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Long-term Changes in Fruit Phenology in a West African Lowland Tropical Rain Forest are Not Explained by Rainfall

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ABSTRACT

Decreases in rainfall have been proposed to have a negative impact on tropical rain forests, and West Africa is currently experiencing a decline in rainfall at the multi-decadal scale. Here, we present analyses of a long-term dataset on the plant fruiting status from individuals of 44 species of the tropical rain forest of Taï National Park, Côte d'Ivoire. This study includes records of 1401 individuals collected at monthly intervals for over 12 yr, 984 of which survived throughout the entire study period. The aims of this study were to: (1) quantitate inter-annual trends in species and forest scale fruit presence; and (2) test the importance of rainfall in explaining inter-annual fruit presence variability. Long-term upward trends in the expected proportion of individuals with fruits were found for the majority of species, while no significant downward trends were detected, driving a significant upward trend at the community level. Peak production months of the upward trending species were not associated with the dry or wet season. Significant rainfall correlations with the total proportion of individuals showing fruit were generally negative, with only five species showing significant positive correlations. Taken together, these results suggest that the observed inter-annual trends and variability of fruit abundance are currently not associated with rainfall. We discuss several parsimonious and complex alternative explanations.

Abstract in French is available in the online version of this article.

Key words: climate change; phenophase; plant community; seasonality; Taï National Park.

Analyses of tropical forest plant community metrics such as mortality and recruitment (Phillips & Gentry 1994, Phillips *et al.* 2002), aboveground biomass (Lewis *et al.* 2004b), and fruit abundance (Chapman *et al.* 2005) all indicate systems in flux. Because of their importance for plant reproductive patterns, and as an indicator of the frugivore resource environment (van Schaik *et al.* 1993), characterizing short and long-term reproductive effort by plants provides insight into many aspects of tropical forest ecosystems and clues as to how they might respond to climate change process as currently impacting tropical forests (Lewis *et al.* 2004a, Malhi & Wright 2004, Chapman *et al.* 2005, Wild *et al.* 2005, Lloyd & Farquhar 2008).

For primary tropical forests, long-term information on patterns of plant reproductive effort is sparse, as evidenced by a recent review by Lewis *et al.* (2009a) which included only two such studies (of fruits by Chapman *et al.* 2005 and flowers and fruits by Wright & Calderón 2006). This article aims to contribute to the understanding of long-term trends in fruiting patterns in tropical forests by presenting data and analyses of fruit presence-absence data from individual plants in Taï National Park (TNP), Côte d'Ivoire. TNP is the largest contiguous protected primary lowland tropical rain forest remaining in West Africa, providing a rare opportunity to examine inter-annual fruiting patterns from mature trees in an undisturbed tropical ecosystem. Throughout this article, the term trend is used *sensu* the time series literature, and in particular we identify a trend as the long-term, persistent change in the probability of observing fruit (see equation 1 below).

Understanding how causal drivers operate to shape trends and the dynamics of fruit presence and abundance in tropical systems is a complex and multifaceted problem. Abiotic factors impacting plant physiology such as light (Wright & van Schaik 1994, Wild *et al.* 2005), temperature (Malhi & Wright 2004), atmospheric carbon (Lloyd & Farquhar 2008) and nitrogen (Hietz *et al.* 2011), and rainfall (Lewis *et al.* 2004a), are all in flux and can contribute to fruit production effort. In West African tropical forests there is evidence of increased aboveground woody biomass in recent decades (Lewis *et al.* 2009b), and biomass has been shown to positively correlate with increased fruit production (Chapman *et al.* 1992). While this suggests that the predicted increases in biomass for West African forests will translate into increased reproductive effort, the substantial fine scale spatial variation in fruit production patterns observed by Chapman *et al.* (2005) reinforces the need for caution in making predictions about forest response at small scales.

Laying on top of abiotic determinants are ecological processes such as pollinator and frugivore population dynamics that also contribute to fruiting presence and abundance patterns (Rathcke & Lacey 1985, Ims 1990). The mechanistic complexity determining fruit production is compounded by the possibility of interactions amongst causal factors, such as between light and carbon (Ramanathan & Carmichael 2008) or pollination and regional climate forcing (Satake & Iwasa 2002).

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Because rainfall is a relatively dynamic covariate at TNP we are interested in testing whether rainfall correlates with reproductive effort by plant species as measured by fruit presence. While making specific predictions about the response of fruits to trends in rainfall dynamics is challenged by the complexity and diversity of tropical forests and potential nonlinearity in the response of plants to other abiotic and biotic changes, some evidence about the impact of water on tropical forest plant species' reproductive effort is available. Wright and Calderón (2006) found that the seed production response of a lowland moist tropical forest to El Niño driven changes in precipitation to depend on its severity, presumably related to tensions between benefits of increased light availability and costs of decreased moisture, but otherwise found no evidence of systematic long-term trends. The long-term study by Chapman *et al.* (2005) on fruiting patterns in an east Africa tropical forest showed that the direction of change in fruit abundance depended on the decade of analysis, with a positive trend between 1990–2002 and inferentially associated with recent increasing rainfall. A short-term canopy water addition experiments by Díaz and Granadillo (2005) also indicated an overall positive association between water availability and fruit production in three tree species of the tropical dry forests of Venezuela.

At TNP, rainfall is currently showing a long-term decline over the last 40 yr, matching a regional West African trend identified in Malhi and Wright (2004), although this decline has become relatively stable in the Côte d'Ivoire region during the past 10 yr (Fig. 1). At TNP, any persistent effects of rainfall trends may not be consistent across species even though there is statistically significant fruiting seasonality setting peak fruiting at the transition between the wet and major dry season for many species (Anderson *et al.* 2005). As West Africa gets hotter and drier, predicting the consequences for short and long-term climate change on forests is aided by trend analyses of fruiting dynamics. As quantitating intra- and inter-annual fruiting patterns is a first step to identifying plausible and implausible mechanisms of fruit production and for making cross system comparisons for comparative research on plant and animal ecology, the aims of this study were to: (1) to quantitate inter-annual trends in species and forest scale fruit presence probabilities; and (2) test the importance of rainfall in explaining inter-annual fruit presence variability.

METHODS

Phenology data collection.—Phenology data were collected within TNP at approximately 5°50′ 47″ N and 7°18′ 44″ W by the Taï Chimpanzee Project (Boesch & Boesch-Achermann 2000) along a network of forest trails. These trails allowed repeated observations of individually marked trees spread throughout approximately 30 km^2. The fruiting phenology data used here are essentially the result of continued monitoring of trees used in the dataset of the phenology study at TNP reported by Anderson *et al.* (2005). Species were selected based on their importance as dietary food items of western chimpanzees (*Pan troglodytes verus*) (Table S1). A broadly inclusive botanical study on species rarity found most plant species in the survey area to be relatively rare, with the dietary species of chimpanzees to be amongst the most abundant species. Two exceptions of relatively abundant species not included in this study are *Corynanthe pachysceras* and *Diospyros canaliculata*, but overall the species included here generally represent the most common woody fruiting species of TNP.

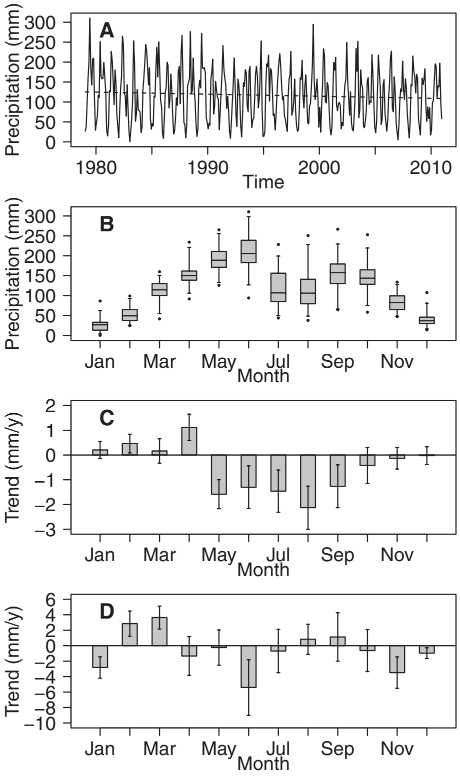

FIGURE 1. Rainfall patterns based on NASA precipitation models. (A) Monthly rainfall totals as a time series line plot. The dashed line shows the long-term modeled decline in rainfall. (B) Box plots of rainfall totals by month summarize the seasonality in rainfall, with the central horizontal line drawn at the median, the box extending to the interquartile range boundaries, whiskers extending between the 0.025 and 0.975 quantiles, and points denoting outliers. Panels (C-D) illustrate monthly inter-annual linear trend estimates of rainfall change (mm/y) with whiskers extending to ± one standard deviation for the time periods 1979–2010 (panel C) and using data from January 1998 to October 2010 which coincides with the phenology study (panel D).

Observations of marked individuals for each species were made using binoculars to assign monthly fruit rank scores. Individual plants were given rank values of 0, 1, 2, 3, and 4, where 0 corresponds to no fruits observed, and 1, 2, 3, and 4 corresponds to 1–25 percent, 26–50 percent, 51–75 percent, and 76–100 percent of tree crown filled with fruits, respectively. Monitored individuals were selected based on evidence of reproductive maturity and a species-specific diameter at breast height (dbh) threshold (Table S1). In general, individuals as large as possible were chosen to ensure data were collected from mature and typically productive trees.

Data collection was initiated in 1997 and is ongoing, with trees that died or were lost (political instability resulted in several extended periods of research discontinuities) generally being replaced to maintain sample sizes. We selected the subset of time from January 1998 until October 2010 for the data analysis here based on a goal to obtain the greatest number of individuals continuously living over the longest time period while minimizing the proportion of missing data values related to political instability. This resulted in 1401 individuals representing 44 species, with average total study duration from first to last observation of approximately 140 mo per individual. Because plants may change their typical reproductive strategies toward the end of life, we also carried out all analyses presented here using the subset of data that included only individuals that survived throughout the study. This filter retained 984 individual plants from the 44 species, of which 39 species were represented by at least five individuals (whose species level estimates are assumed to be more reliable). Analyses of this subset of individuals found no differences from the analyses of the full dataset presented here.

Phenology data pre-processing.—Rank score data were converted to presence-absence data. Categorical rank score data are difficult to statistically analyze under the aims and models of this study but bivariate data are not. This conversion also facilitates graphical comparison with the other comparatively long-term fruit African tropical phenology study reported in Chapman *et al.* (2005). By treating the rank scores as ratio scale data and shifting the ordinal scales to the midpoints of each bin, we observed graphically that the intra-annual fluctuations and the inter-annual trend of these means were comparable to the bivariate data graphs presented in Figure 2. Figure 2 illustrates several different summary plots of the proportion of individuals with fruit at the forest community level of aggregation, and shows a clear long-term upward trend between years (Fig. 2B) as well as intra-annual seasonality (Fig. 2C). The Inter-annual trend model described below quantitates the significance of this trend and those of each species while controlling for seasonal periodicity and individual heterogeneity in fruit production effort.

For analyses involving rainfall data used to test relationships between cumulative rainfall and the whether an individual i of species s showed fruit in year t, some care is needed in binning monthly samples into an indicator variable on the yearly fruit bearing state. For example, if an individual is identified as showing fruit for several months before and after the peak fruiting event during a particular year t, it would not be correct to define the year break point at the peak fruiting month and attribute the observed nonzero fruiting presence score following this month to a positive fruiting presence status for year $t + 1$. Observation error and missing data presented further difficulty in identifying clear sequences of fruit presence associated with each specific year. Thus, we proceeded as follows. First, the peak fruiting month for each species was obtained as the month with the highest mean number of individuals showing fruit. Then for each year t, each individual plant i of the species was recorded as showing fruit if it showed fruit at least once during the continuous time period from 7 mo prior to 4 mo subsequent to the peak fruiting months, inclusive. This ensured that any individual who showed fruit at least once during the year associated with the species defined peak fruiting time was marked as having shown fruit for that year but not to the subsequent year $t + 1$.

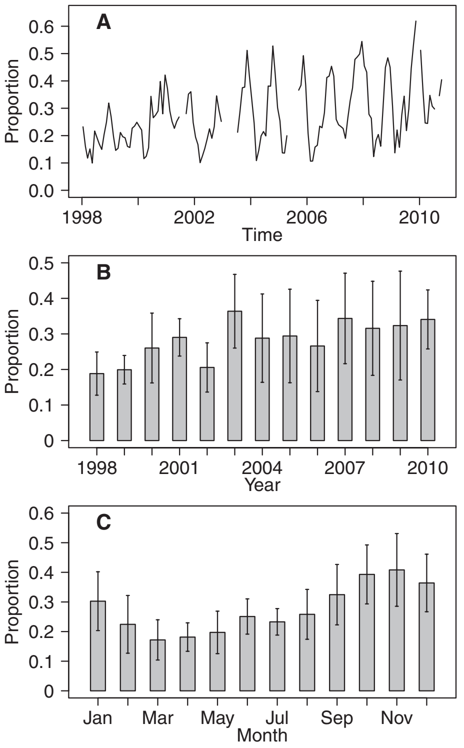

FIGURE 2. The proportion of individuals from the forest community bearing fruit are shown as time series data (A), yearly means (B), and monthly means (C); bars extend to the mean and vertical lines extend from the mean to ±1 SD.

Rainfall data.—TNP rainfall averages between 1700–2100 mm per year (Kasparek 2000) from 3 to 7 relatively dry months per year. As such, TNP is a relatively dry tropical rain forest based on the classification scheme of Reich (1995). Although monthly cumulative rainfall data were taken at a research camp adjacent to the phenology study site from August 1987 to July 2009 by the Taï Chimpanzee Project (Boesch & Boesch-Achermann 2000), in addition to occasional months of unreliable data collection most months during 2003–2005 were not recorded. We obtained rainfall data from NASA's rainfall archives (http://disc2.nascom.nasa.gov/Giovanni/tovas/) from 1979 to October 2010 at 2.5° × 2.5° resolution. Absolute total rainfall varies substantially across TNP (Kasparek 2000) and the NASA-derived monthly rainfall estimates were generally substantially less than observed rainfall totals collected on site. The NASA-derived estimates were well correlated with the available site collected rainfall data (Pearson correlation 0.72), so that the NASA-derived data can be safely assumed to be fairly accurate rainfall proxy needed in the regression analyses. A parallel analysis relying on the site collected rainfall data revealed similar results compared with the ones presented here, but with more species showing a nonsignificant relationship with rainfall as would be expected with reduced sample sizes.

Detrending analysis of the rainfall data based on model equation 1 (described next) using an identity link function for g revealed a significant decline over the period 1979–2010 (trend coefficient = −0.04, std. error = 0.02, *P*-value = 0.03). This downward trend diminished over the years 1998–2010 (trend coefficient = −0.01, std. error = 0.06, *P*-value = 0.91). Figure 1 summarizes the rainfall dynamics at TNP, and based on the median monthly rainfall patterns, we define here the major long dry season to be from November to February, a short dry season during July and August, and the wet seasons during March to June and September to October.

INTER-ANNUAL TREND MODELS.—Because the onset and duration of fruit presence results from, amongst other factors, the convolution between timing and synchrony in flowering and fruit maturation times, characteristics such as the peakedness in curves describing the seasonality of fruit presence probabilities can in theory be quite variable across species and scales of biological aggregation. At TNP, dissertation work by Zoro Goné Bi found that species can exhibit aseasonal, annually seasonal, and supra-annual production. Anderson *et al.* (2005) also identified a significant annual seasonal fruiting cycle in the percentage of individuals with fruits at the forest community scale using regression on trigonometric functions. Here, to control for diverse patterns of seasonal variation in a unified way across species while estimating the direction and significance of inter-annual trends, we used a semi-parametric generalized additive model framework (Hastie & Tibshirani 1986, Wood 2006).

Specifically, let $y_{i,t}$ be a bivariate random variable indicating fruit presence for each individual i at month t. The semi-parametric model

$$g(\mathrm{E}[y_{i,t}]) = \beta_0 + \beta_1 x_t + s(m_t) + b_i \tag{1}$$

was used to model fruiting presence for individuals at the species level for each species separately and for the entire forest community. The model given in equation (1) consists of: the logit link function g of the expected value $\mathrm{E}[y_{i,t}]$ of $y_{i,t}$; a linear parametric trend $\beta_0+\beta_1 x_t$ with parameters β_j, $j = 0, 1$, that is a function of a cumulative time index x_t; a nonparametric smooth periodic function $s(m_t)$ of the month of the year m_t at time t, with period of 12 mo; and individual random effects b_i in the intercept of the trend component with which are normally distributed with mean 0 and standard deviation to be estimated. Residuals r_t are assumed to be independent and normally distributed with mean zero and variance-covariance matrix Σ.

Several potential shortcomings of the models described by equation (1) that we considered are the following. The most obvious one is the lack of including temporal autocorrelation in the residuals r_t. For models of the type represented by equation (1), current software that facilitates inclusion of autocorrelation uses older model fitting methods based on penalized quasi-likelihood, which make significance testing difficult, can lead to biased estimates for bivariate response data, and sometimes lead to numerical stability issues (Wood 2008). To assure that temporal autocorrelation did not bias trend estimates, we compared trend results from a model allowing temporal autocorrelation in the residuals to the random effects models presented here (see section *Model fitting and output* for an overview and references on the code used). Comparing trend terms between models with and without autocorrelation indicated practically no difference in these estimates, and hence we chose to proceed a model that allows more recent numerical fitting techniques to allow for classical null hypothesis testing of parameter significance (Wood 2006).

A second limitation for some species is the choice of fixing the smooth function $s(m_t)$ to a cyclic period of 12 mo. Changing this from, for example, 12 mo to 24 mo still produced annual periodic smooths for species that based on graphical examination would best be classified as having supra-annual production patterns (*e.g.*, *Diospyros mannii*, shown in Fig. S1); these species seem to have enough nonzero production during the intermediate years between the supra-annual fruiting events to drive estimates of $s(m_t)$ toward a bimodal function over a 24-mo domain. In general, specifying a 12-mo rather than a 24-mo period for the cyclic smooth $s(m_t)$ showed stronger convergence between the smooth functions and the peak fruiting patterns when compared against raw plots of the data.

INTER-ANNUAL VARIABILITY AND RAINFALL MODELS.—We tested whether cumulative rainfall based on the 11 mo prior to and including the species defined peak production time impacted the number of individuals showing fruit for each year using a generalized linear mixed model (GLMM) framework (Bolker *et al.* 2009). These models were implemented following the guidelines of the 2011 updated supplementary material in Bolker *et al.* (2009). Let $p_{i,t,s}$ be the bivariate response variable of fruit presence or absence for individual i during year t of species s (as described in the *Phenology data pre-processing* section above), and denote the rainfall covariate indice by r_t. The model is

$$g(\mathrm{E}[p_{i,t,s}]) = \beta_0 + \beta_1 r_t + b_i \tag{2}$$

where g is the logit link function, β_0 and β_1 are the fixed effects, and b_i are the random intercept terms for each individual plant and are assumed to be normally distributed with mean 0 and standard deviation to be estimated. Our interest is in inference about the fixed effect parameter β_1, and in particular its sign and significance, the significance of which was tested using a likelihood ratio test between a model with and without this term (Table S1).

MODEL FITTING AND OUTPUT.—All models were fit using the R v.2.14.1 programing environment (R Development Core Team 2012). The trend models given by equation (1) were fit using the gamm4 function in the gamm4 package v. 0.1–6 (Wood 2011a,b) based on maximum likelihood methods. Models with temporal autocorrelation were fit using the gamm function in the mgcv package version 1.7–19 (Wood 2004). Cyclic cubic basis functions were used for estimating s, with a maximum of eight knots (Wood 2006, 2011b). The rainfall models given by equation (2) were fit by maximum likelihood using the lmer function from the lme4 package version 0.999999–0 (Bates *et al.* 2012). Rainfall covariate data were transformed to a standard normal deviate to facilitate numerical stability. Both trend and rainfall model results were not correlated with sample sizes across species.

For all models our main interest is about inference on the fixed effect parameter β_1 which captures the effect and significance of trends and rainfall, respectively. The models and analyses conducted here, however, provide considerably more output of biological interest (*e.g.,* differences in the smooth term estimates across species and random effects reflecting intraspecific heterogeneity). For each species, extensive model output details and summary data plots as in Figs. 2 and 3 are provided in Figure S1.

RESULTS

INTER-ANNUAL TRENDS.—Twenty-nine species showed significant positive trends at the 0.05 significance level, while the six species with a negative trend coefficient all had P-value estimates greater than 0.05 (Fig. 4A; Table S1). The months of peak fruiting times for species showing positive slope estimates in the inter-annual trend term of equation (1) were distributed throughout the year. Months with the most peak fruiting events (coinciding with the transition from wet to dry seasons) showed higher proportions of upward trending species (Figs. 2B and 4; Table S1) than other months. All species showed a significant intra-annual smooth term describing either regular annual or biannual fluctuations in fruiting presence (Fig. S1). With the exception of *Dialium guineense* (sample size $N_s = 3$) and *Elaeis guineensis* (sample size $N_s = 4$), random effects standard deviation estimates were well away from zero (mean = 9.327, min = 0.130, max = 35.052), highlighting the role of individual heterogeneity.

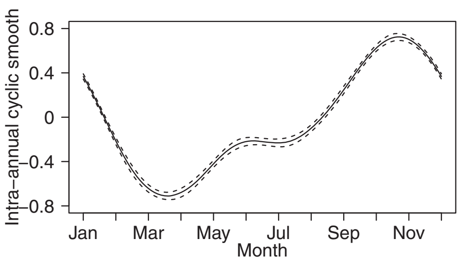

FIGURE 3. Estimated intra-annual periodic function $s(m_t)$ of equation (1) for the forest community (solid line), with approximate 95 percent Bayesian credible intervals delimited by dashed lines on the linear predictor scale of model equation (1). This shows that while forest wide fruit production is seasonal with a single primary peak in November, the underlying shape of this function is driven by the multimodal distribution of peak fruiting times at the species level (Fig. 4B) and hence is not symmetric about this peak.

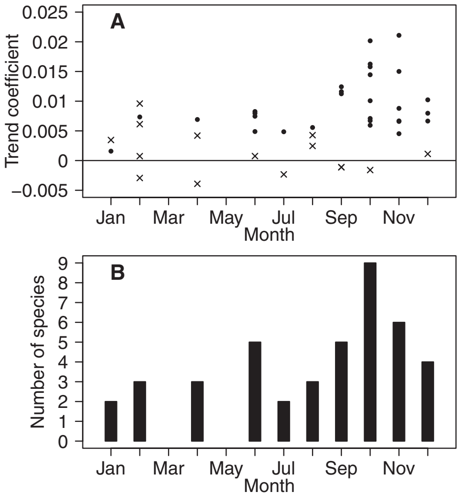

FIGURE 4. (A) Inter-annual trend coefficients on a linear scale by peak fruiting month. Significant (points) or nonsignificant (crosses) trends are based on a 0.05 P-value significance threshold. (B) Counts of the number of species with peak fruiting times by month.

At the community level, the upward inter-annual trend in the proportion of individuals with fruit observed in Figure 2B is highly significant (β_1 estimate 0.006, SE <0.001, z-value 42.642, P-value < 0.001). Model predictions of the parametric trend component at the first and last time points are 0.147 and 0.307, a percentage increase of 108.063 percent. The regular intra-annual oscillations clear by eye (Fig. 2C) are reflected by a highly significant smooth term s (χ^2 test statistic 4960, estimated df 6, P-value < 0.001). This oscillation occurs over a 12-mo period and peaks at approximately the end of October near the beginning of long dry season (Fig. 3). It is worth noting its asymmetry driven by the underlying distribution of peak fruiting times throughout the year at the species level (Fig. 4B), and re-affirming the utility of nonparametric techniques for controlling for seasonality in fruiting presence studies such as these.

FRUITING RELATIONSHIP WITH RAINFALL.—Table S1 and Figure S1 provide extensive results from the rainfall models which we summarize here. Using a P-value threshold of 0.05, cumulative rainfall was significantly negatively correlated with annual production at the species level for 22 species, with five species showing significant positive correlations. Of the five species with a significant positive association with rainfall, three have peak fruiting during the dry season and two during the wet season. Of the 22 species with a negative association with rainfall, 11 show peak fruiting during the dry season and 11 during the wet season. For species with no statistical association with rainfall, four show peak fruiting during the dry season and 13 show peak fruiting during the wet season. Taken together, these findings indicate that no relationship exists between the presence and direction of a significant rainfall effect and the season of peak fruiting at the species level.

DISCUSSION

Our results corroborate and extend the findings by Anderson *et al.* (2005), who also found forest community oscillations in fruiting presence with a 12-mo period, peaking approximately in November during the end of the short wet season and prior to the long dry season. Here, by letting the data speak using a nonparametric construction of $s(m_t)$ rather than *a priori* assuming symmetric trigonometric functions, we found an asymmetric and somewhat bimodal intra-annual fluctuation (Fig. 3), reflecting the underlying distribution of peak fruiting times throughout the year (Fig. 4B). Furthermore, we were able to scale up the analysis from measuring co-oscillation between two monthly resolved time series to the analyses of inter-annual trends and seasonal impacts of rainfall. In sum, these analyses quantitatively disentangle seasonal fluctuations from long-term trends while accounting for individual heterogeneity, and document an upward inter-annual trend in the proportion of individuals with fruits for most study species and the forest community despite declining rainfall.

A parsimonious explanation of the observed upward fruiting trends is that as the plants age, they are simply more capable of producing fruit. Because the trees included in this study were all selected based on evidence of reproductive maturity, the trends observed here under such an explanation would have to be the result of continued increases in fruit presence, and not solely because they had matured from nonproducing to producing trees. The average time until fruit was detected across all individuals was approximately 17 mo, diminishing the likelihood that individuals reaching reproductive maturity during the course of this study as the explanation for the observed upward trends. Any biomass increases related to aging that could produce concomitant increases in fruit seems unlikely given the observed rates of increase in fruit production, but remains an open possibility.

Another explanation for the source of the inter-annual variability is rainfall, yet the statistical correlations between rainfall and fruit production tended to be negative, pointing in the opposite direction. While there is no conceptual uncertainty that at some threshold declines in rainfall will negatively impact fruit production, whether because of an immediate lack of the necessary water resources or because of a multi-year cumulative stress effect, our analyses suggest this is not currently an overwhelmingly important driver of fruit production and trends at TNP. In fact, the transition months between the wet to dry seasons and for which the clearest unambiguous declines in rainfall are observed (Fig. 1D) also show a high proportion of significantly upward trending species (Fig. 4A).

The observations made so far in the discussion suggest that changes in irradiance as a likely explanation for the fruit phenology patterns are observed here. The optimal timing of leaf and flower production often coincides with seasonal peaks in irradiance in tropical forest species (van Schaik *et al.* 1993, Wright & van Schaik 1994). Most upward trending species are reproducing during the wet seasons when water availability is presumably not limiting, and any decreased rainfall that is accompanied by decreased cloud cover could lead to increased irradiance, stimulating increased levels of photosynthesis. Further supporting the hypothesis that light is constraining fruit production at TNP is the observation that peak flowering tends to coincide with the solar zenith (occurring approximately in late March and September) (Anderson *et al.* 2005), with subsequent peak fruiting being offset (Fig. 4B) with the solar zenith. There is also a general positive trend in light availability in tropical forests regions in general (Wild *et al.* 2005, Wright 2005); if this trend continues and light is the limiting factor, we can predict that fruit production should continue to increase until other factors constrain it.

Persistent changes in ecological factors can also determine fruit presence changes. Dramatic declines in arboreal frugivore populations, such as experience by the local chimpanzee population (C. Boesch, unpubl. data) also can explain the observed increases of fruits. While much remains unknown about the complete frugivore community and the component population trajectories, one could predict that in the short-term fruit presence will increase as the impact of frugivore consumption declines. Likewise, pollinator community and population dynamics are poorly documented, yet are also important in the reproductive output and synchrony of tropical forests (Bawa 1990).

Whether the observed changes in fruiting patterns of the polycarpous plants studied here are driven by the increases in CO_2 and light on growth and physiology, changes in the community and population densities of pollinators and frugivores, or the interactions between these, understanding West African tropical forest fruit production changes will need further fine scale, long-term studies in all these respects.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Species names and summary of model results.*

FIGURE S1. Species level graphics and additional model results.

LITERATURE CITED

Anderson, D. P., E. V. Nodheim, T. C. Moermond, Z. B. Goné Bi, and C. Boesch. 2005. Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. Biotropica 37: 631–640.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes. Available at http://cran.r-project.org/web/packages/lme4/index.html (accessed 31 Oct 2012).

Bawa, K. S. 1990. Plant-pollinator interactions in tropical rain forests. Annu. Rev. Ecol. Syst. 21: 399–422.

Boesch, C., and H. Boesch-Achermann. 2000. The chimpanzees of the Taï Forest: Behavioural ecology and evolution. Oxford University Press, Oxford.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends Ecol. Evol. 24: 127–135.

Chapman, C. A., L. J. Chapman, T. T. Struhsaker, A. E. Zanne, C. J. Clark, and J. R. Poulsen. 2005. A long-term evaluation of fruiting phenology: Importance of climate change. J. Trop. Ecol. 21: 31–45.

Chapman, C. A., L. J. Chapman, R. Wangham, K. Hunt, D. Gebo, and L. Gardner. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24: 527–531.

Díaz, M., and E. Granadillo. 2005. The significance of episodic rains for reproductive phenology and productivity of trees in semiarid regions of northwestern Venezuela. Trees 19: 336–348.

Hastie, T., and R. Tibshirani. 1986. Generalized additive models (with discussion). Stat. Sci. 1: 297–318.

Hietz, P., B. L. Turner, W. Wanek, A. Richter, C. A. Nock, and J. S. Wright. 2011. Long-term change in the nitrogen cycle of tropical forests. Science 334: 664–666.

Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. Trends Ecol. Evol. 5: 135–140.

Kasparek, M. 2000. Flore du Parc National de Taï (Côte d'Ivoire). Verlag, Heidelberg.

Lewis, S. L., J. Lloyd, S. Sitch, E. T. A. Mitchard, and W. F. Laurance. 2009a. Changing ecology of tropical forests: Evidence and drivers. Annu. Rev. Ecol. Syst. 40: 529–549.

Lewis, S. L., G. Lopez-Gonzalez, B. Sonké, K. Affum-Baffoe, T. R. Baker, L. O. Ojo, O. L. Phillips, J. M. Reitsma, L. White, J. A. Comiskey, K. M.-N. Djuikouo, C. E. N. Ewango, T. R. Feldpausch, A. C. Hamilton, M. Gloor, T. Hart, A. Hladik, J. Lloyd, J. C. Lovett, J.-R. Makana, Y. Malhi, F. M. Mbago, H. J. Ndangalasi, J. Peacock, K. S.-H. Peh, D. Sheil, T. Sunderland, M. D. Swaine, J. Taplin, D. Taylor, S. C. Thomas, R. Votere, and H. Wöll. 2009b. Increasing carbon storage in intact African tropical forests. Nature 457: 1003–1007.

Lewis, S. L., Y. Malhi, and O. L. Phillips. 2004a. Fingerprinting the impacts of global change on tropical forests. Philos. Trans. R. Soc. Lond., Ser. B 359: 437–462.

Lewis, S. L., O. L. Phillips, T. R. Baker, J. Lloyd, Y. Malhi, S. Almeida, N. Higuchi, W. F. Laurance, D. A. Neill, J. N. M. Silva, J. Terborgh, A. Torres Lezama, R. Vásquez Martinez, S. Brown, J. Chave, C. Kuebler, P. Núñez Vargas, and B. Vinceti. 2004b. Concerted changes in tropical forest structure and dynamics: Evidence from 50 South American long-term plots. Philos. Trans. R. Soc. Lond., Ser. B 359: 421–436.

Lloyd, J., and G. D. Farquhar. 2008. Effects of rising temperatures and [$C0_2$] on the physiology of tropical forest trees. Philos. Trans. R. Soc. Lond., Ser. B 363: 1811–1817.

Malhi, Y., and J. Wright. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. Philos. Trans. R. Soc. Lond., Ser. B 359: 311–329.

Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. Science 263: 954–958.

Phillips, O. L., Y. Malhi, B. Vinceti, T. Baker, S. L. Lewis, N. Higuchi, W. F. Laurance, P. Núñez Vargas, R. Vásquez Martinez, S. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 2002. Changes in growth of tropical forests: Evaluating potential biases. Ecol. Appl. 12: 576–587.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org (accessed 5 Oct 2012).

Ramanathan, V., and G. Carmichael. 2008. Global and regional climate changes due to black carbon. Nat. Geosci. 1: 221–227.

Rathcke, B., and E. P. Lacey. 1985. Phenologial patterns of terrestrial plants. Annu. Rev. Ecol. Syst. 16: 179–214.

Reich, P. B. 1995. Phenology of tropical forests: Patterns, causes, and consequences. Can. J. Bot. 73: 164–174.

Satake, A., and Y. Iwasa. 2002. The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. J. Ecol. 90: 830–838.

van Schaik, C., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. Annu. Rev. Ecol. Syst. 24: 353–377.

Wild, M., H. Gilgen, A. Roesch, A. Ohmura, C. N. Long, E. G. Dutton, B. Forgan, A. Kallis, V. Russak, and A. Tsvetkov. 2005. From dimming to brightening: Decadal changes in solar radiation at Earth's surface. Science 308: 847–850.

Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Am. Stat. Assoc. 99: 673–686.

Wood, S. N. 2006. Generalized Additive Models: An Introduction with R. Chapman & Hall, Boca Raton, Florida.

Wood, S. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. J. R. Stat. Soc. Ser. B 70: 495–518.

Wood, S. 2011a. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B 73: 3–36.

Wood, S. 2011b. gamm4: Generalized additive mixed models using mgcv and lme4. Available at http://cran.r-project.org/web/packages/gamm4/index.html (accessed 5 Oct 2012).

Wright, S. J. 2005. Tropical forests in a chaning environment. Trends Ecol. Evol. 20: 553–560.

Wright, S. J., and O. Calderón. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. Ecol. Lett. 9: 35–44.

Wright, S. J., and C. van Schaik. 1994. Light and the phenology of tropical trees. Am. Nat. 143: 192–199.