LETTER

Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest

S. J. Wright* and Osvaldo Calderón

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, Panamá
Correspondence: E-mail: wrightj@si.edu

Abstract

It has recently been reported that humid tropical forests are changing rapidly in response to global anthropogenic change and that these forests experience greater tree mortality and even fire during droughts associated with El Niño events. The former reports are controversial largely because a single method has been used – repeated censuses of tree plots. The latter reports focus on recent extreme El Niño events. Here, we show that flower and seed production both increase during El Niño events in an old-growth tropical forest in Panama. Flower production, but not seed production, has also increased over the past 18 years. The sustained increase in flower production was greater for 33 liana species than for 48 tree species. These results indicate that moderate El Niño events favour seed production, document long-term increases in flower production for the first time, and corroborate long-term increases in the importance of lianas using independent methods. Changes in levels of solar irradiance might contribute to all three patterns.

INTRODUCTION

Dramatic changes have been reported in the dynamics and structure of humid, old-growth tropical forests over the past 2–3 decades. These changes include shifts in tree species composition and increases in just 10 years of *c.* 50%, 40%, 20%, 5% and 2% in the number of large lianas, tree recruitment rates, tree mortality rates, above-ground biomass and stem density respectively (Phillips *et al.* 2002a; Baker *et al.* 2004; Laurance *et al.* 2004; Phillips *et al.* 2004). These changes are controversial in part because the evidence comes from a single method – repeated censuses of tree plots (Clark 2002; Phillips *et al.* 2002b; Nelson 2005; Wright 2005a). Moreover, the causes of these changes even if they can be corroborated using independent methods remain uncertain largely because plant responses to natural, interannual climate variation are poorly understood for humid tropical forests.

The El Niño Southern Oscillation (ENSO) is the greatest source of interannual climate variation in the tropics. The ENSO brings similar climate anomalies to a large portion of the humid tropics including southern Mesoamerica, the northern and eastern Amazon, Southeast Asia, New Guinea,

northern Australia and parts of equatorial West Africa (Kiladis & Diaz 1989; Malhi & Wright 2004). These shared climate anomalies include reduced cloud cover and rainfall and increased solar irradiance and temperature during El Niño events and the opposite during La Niña events (Aceituno 1988; Kiladis & Diaz 1989). Plants will respond because plant metabolism varies with temperature, moisture availability and light availability. Extended droughts associated with recent severe El Niño events have caused elevated tree mortality and even led to fire in selected humid tropical forests (Condit *et al.* 1995; van Nieuwstadt & Sheil 2005). Greater temperatures increase respiration costs (Clark *et al.* 2003), which could also limit net primary production during El Niño events. However, reduced cloud cover and greater solar irradiance could relieve light limitation.

There is clear evidence that light limits net primary production in humid tropical forests. Light limits photosynthetic carbon uptake because leaf area indices (m^2 of leaf area per m^2 of ground area) range from four to six or seven and most leaves are heavily shaded. Over the course of a day, forest-wide carbon uptake increases steadily with solar irradiance, which varies as cloud cover and solar angle change (Loescher *et al.* 2003). Seasonal changes in cloud

cover also affect net primary production; for example, forest-wide carbon uptake varies seasonally with cloud cover and solar irradiance penetrating the atmosphere in simulations of South American net primary production (Raich *et al.* 1991). Over the course of 2 years, we experimentally augmented light levels experienced by an upper canopy tree species whenever cloud cover reduced photosynthetically active irradiance by >700 μE m^{-2} s^{-1}. Responses included increased maximum photosynthetic potentials, realized carbon uptake, branch extension growth, numbers of reproductive buds and fruit mass (Graham *et al.* 2003). Natural interannual variation in cloud cover and solar irradiance should have similar effects. In sum, the ENSO causes coordinated changes in temperature, moisture and light availability that potentially have opposing effects on plant function in many humid tropical forests.

Tropical forest plants have not previously been evaluated with sufficient frequency through even a single ENSO cycle to resolve the net effects of these coordinated changes (Wright 2005b). Attempts to model net primary production have been inconclusive; for example, net primary production over the Amazon Basin decreased during El Niño events in one regional model and increased in another (Tian *et al.* 1998; Behrenfeld *et al.* 2001). Long-term monitoring of flower and seed production may help to resolve the net effects of ENSO-related climate variation. Reproduction tracks interannual variation in climate in many plant species (Kelly & Sork 2002) and should respond to the full range of ENSO variation as well as to anthropogenic climate change. We have monitored the rain of flowers and seeds at 1-week intervals since January 1987 on Barro Colorado Island (BCI), Panama. The 18-year record now includes six El Niño and three La Niña events as well as 155 218 flower records and 1 035 370 individual seeds and fruit identified to species. We use these data to document seasonal, interannual and long-term variation in reproduction and to explore the relationship between ENSO climate variation and interannual variation in reproduction. The ENSO has shifted toward El Niño conditions in recent decades and further change may occur with global warming (Federov & Philander 2000; Schöngart *et al.* 2004; Collins 2005). Thus, any relationship between ENSO and plant reproduction could contribute to directional changes in the dynamics and structure of old-growth tropical forests.

METHODS

Study site and climate

The old-growth forest on BCI (9°10′ N, 79°51′ W) has escaped fire and agriculture for >1500 years (Piperno 1990). Temperatures average 27 °C in April and 26 °C in the other 11 months. Annual rainfall averages 2600 mm, and a 4-month dry season begins in December. We use 'meteorological' years, which begin on 1 December, to capture this seasonality. Rainfall, temperature and solar irradiance were recorded with a rain gauge (US Forest Service 5100–4515A), a temperature sensor (Vaisala HMP45AC, Helsinki, Finland) and a pyranometer (Li-Cor Silicon Pyranometer, Lincoln, NE, USA), respectively, mounted on a tower just above the forest canopy. Temperature and irradiance were recorded every 15 min and averaged or summed respectively. Reliable irradiance data are only available from January 1990.

Plant reproduction

The rain of flowers and seeds was censused weekly between 1 January 1987 and 31 March 2005 using 200 traps located within a 50-ha plot where trees and shrubs are mapped and identified (Wright *et al.* 2005). Each trap consisted of a square 0.5-m^2, open-topped, 1-mm mesh bag supported by a polyvinyl chloride (PVC) frame. Distances between nearest traps averaged 18.9 m (± 3.6 m = 1 SD). Reproductive parts were identified to species; the presence of flowers was recorded; and fruits and seeds were counted and further categorized as immature, mature (endosperm filled), or damaged by animals. The number of species flowering (fruiting) equalled the number of species recorded as a flower (mature seed or fruit) each month (see Table S1).

The level of production was estimated for the 33 liana species and 48 tree species with both flowers and seeds or fruit captured in 10 or more traps in any single year. This criterion insured that four or more reproductive individuals were located close to traps. This was verified for trees and shrubs by superimposing locations of large, potentially reproductive individuals and of traps that captured conspecific flowers, seeds and fruit. Many more individuals of each species inhabited the 50-ha plot. Flower production equalled the number of flower presences (see Table S2). Seed production equalled the number of seeds captured plus the number of mature fruit captured multiplied by a species-specific mean seed-to-fruit ratio (See Table S2). Annual production estimates were assigned to meteorological years using mean flowering dates (Wright *et al.* 2005). Annual production estimates were converted to standard normal deviates to place all 81 species on a common scale for graphical purposes only.

ENSO indices

The Southern Oscillation Index (SOI) and four sea surface temperature (SST) indices (ENSO12, ENSO3, ENSO34 and ENSO4) were obtained from the US National Weather Service Climate Prediction Center (http://www.cpc.ncep.noaa.gov/data/indices). The SST indices are inversely

related to the SOI and refer to different portions of the equatorial Pacific. ENSO12 is the area defined by 80°–90° W and 0°–10° S, ENSO3 by 90°–150° W and 5° N–5° S, ENSO4 by 150° W–160° E and 5° N–5° S and ENSO34 by 120 W°–170° W and 5° N–5° S. The ENSO12 and ENSO3 areas are closest to Panama. El Niño and La Niña events occurred when the 5-month running average of the ENSO34 Index, defined as the monthly departure from its long-term mean for the 1971–2000 base period, exceeded + 0.5 °C or was less than −0.5 °C for at least eight consecutive months respectively. This definition follows Trenberth (1997) except a current base period, greater ENSO34 anomalies (± 0.5 vs. ± 0.4 °C) and longer lasting anomalies (8 vs. 6 months) were used to isolate stronger events likely to influence Panama.

Analyses

Seasonality was removed from each time series using additive monthly factors. An additive monthly factor is a fixed number of units above or below the overall mean value of the series for each month. Cross correlations were then performed to evaluate three hypotheses for lags of 0–12 months. First, the hypothesis that the ENSO influences BCI climate was evaluated using 15 cross correlations between the five ENSO indices and irradiance, temperature and rainfall. Second, the hypothesis that the ENSO influences plant reproduction was evaluated using 10 cross correlations between ENSO indices and numbers of species flowering and fruiting. Third, the hypothesis that climate influences reproduction was evaluated using six cross correlations between irradiance, temperature, rainfall and numbers of species flowering and fruiting. Table S1 holds the data used in the cross correlation analyses.

The null hypotheses that production was constant among years and lifeforms (lianas vs. trees and shrubs) were evaluated by subjecting the time series of annual flower and seed production to one-way repeated measures analyses of variance. The 33 liana and 48 tree and shrub species were replicates, lifeform was the grouping factor, and year was the repeated measures factor. This analysis will identify a long-term trend if the repeated measures on year are significant. Logarithms of flower and seed production normalized residuals. Table S2 holds the data used in the repeated measures analyses.

RESULTS

Climate and plant reproduction are strongly seasonal on BCI. The number of species recorded flowering or fruiting lagged the seasonal pattern of irradiance by 1 month and was nearly the mirror image of the seasonal pattern of
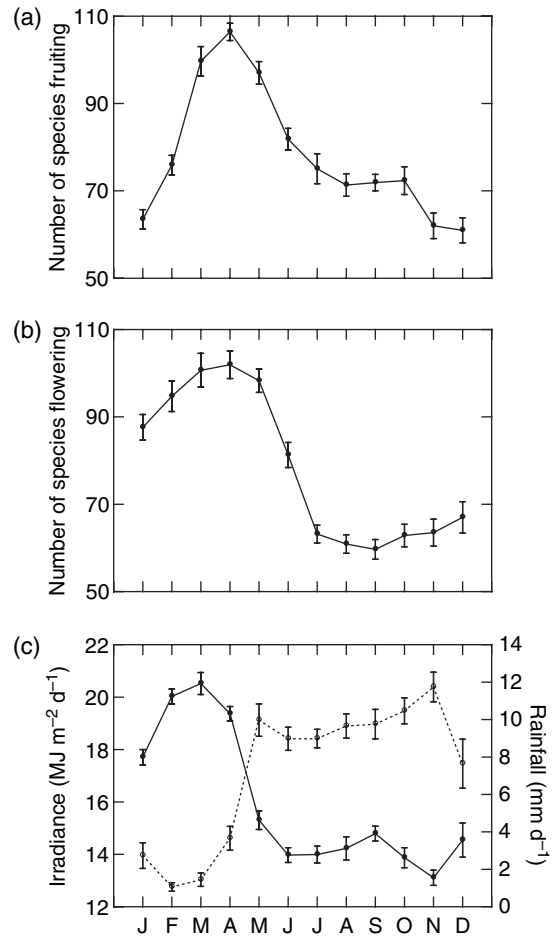

Figure 1 Seasonality of number of fruiting species (panel a), flowering species (panel b), rainfall (dashed line in panel c) and irradiance (solid line in panel c) on Barro Colorado Island, Panama. Number of species refers to species captured each month in 200 0.5-m^2 traps. Symbols represent monthly means (± 1 SE). Flowering, fruiting and rainfall are for 18 years from March 1987 to February 2005. Irradiance is for 15 years from January 1990 to December 2004.

rainfall (Fig. 1). This seasonality of climate and plant reproduction occurs in many humid tropical forests and is consistent with the hypothesis that many forest species time reproduction to coincide with the annual dry-season irradiance peak and to avoid the prolonged wet-season irradiance low (van Schaik et al. 1993; Wright & van Schaik 1994). Irrigation throughout five consecutive dry seasons failed to alter the timing of reproduction by canopy trees and lianas on BCI further indicating that seasonal changes in moisture availability have little influence on the timing of reproduction for most canopy species (Wright & Cornejo 1990). All monthly time series were transformed to remove these seasonal patterns before performing further analyses.

	Temperature		Rainfall		Irradiance	
	r*	Lag† (months)	r*	Lag† (months)	r*	Lag† (months)
SOI‡	n.s.		**0.253**	3	**−0.210**	2
ENSO12§	**0.482**	−2	−0.162	1	**0.376**	−1
ENSO3§	**0.353**	−2	**−0.221**	1	**0.333**	0
ENSO34§	**0.187**	−2	**−0.231**	1	**0.249**	0
ENSO4§	n.s.		−0.175	1	n.s.	

Table 1 Cross correlations among monthly values of rainfall, mean temperature and solar irradiance recorded on Barro Colorado Island, Panama and five indices of the El Niño southern oscillation

Seasonality was removed from each time series before performing cross correlations (see methods: analyses).

*Bold correlation coefficients are significant at $P < 0.01$. The remaining correlation coefficients are significant at $P < 0.05$ or not significant (entry is 'n.s.').

†Negative lags signify that variation in the local climate preceded variation in the El Niño Southern Oscillation Index.

‡The Southern Oscillation Index refers to the standardized difference in atmospheric pressure between Tahiti and Darwin, Australia.

§The four ENSO indices are inversely related to the SOI and refer to sea surface temperatures over different portions of the equatorial Pacific. ENSO12 is the area defined by 80°–90° W and 0°–10° S, ENSO3 by 90°–150° W and 5° N–5° S, ENSO4 by 150° W–160° E and 5° N–5° S and ENSO34 by 120° W–170° W and 5° N–5° S.

The ENSO influences BCI climate. Twelve of the 15 cross correlations between ENSO indices and irradiance, temperature or rainfall were significant (Table 1). The strongest cross correlations were for BCI temperature and SST indices for the two regions of the Pacific closest to Panama. The sign of the cross correlation coefficients indicate that irradiance and temperature tended to increase while rainfall tended to decrease during the El Niño phase of the ENSO. Table 1 only reports the lags with the largest cross correlation coefficients. In fact, the timing of high temperatures, high solar irradiance and low rainfall broadly coincided with the timing of high SSTs in the equatorial Pacific – the relevant cross correlations being significant for a range of lags centred on a lag of zero months. The number of significant lags for the different ENSO indices was 4–5, 4–14 and 6–23 months for rainfall, irradiance and temperature, respectively. These relationships between BCI climate and the ENSO closely resemble regional relationships (Aceituno 1988; Kiladis & Diaz 1989; Malhi & Wright 2004).

The ENSO also appears to influence the number of plant species reproducing on BCI. All 10 cross correlations between ENSO indices and numbers of species flowering or fruiting were significant (Table 2). The number of species fruiting did not evince a long-term trend, peaked during all six El Niño events, and fell to low levels during all three La Niña events in the 18-year record (Fig. 2a). The number of species fruiting also peaked 1–2 months after the SOI and coincided broadly with the four SST indices in the cross-correlation analyses (Table 2). In contrast, the number of species flowering tended to increase over the 18-year record

and peaked relative to contemporaneous background levels during five of six El Niño events (Fig. 2b). The number of species flowering also peaked 3–4 months before the SOI and 6–8 months before the SST indices in the cross correlation analyses (Table 2). Interannual variation in BCI climate must mediate these relationships between ENSO indices and numbers of species reproducing.

The final set of cross correlations evaluated this possibility. Four of the six cross correlations between the number of species flowering and fruiting and temperature, irradiance and rainfall were significant (Table 2). Numbers of both flowering and fruiting species were positively related to temperature for lags of 11 to −11 months (note Table 2 only presents the largest cross correlation coefficients). This is inconsistent with the hypothesis that temperature-mediated increases in respiration impact plant carbon balance negatively (Clark *et al.* 2003) because more not less energy was devoted to reproduction when temperatures were higher. The number of species fruiting was also positively related to irradiance 2–3 months earlier. This is consistent with the hypothesis that light levels limit fruit production (Wright & van Schaik 1994; Graham *et al.* 2003). The number of species fruiting was negatively related to rainfall 2 months earlier. The rainfall-fruiting species cross correlation may be an artifact of the stronger positive irradiance-fruiting species relationship for the same 2-month lag and the very strong negative irradiance-rainfall relationship (data in Table S1). The final two cross correlations between number of species flowering and rainfall and irradiance were insignificant. The absence of a relationship between interannual variation in rainfall and number of

Table 2 Cross correlations among monthly values of the number of species flowering and fruiting on Barro Colorado Island (BCI), Panama; five indices of the El Niño Southern Oscillation; and rainfall, mean temperature and solar irradiance recorded on BCI

	Number of species flowering		Number of species fruiting	
	$r*$	Lag† (months)	$r*$	Lag† (months)
SOI‡	−0.149	3	**−0.304**	−2
ENSO12§	**0.207**	8	**0.357**	−3
ENSO3§	**0.246**	8	**0.405**	−3
ENSO34§	**0.238**	7	**0.381**	−1
ENSO4§	**0.210**	7	**0.322**	−3
Rainfall	n.s.		**−0.209**	−2
Temperature	**0.394**	7	**0.467**	−2
Solar Irradiance	n.s.		**0.315**	−2

Seasonality was removed from each time series before performing cross correlations (see methods: analyses).
*Bold correlation coefficients are significant at $P < 0.01$. The remaining correlation coefficients are significant at $P < 0.05$ or not significant (entry is 'n.s.').
†Negative lags signify that variation in the number of reproductive species preceded variation in local climate or the El Niño Southern Oscillation Index.
‡The Southern Oscillation Index refers to the standardized difference in atmospheric pressure between Tahiti and Darwin, Australia.
§The four ENSO indices are inversely related to the SOI and refer to sea surface temperatures over different portions of the equatorial Pacific. ENSO12 is the area defined by 80°–90° W and 0°–10° S, ENSO3 by 90°–150° W and 5° N–5° S, ENSO4 by 150° W–160° E and 5° N–5° S and ENSO34 by 120° W–170° W and 5° N–5° S.

species flowering is inconsistent with hypotheses that drought is a proximate cue for flowering or that heavy rainfall inhibits flowering (Foster 1982). The number of reproductive species was most strongly related to temperature, possibly because temperature integrates environmental conditions.

The ENSO also influenced quantitative levels of flower and seed production for the 81 species captured as both flowers and seeds or fruit in 10 or more traps in at least one calendar year. Flower production increased steadily over 17 years for both lianas and trees (Fig. 3). The sustained increase was more rapid for 33 liana species than for 48 tree species ($F_{16,1264} = 4.59$, $P < 0.001$ for the lifeform–year interaction) and was temporally consistent across species within both lifeforms (Fig. 3). Flower production was particularly strong during both years of the 1991–1992 and the first year of the 1997–1998 El Niño events (Fig. 3).

Seed production did not evince a long-term trend but did respond to the same two El Niño events (Fig. 4). Seed
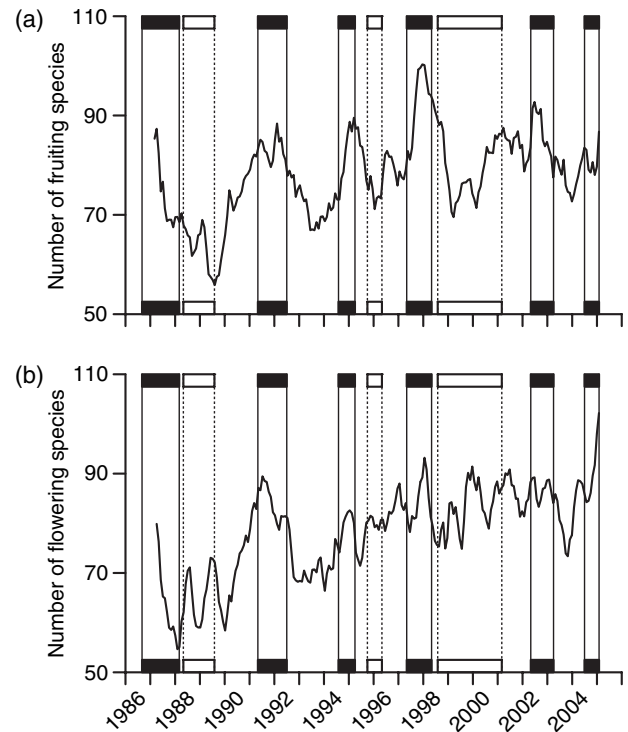

Figure 2 The number of species recorded fruiting (panel a) and flowering (panel b) each month for 18 years on Barro Colorado Island, Panama. El Niño (black boxes and solid vertical lines) and La Niña (open boxes and dotted vertical lines) events occurred when sea surface temperature anomalies in the ENSO34 region were >0.5 °C or less than −0.5 °C for at least eight consecutive months, respectively. The number of fruiting species was relatively high during six El Niño events and relatively low during three La Niña events. The number of flowering species increased over 18 years. Numbers of species were recorded in weekly censuses of 200 0.5-m^2 traps and are represented by 5-month running mean values calculated after removing seasonality.

production was temporally consistent across all 81 species including lianas and trees ($F_{16,1264} = 0.92$, $P = 0.55$ for the lifeform–year interaction; $F_{16,1264} = 3.39$, $P < 0.001$ for year) and was particularly strong during 1992 and 1997 (Fig. 4). The increase in flower but not seed production (Figs 3 and 4) may reflect repeated, low-cost flowering as environmental conditions slowly improved and opportunistic, high-cost fruit production when conditions were most favourable during El Niño years.

Levels of reproduction are likely to integrate conditions over several months. To evaluate this possibility, irradiance anomalies were defined as the current monthly value minus the long-term mean value for the same month and summed over 3- to 19-month windows. Anomalies that lag the years of high seed production are relevant here because prolonged flower-to-fruit development times of up to 11 months meant that, although each species flowered during the year
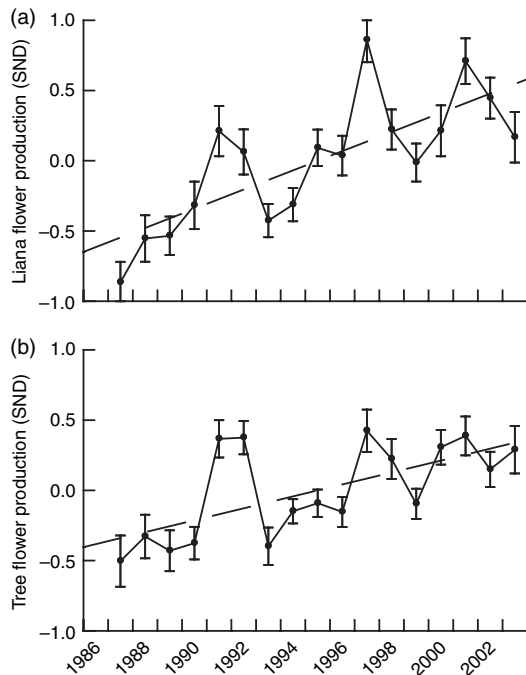
Figure 3 The production of flowers for 33 liana species (panel a) and 48 tree species (panel b) over 17 years on Barro Colorado Island, Panama Flower production increased for both lifeforms, with the increase being more rapid for lianas. Flower production was also relatively large in 1991, 1992 and 1997. Flower production was quantified as the number of times flowers were present in weekly censuses of 200 0.5-m^2 traps. To place all species on the same scale, annual flower production was converted to standard normal deviates for each species. Symbols represent the mean standard normal deviate ($\pm$ 1 SE) for each year.
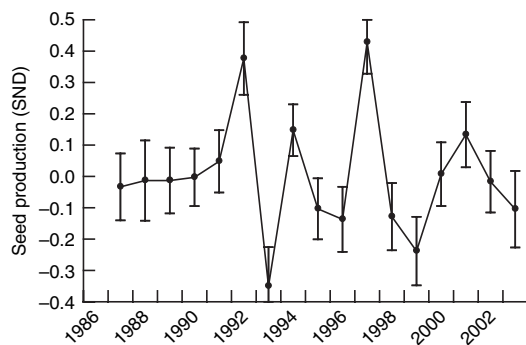

Figure 4 The production of seeds for 81 tree and liana species over 17 years on Barro Colorado Island, Panama. Seed production was greatest in 1992 and 1997. Seed production was quantified as the number of seeds captured plus the number of fruit captured multiplied by the species-specific mean number of seeds per fruit in weekly censuses of 200 0.5-m^2 traps. To place all species on the same scale, logarithms of annual seed production were converted to standard normal deviates for each species. Symbols represent the mean standard normal deviate ($\pm$ 1 SE) for each year.

of high production, many species actually filled and dispersed seeds later. The 1991–1992 and 1997–1998 El Niño events included the years of greatest flower and seed production and were characterized by relatively large positive irradiance anomalies for the shorter windows and by progressively larger positive anomalies for the longer windows (Fig. 5). The 1997 irradiance anomaly was particularly noteworthy – irradiance exceeded the long-term mean by 30% over the 8-month rainy season.

DISCUSSION

Plant responses to the El Niño southern oscillation

The ENSO causes similar and simultaneous anomalies in temperature, rainfall and irradiance over a large portion of the humid tropics with higher irradiance, higher temperature and lower rainfall during El Niño events and the opposite during La Niña events (Aceituno 1988; Kiladis & Diaz 1989; Malhi & Wright 2004). Plant production may increase during El Niño events if greater irradiance relieves light limitation or decrease if reduced rainfall causes water stress or if higher temperatures increase respiration costs.

A recent literature review suggests forest-wide responses vary modally in response to the range of severity of climate anomalies observed during El Niño events (Wright 2005b). Extreme drought during severe El Niño events caused elevated tree mortality and even fire in several humid tropical forests (Condit et al. 1995; van Nieuwstadt & Sheil 2005; Wright 2005b). In contrast, climate anomalies during more moderate El Niño events may favour tree growth. Annual tree growth rings tended to be greatest during El Niño events for both floodplain forests of the Amazon and terra firme forests of central Panama (Devall et al. 1996; Schöngart et al. 2004). Drought indirectly causes the pattern observed for floodplain forest – low river levels favour floodplain tree growth (Schöngart et al. 2004).

The relationship between El Niño and tree growth rings was more complex in Panama. Annual growth rings spanned 33 years and eight El Niño events at a site 2 km from BCI (Devall et al. 1996). Six mild El Niño events included five of the seven largest annual growth increments, a statistically improbable coincidence (Fisher Exact Test, $P < 0.001$). Tree growth rates were also elevated during the 1997–1998 El Niño event nearby on BCI (Condit et al. 2004). The two remaining El Niño events in the annual growth ring record coincided with the two most severe droughts in the 82-year BCI rainfall record (in 1976–1977 and 1982–1983), the smallest annual tree growth increment (in 1976), and elevated tree mortality (in 1982–1983; Condit et al. 1995; Devall et al. 1996). To summarize, tree growth in central Panama is enhanced during moderate El Niño events but reduced when severe drought coincides with an El Niño event.
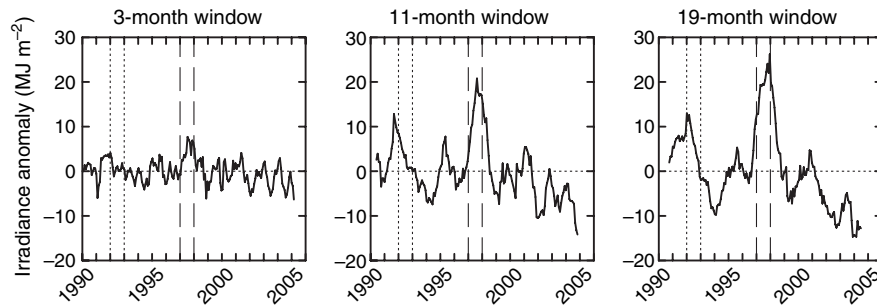
Figure 5 Irradiance anomalies recorded for 3-, 11- and 19-month windows for Barro Colorado Island, Panama. Community-wide seed production was very high in 1992 (dotted vertical lines) and 1997 (dashed vertical lines). The dotted horizontal line represents an anomaly of zero. Anomalies equal the sum over 3, 11 or 19 months of the difference between current irradiance and mean irradiance for the same month. Mean monthly irradiance was calculated for 1990 through 2004 inclusive.

Plant reproduction is also enhanced during El Niño events in Borneo (Curran *et al.* 1999; Sakai 2002) and Panama (this study). Reproduction occurs on very different schedules in these forests. In Borneo, most tree species reproduce supra-annually and synchronously in general flowering events, general flowering and El Niño events are strongly associated, and El Niño climate anomalies are hypothesized to provide the proximate cue that initiates reproduction (Curran *et al.* 1999; Sakai 2002). In Panama, normal seasonality provides the cues that initiate reproduction and most species reproduce annually at a characteristic time of year (Wright & Calderón 1995; Wright *et al.* 2005); however, seed production is greatest during particularly sunny El Niño years (Figs 4 and 5). van Schaik (1986) suggested that increased light availability may also favour plant reproduction during El Niño events in Borneo.

Integrating these observations, we hypothesize that forest-wide plant growth and reproduction will be reduced during extreme El Niño events that bring severe drought, enhanced during moderate El Niño conditions that relieve light limitation, and reduced by La Niña conditions that intensify light limitation. This hypothesis should apply equally well to humid tropical forests in southern Mesoamerica, the northern and eastern Amazon, Southeast Asia, New Guinea, northern Australia and parts of equatorial West Africa where ENSO climate anomalies are similar (Kiladis & Diaz 1989; Newbery *et al.* 1998; Malhi & Wright 2004).

Plant responses to anthropogenic change

Recent reports that the structure and dynamics of old-growth tropical forests are changing are controversial because the evidence comes from a single methodology – repeated censuses of woody stems in fully enumerated plots – and concerns a single component of net primary production – the net wood growth increment (Clark 2002;

Phillips *et al.* 2002b; Nelson 2005; Wright 2005a). Here, we used passive litter traps to assess a second component of forest production. This offers an opportunity to corroborate earlier reports of changes in forest structure and dynamics.

The original plot-based report indicated that large lianas are increasing rapidly in importance in western Amazonian forests (Phillips *et al.* 2002a). Specifically, the basal area of lianas and trees increased by 4.58% year^{-1} and 0.34% year^{-1}, respectively, between *c.* 1980 and 2000 (Phillips *et al.* 2002a). We observed similar increases in flower production of lianas and trees of 4.1% year^{-1} and 1.8% year^{-1}, respectively, on BCI between 1987 and 2003 (Fig. 3). The relative contribution of lianas to overall leaf litter production also increased by *c.* 50% over 17 years at a second old-growth forest site on BCI (Wright *et al.* 2004). These increases measured using independent methods corroborate the increasing importance of lianas in old-growth tropical forests as well as increasing flower production by both lianas and trees.

There has been one other recent attempt to relate long-term changes in plant reproduction in a tropical forest to anthropogenic climate change. Chapman *et al.* (2005) combined 1970–1983 and 1990–2002 censuses of the reproductive status of focal trees from the Kibale National Park, Uganda. The proportion of the monitored population fruiting decreased from 1970 to 1983 and then increased from 1990 to 2002. These trends are difficult to evaluate for two reasons. First, the two censuses used different criteria to include individuals. Nine between-census comparisons of similarly sized individuals of the same species were possible. The proportion of individuals fruiting decreased steadily for six species, increased for two species, and was consistently low for the ninth species (Chapman *et al.* 2005). The second reason these trends are difficult to evaluate concerns the treatment of trees that died during the censuses. Typically *c.* 2% of tropical trees die each year. If trees tend to be sterile (fertile) for several years immediately before they die, then their loss would cause an apparent increase (decrease)

in the proportion of the monitored population that was reproductive through time. It is essential to evaluate the performance of individuals that are removed from focal tree censuses to document long-term trends.

Sustained changes in tropical forest dynamics were initially attributed to rising atmospheric CO_2 concentrations (Phillips & Gentry 1994). The potential contribution of elevated CO_2 to above-ground biomass was subsequently evaluated using forest dynamics models (Chambers *et al.* 2004). These models incorporated mortality, recruitment and growth rates observed for trees from the central Amazon and then added the maximum 25% increase to growth rates that has been observed experimentally when CO_2 is doubled in the presence of ample light, water and nutrients. Model simulations showed that this maximum potential contribution of elevated CO_2 to above-ground biomass equalled just 16% of the increase actually observed for the same sites (I obtained 16% using the above-ground biomass changes reported for the same 17 Biological Diversity of Forest Fragments Project and Bionte sites by Baker *et al.* (2004) and their assumption that 50% of above-ground biomass is carbon). In the only CO_2 fertilization experiment performed with tropical trees, branch-level carbohydrate concentrations increased and photosynthesis was quickly down regulated in fully sun exposed, upper canopy branches (Lovelock *et al.* 1999). Thus, the one relevant experiment suggests that rising atmospheric CO_2 concentrations will not influence the productivity of old-growth tropical forests. Additional tropical CO_2 fertilization experiments are badly needed.

A second possible cause of sustained changes in forest dynamics is that a much more potent limiting factor – light – has also increased (Lewis *et al.* 2004). Solar irradiance penetrating the atmosphere and measured at the Earth's surface decreased by 4–6% between *c.* 1960 and 1990 – a phenomenon dubbed global dimming (Stanhill & Cohen 2001). This trend has reversed from 1990 to 2002 – a phenomenon recently dubbed global brightening (Wild *et al.* 2005). Satellite-based measurements of the radiative balance of the upper atmosphere confirm that solar irradiance reaching the Earth's surface decreased between 1983 and 1990 and increased between 1990 and 2001 (Wielicki *et al.* 2002, 2005; Pinker *et al.* 2005). Speculation about the causes of global dimming includes anthropogenic increases in atmospheric aerosol loadings and possibly cloud cover (Stanhill & Cohen 2001). Speculation about causes of global brightening include reduced aerosol loadings associated with air pollution control, the decline of the Eastern European economy, and recovery from the June 1991 explosion of Mt Pinatubo (Wild *et al.* 2005). In any event, the recent increase in solar irradiance is not evident on BCI where instead ENSO-related variation overwhelms any long-term trend in solar irradiance (Fig. 5).

To summarize, this study provides independent evidence that production by trees and lianas and the relative importance of lianas are increasing on a decadal time scale in old-growth, humid tropical forests. The ENSO has shifted toward more frequent and more severe El Niño events in recent decades (Federov & Philander 2000; Schöngart *et al.* 2004). The shift toward El Niño conditions, recent increases in solar irradiance, and increases in atmospheric CO_2 concentrations may all contribute to changes in the structure and dynamics of old-growth tropical forests (Lewis *et al.* 2004). Further changes in the ENSO might occur with global warming (Federov & Philander 2000; Collins 2005). This will further alter flower and seed production, which will in turn alter the abundances of pollinators, frugivores and granivores (Curran *et al.* 1999; Wright *et al.* 1999; Ticktin 2003) and shift the competitive balance among plant species when seed production limits recruitment (Svenning & Wright 2005; Muller-Landau 2006). These possible changes in the dynamics of tropical forests are of central importance, and the search for their signal in additional independent data sets should be a high priority.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from http://www.Blackwell-Synergy.com:

Table S1 Monthly time series of ENSO indices, BCI climate, and numbers of species flowering and fruiting.

Table S2 Annual time series of flower records and seed production for 81 BCI species.