to the model, the predictive capability of the model was improved. The model predicted a peak in flowering in April and May 1999, but flowering was very low at this time.

The variables that best predicted the percentage of species bearing ripe fruit were the cosine and sine functions with a periodicity of 12 mo, the cumulative rainfall in the preceding 12–15 mo, and the mean minimum temperature in the preceding 2–5 mo (Table 2). An autoregressive order 1 covariance structure was built into this model, as the Durbin–Watson autocorrelation statistic was significant ($d = 1.33$, $N = 37$ mo, $P < 0.05$). This regression model accurately predicted fruiting peaks in December and January (Fig. 2b). However, the model did not predict well the reduced fruit production in December 1998 and January 1999. The percentage of species in fruit began to increase in the short wet season of September and October, and peaked in the middle of the long dry season. By the end of the dry season in March, the percentage of species in fruit had begun to or had already decreased substantially. While the cosine and sine functions predicted that the troughs in fruiting should occur in June and July, the observed troughs occurred in May in each year of the study.

Fruit abundance (A_m) was best predicted by the cosine and sine functions with periodicity of 12 mo, the cumulative rainfall in the preceding 4–7 mo, and the mean minimum temperature in the preceding 10–13 mo ($R^2 = 0.72$, $N = 39$ mo, $P < 0.0001$). Fruit abundance was negatively related to rainfall in the preceding 4–7 mo, and positively related to the mean minimum temperature in the preceding 10–13 mo (Table 3). The Durbin–Watson autocorrelation statistic was nonsignificant ($d = 2.33$, $N = 39$ mo, $P > 0.05$); therefore a standard regression model was applied. The timing of peaks in fruit abundance corresponded (Fig. 2c) to the peaks in the percentage of species with ripe fruit (Fig. 2b), which were centered in the long dry season (November–March). The period of low fruit abundance varied interannually, but tended to occur between the end of the wet season and continued through the end of the short dry season (May–August).

The percentage of species that were flushing new leaves in a given month was best predicted by the cosine and sine functions with periodicity of 12 mo, the mean minimum temperature in the current month and the preceding 1–3 mo, and the cumulative rainfall in the preceding 7–10 mo ($R^2 = 0.85$, $N = 23$ mo, $P < 0.0001$). Rainfall in the preceding 7–10 mo had a negative relationship with leaf flushing, while the relationship with the mean maximum

TABLE 1. *Significant predictor variables of the percent of species in flower in a given month. All potential interaction effects between independent variables were nonsignificant. Presented results are from a type III test of fixed effects.*

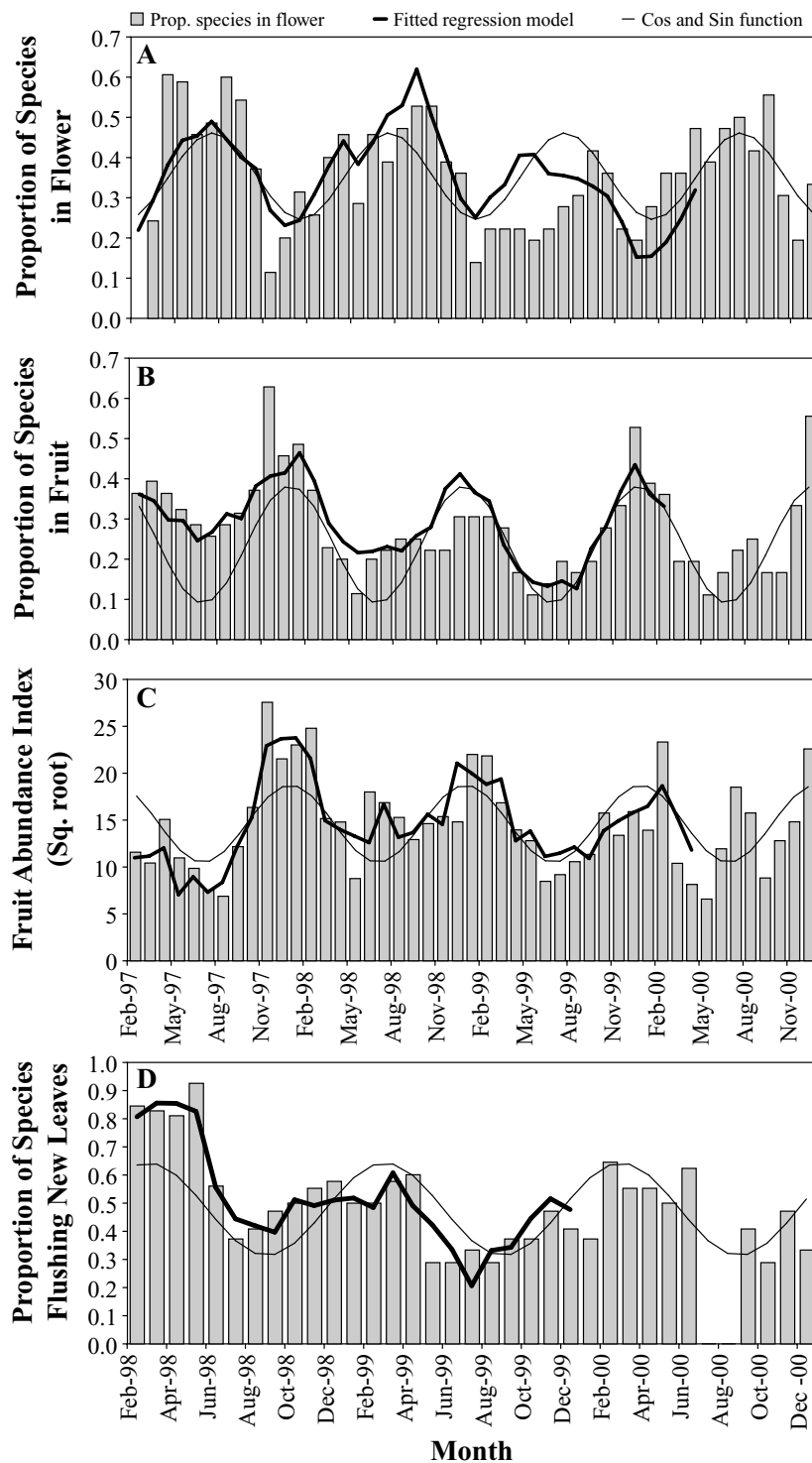| Source	Coefficient	N	F-value	P-value
Mean min. temp. in the preceding 4–7 mo	0.0495	39	8.27	0.0068
$X_{cp} = \cos(\frac{2\pi t}{12})$	−0.1051	39	7.44	0.0099
$X_{sp} = \sin(\frac{2\pi t}{12})$	0.04291	39	1.08	0.3067

FIGURE 2.   Two regression lines predicting the phenophase in each month of the study. The thin line in each of the graphs is the model that includes only the cosine and sine functions with a periodicity of 12 mo, which demonstrates the entrained phenology cycles. (a) Predicting of the proportion of species presenting flowers, and the bold line is the model that includes mean minimum temperature in the preceding 4–7 mo as well as the cosine and sine functions in the. (b) Predicting the proportion of species bearing ripe fruit, and the bold line is the model that includes mean minimum temperature in the preceding 2–5 mo, rainfall in the preceding 12–15 mo, and the cosine and sine functions. (c) Predicting the fruit abundance index, and the bold line is the model that includes mean minimum temperature in the preceding 11–13 mo, rainfall in the preceding 4–7 mo, and the cosine and sine functions. (d) Predicting the percentage of species flushing leaves, and the bold line is the model that includes mean minimum temperature in the preceding 1–3 mo, rainfall in the preceding 7–10 mo, and the cosine and sine functions.

TABLE 2. *Significant predictor variables of the percentage of species in fruit in a given month. All potential interaction effects between independent variables were nonsignificant. Presented results are from a type III test of fixed effects.*

Source	Coefficient	N	F-value	P-value
Mean min. temp. in the preceding 2–5 mo	0.03058	37	6.67	0.0148
Rainfall in preceding 12–15 mo	0.000298	37	9.23	0.0047
$X_{cp} = \cos(\frac{2\pi t}{12})$	0.1656	37	29.53	0.0001
$X_{sp} = \sin(\frac{2\pi t}{12})$	0.03227	37	0.99	0.3280

TABLE 3. *Significant predictor variables of the fruit abundance index in a given month. All potential interaction effects between independent variables were nonsignificant. Presented results are from a type III test of fixed effects.*

Source	Coefficient	N	F-value	P-value
Mean min. temp. in preceding 10–13 mo	31.966	39	21.71	<0.0001
Rainfall in preceding 4–7 mo	−0.9718	39	33.26	<0.0001
$X_{cp} = \cos(\frac{2\pi t}{12})$	9.2089	39	76.69	<0.0001
$X_{sp} = \sin(\frac{2\pi t}{12})$	−2.19619	39	10.34	0.0028

temperature in the current and the three preceding months was positive (Table 4). An autoregressive covariance structure was not used in this analysis as the Durbin–Watson autocorrelation statistic was nonsignificant ($d = 2.42$, $N = 23$ mo, $P > 0.05$). A square root transformation was performed on the dependent variable in order to stabilize the variance. The sample size of this analysis was smaller than the preceding analyses, because we began the data collection of leaf phenology 1 yr after the fruit and flower phenologies were initiated. Furthermore, because leaf flushing in a given month was related, at least in part, to the mean minimum temperature in that month, the analysis ended where the data collection on the meteorological variables stopped.

The peak in leaf flushing varied substantially from year to year, but tended to occur between February and June (Fig. 2d). This

TABLE 4. *Significant predictor variables of the percentage of species flushing new leaves in a given month. All potential interaction effects between independent variables were nonsignificant. Presented results are from a type III test of fixed effects.*

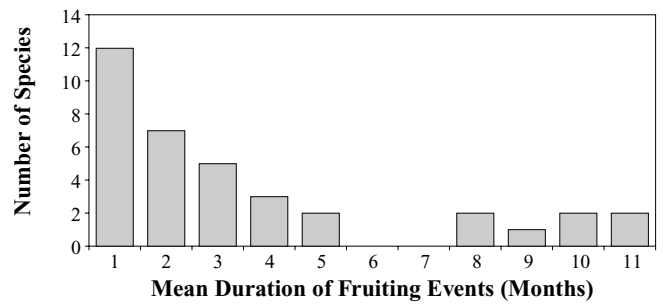| Source	Coefficient	N	F-value	P-value
Mean min. temp. in current and preceding 1–3 mo	0.03256	23	16.54	0.0007
Rainfall in preceding 7–10 mo	−0.0005898	23	24.84	<0.0001
$X_{cp} = \cos(\frac{2\pi t}{12})$	0.08714	23	14.67	0.0012
$X_{sp} = \sin(\frac{2\pi t}{12})$	0.01717	23	0.06	0.8150

FIGURE 3.   Histogram displaying the number of species in each category of mean fruiting duration. The 36 analyzed species fall into one of two groups: short- or long-fruiting duration.

coincided with the end of the long dry season and the entire wet season (Fig. 1). The cosine and sine functions, without the weather variables in the model, predicted peaks in the percentage of species with young leaves in February and March (end of long dry season), and troughs in August and September (end of short dry season). Deviations from the cosine/sine cycle were largely accounted for by the inclusion of meteorological variables in the regression model (Fig. 2d).

Results of regression of the mean duration of fruiting events against the mean DBH of each species demonstrated a significant positive relationship ($R^2 = 0.22$, $N = 36$ species, $P = 0.0036$). Most species had a mean fruiting duration of less than or equal to 5 mo, but a distinct group of seven species had a much longer fruiting duration (Fig. 3; Appendix 1). Based on this natural break in the frequency distribution of fruiting duration, we divided all of the tree species into two groups: the first were the species with mean fruiting duration of ≤5 mo; and the second were the seven species with a mean fruiting duration of >5 mo. Species with a short mean fruiting duration tended to have their fruiting peaks in the long dry season (November–February; Fig. 4). Six of the seven species with long-fruiting duration had a fruiting peak in the month of June. Otherwise, the fruiting peaks for long-fruiting group were spread throughout the year. However, when the relative contribution of the
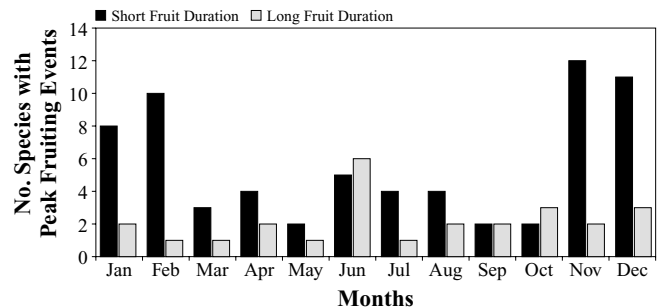

FIGURE 4.   The number of species that had peak fruiting events in each month of the year. White columns are species with relatively short-fruiting durations, and black columns are species with long-fruiting durations.
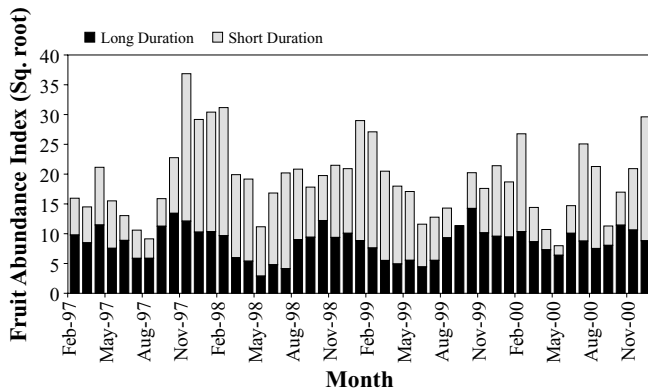
FIGURE 5.   Fruit abundance index for each month of the study, illustrating the relative contribution of species that have short-fruiting duration (white), versus species with long-fruiting duration (black).

two groups to the fruit abundance index was examined over time, it was apparent that both groups had troughs in fruit abundance beginning at the end of the wet season and continuing through the short dry season (May–August; Fig. 5).

DISCUSSION

Consistent and predictable annual cycles in the biotic and abiotic factors that affect tree growth and reproduction over evolutionary time are expected to shape tree phenology patterns. The flower, fruit, and leaf-flushing phenophases examined in this study all demonstrated significant 12-mo periodicity in their cycles. Deviations from the typical cycle were largely attributable to short-term fluctuations in rainfall and/or temperature. The selection of monitored tree species was biased in that the fruits of all species were consumed by chimpanzees; however, these species represent the majority of stems and basal area of trees in the forest. Therefore, we are confident that the tree phenology patterns presented here reflect the dominant patterns in the forest.

FLOWERING PHENOLOGY.—The broad peak in flowering began with the northward zenithal passing of the sun in early April, and ended with the southward zenithal passing in early September, which supports the insolation–limitation hypothesis (van Schaik et al. 1993). Although these peaks coincided with wet periods, the percentage of trees flowering remained relatively high throughout the short dry season. The water stress in the short dry season may not have been high enough to inhibit flowering, which is consistent with findings in other habitats with semiannual wet seasons (Sun et al. 1996, Chapman et al. 1999). However, the observation that the percentage of species in flower was lowest in the long dry season, when water stress was greatest (Fig. 1), suggests that flowering may be inhibited by water stress, as has been observed in tropical dry forests (Borchert 1983, Borchert 1994). Deviations from the typical annual flowering phenology cycle were partially attributable to

fluctuations in the mean minimum temperature in the preceding 4–7 mo. Therefore, individuals within a species may have synchronized flowering because of the temperature cue (Tutin & Fernandez 1993, Chapman et al. 1999).

FRUITING PHENOLOGY.—Fruiting phenology is partially, but not entirely contingent on the flowering phenology. The time interval between pollination and fruit maturation varies between species (Chapman et al. 1999), and several biotic and abiotic factors may inhibit fruit maturation. There were multiple instances in this study where flowering events were not followed by fruiting events. S. owariense and D. thurifera both flowered several times, but neither of them ever fruited.

The fitting of the cosine and sine functions to both the percentage of species in fruit and the fruit abundance index demonstrated that fruiting peaks occurred consistently in the long dry season (November–February). Fruiting began to increase with the onset of the wet season in September, but the peaks in fruiting consistently occurred in the dry season (Fig. 2b and c). This is similar to the patterns observed in Rwanda (Sun et al. 1996), but is not in accordance with other phenology studies in the tropics in which fruiting peaks have been reported to occur in the wet season (Foster 1982, Terborgh 1983, Heideman 1989, Tutin et al. 1991, Chapman et al. 1999). The pattern at Taï does not support the hypothesis that high water availability is necessary at the time of fruiting to enhance fruit maturation (Lieberman 1982, Rathcke & Lacey 1985) and germination success (assuming no seed dormancy; van Schaik et al. 1993, Justiniano & Fredericksen 2000). An alternative possibility is that dry periods result in increased defoliation and tree mortality, which could improve conditions for seedling recruitment in the understory (Williamson 2002).

The phenology patterns of the percentage of species in fruit and the fruit abundance index were very similar; however, these cycles were sensitive to weather variables at different times. The difference between these two response variables is the fruit abundance index factors in population densities and mean basal area of all the tree species. Consequently, the temporal variation in fruit abundance should be greatly influenced by the phenology of relatively common and/or large-sized species. Rainfall in the preceding 12–15 mo had a positive relationship with the percentage of species in fruit, whereas there was a negative relationship between rainfall in the preceding 4–7 mo and the fruit abundance index. This finding suggests that the severity of the preceding dry season influenced the percentage of species that would fruit, and that the fruiting response of species (fruit abundance index) was sensitive to rainfall in the preceding 4–7 mo. We found that both the percentage of species in fruit and the fruit abundance index were positively related to the mean minimum temperature in the preceding months, contrary to a negative relationship in Uganda (Chapman et al. 1999). The effect that temperature has on fruiting may be secondary to its effect on flowering. Both rain and temperature were nonsignificant predictors of fruiting when the cosine and sine functions were removed from the regression model. This suggests that they were not the primary factors influencing fruiting, but that they did explain deviations from the normal annual fruiting cycle.

LEAF PHENOLOGY.—The fitting of the cosine and sine functions to the percentage of species flushing new leaves demonstrated a consistent annual peak beginning in the long dry season and extending into the wet season (February–April). Most leaf fall is expected to occur during times of high water stress (Borchert 1992); at Taï, this was from November to March (Fig. 1). Leaf flushing in the dry season, when water stress is still high, before the seasonal increase in insect biomass, may be a plant adaptation to minimize herbivory on young vulnerable leaves (Aide 1992, Murah & Sukumar 1993, Coley & Barone 1996). Herbivorous insect biomass is greatest in the wet months (due to susceptibility to desiccation in dry months), and predictably, leaf damage by insects has been shown to be greatest in the wet months (Aide 1992, Murah & Sukumar 1993).

The insolation–limitation hypothesis predicts that leaf flushing should coincide with periods of high solar irradiance (van Schaik *et al.* 1993). The leaf-phenology pattern at Taï does not support this hypothesis, as peak leaf flushing begins 2 mo before the solar zenith. However, short-term cloud cover can greatly influence insolation rates, and as the solar zenithal position of the sun coincides with the wet season, clouds may reduce insolation rates at the zenith. Because we did not directly measure irradiance, we could not account for this possibility. However, anecdotally, we were able to charge batteries using solar panels much faster in the wet season than in the dry season. This may be explained by the higher angle of the sun in the sky, and our observation that heavy rainfall was often preceded by several hours of very intense sunlight. In contrast, high diffuse clouds often dominated the dry-season sky.

FRUITING DURATION.—We examined the hypotheses that the fruiting duration of a species was related to its mean DBH, and that large trees were fruiting during the period of fruit scarcity. As expected, trees with short-fruiting duration tended to have peak fruiting months in the long dry season, which corresponds to the pattern exhibited by all monitored species. Although large trees had long-fruiting durations and distributed their fruiting peaks throughout the year, they also had troughs in fruit abundance during periods of fruit scarcity of all the sampled species (Fig. 5). There was substantial interannual variability in the relative contribution of fruit by the two groups during periods of fruit scarcity. The timing of peaks in fruit abundance was offset in the two groups: species of long-fruiting duration peak from September to November, and species of short-fruiting duration peak from November to February. Consequently, both groups are essential for providing a continuous food supply for the vertebrate frugivores in the forests, as was found in Uganda (Chapman *et al.* 1999).

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APPENDIX. *Data on the mean DBH, population density, mean duration of fruiting events, and peak fruiting months for each of the species in the phenology study. Scientific names follow the nomenclature of Lebrun and Stork (1991, 1992).*

Species	Sample size	Mean DBH	Population density (stems/ha)	Mean fruiting duration (mo)
Calpocalyx aubrevillei	25	41.292	0.764	1
Calpocalyx brevibracteatus	30	18.752	23.142	1.33
Chrysophyllum taïense	27	47.444	3.822	2
Coula edulis	42	23.425	19.363	4
Dacryodes klaineana	28	37.690	1.847	2.33
Daniellia thurifera	7	69.667	0.127	Never fruited
Dialium aubrevillei	36	48.397	4.926	5.67
Diospryos manii	34	13.894	45.648	3
Diospyros sanza-minika	29	23.921	19.193	3
Diospyros soubreana	20	12.075	20.361	2.5
Entandrophragma angolense	11	71.000	0.106	3.25
Ficus elasticoides	7	46.000	0.149	1.4

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APPENDIX. *Continued.*

Species	Sample size	Mean DBH	Population density (stems/ha)	Mean fruiting duration (mo)
Gilbertiodendron splendidum	9	29.306	5.372	1.67
Irvingia gabonensis	7	49.786	0.297	3.25
Irvingia grandifolia	11	59.045	0.234	9.67
Klainedoxa gabonensis	33	64.750	0.425	11.67
Magnistypula butayei	9	27.303	1.996	1.5
Memecylon lateriflorum	28	15.031	14.098	2
Nauclea diderrichii	31	44.048	1.104	8
Nauclea xanthophylon	31	26.808	1.656	4.75
Pachypodanthium staudtii	11	35.250	0.425	2.5
Panda oleosa	8	27.353	0.722	5
Parinari excelsa	30	76.802	0.913	8
Pentadesma butyracea	24	54.433	0.955	10
Pouteria aningeri	8	74.688	0.170	1.33
Pycnanthus angolensis	24	70.103	1.338	10.33
Sacoglottis gabonensis	34	36.571	5.117	11.67
Scotellia klaineana	23	22.647	8.832	1.6
Scytopetalum tieghemii	10	25.708	10.127	2
Sterculia oblonga	7	56.450	0.212	1.5
Strombosia pustulata	22	25.538	6.157	1.33
Synsepalum afzelii	14	24.784	1.720	1
Syzygium owariense	12	26.68	1.08	Never fruited
Tarrietia utilis	24	31.510	12.548	1
Treculia africana	10	34.556	0.191	4
Tricoscypha arborea	23	25.023	4.586	1
Uapaca esculenta	31	46.513	2.399	3.4
Uapaca guineensis	27	45.387	1.125	2