CrossMark

ECOSYSTEM ECOLOGY – ORIGINAL RESEARCH

Growth and reproduction respond differently to climate in three Neotropical tree species

Raquel Alfaro-Sánchez[1] · Helene C. Muller-Landau[2] · S. Joseph Wright[2] · J. Julio Camarero[3]

Abstract The response of tropical forests to anthropogenic climate change is critically important to future global carbon budgets, yet remains highly uncertain. Here, we investigate how precipitation, temperature, solar radiation and dry- and wet-season lengths are related to annual tree growth, flower production, and fruit production in three moist tropical forest tree species using long-term datasets from tree rings and litter traps in central Panama. We also evaluated how growth, flower, and fruit production were interrelated. We found that growth was positively correlated with wet-season precipitation in all three species: *Jacaranda copaia* ($r = 0.63$), *Tetragastris panamensis* ($r = 0.39$) and *Trichilia tuberculata* ($r = 0.39$). Flowering and fruiting in *Jacaranda* were negatively related to current-year dry-season rainfall and positively related to prior-year dry-season rainfall. Flowering in *Tetragastris* was negatively related to current-year annual mean temperature while *Trichilia* showed no significant relationships of reproduction with climate. Growth was significantly related to reproduction only in *Tetragastris*, where it was positively related to previous year fruiting. Our results suggest that tree growth in moist tropical forest tree species is generally reduced by drought events such as those associated with strong El Niño events. In contrast, interannual variation in reproduction is not generally associated with growth and has distinct and species-specific climate responses, with positive effects of El Niño events in some species. Understanding these contrasting climate effects on tree growth and reproduction is critical to predicting changes in tropical forest dynamics and species composition under climate change.

Keywords Dendrochronology · Flower production · Fruit production · Barro Colorado Nature Monument · ENSO

Introduction

Moist tropical forests exhibit considerable spatial and temporal variation in tree growth and productivity, variation which has been related in part to climate and soils (Clark et al. 2013; Graham et al. 2003; Wright and Calderón 2006; Phillips et al. 2009; Wright et al. 2010). Anthropogenic global change is modifying these drivers through rising temperatures, altered cloud cover and rainfall regimes, and increased nitrogen deposition, leading to considerable speculation regarding the impacts on tropical forest dynamics (reviewed by Wright et al. 2010). Interannual variation in climate, such as that associated with El Niño-Southern Oscillation (ENSO) events (Ropelewski and Halpert 1987; Philander 1990; Schöngart et al. 2004), provides an opportunity to investigate how climate affects tree growth (e.g., Brienen et al. 2010) and reproduction in tropical forests (Zimmerman et al. 2007). Interspecific variation in how tree growth and reproduction respond to interannual climate

✉ Raquel Alfaro-Sánchez
r.alfarosanchez@gmail.com

[1] Laboratory of Tree-Ring Research, University of Arizona, 1215 E Lowell St, Tucson, AZ 85721, USA

[2] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama

[3] Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana, 1005, 50192 Saragossa, Spain

⧠ Springer

variation also provides insights into how tree species composition may be altered under future climate change.

Seasonal and interannual variation in rainfall, temperature and solar radiation influence tree growth across the tropics (Worbes 1995, 1999). Higher rainfall has been associated with increased tree growth in wet tropical forests (Feeley et al. 2007; Clark and Clark 2010; Clark et al. 2013). Higher minimum (night-time) temperatures have been associated with lower growth rates, a relationship hypothesized to be due to higher respiratory costs (Clark et al. 2003, 2013; Clark and Clark 2010; Feeley et al. 2007; but see Cheesman and Winter 2013). Warmer daytime temperatures may also contribute to decreased forest productivity by reducing water-use efficiency of canopy leaves (Clark and Clark 2010). Seasonal and interannual variation in solar radiation has also been hypothesized to influence productivity in moist tropical forests through positive effects on photosynthesis (Graham et al. 2003; Nemani et al. 2003; Wright and Calderón 2006). In contrast, cloudy conditions only enhance photosynthesis when the increase due to diffusion of light exceeds the loss due to absorptance and reflection of light (Roderick et al. 2001).

In tropical forests, repeated tree diameter measurements are widely used to provide information on supra-annual variation or (less commonly) interannual variation in radial growth (Clark et al. 2003, Clark et al. 2013; Clark and Clark 2010; Feeley et al. 2007; Dong et al. 2012). However, the vast majority of these tree growth datasets span at most a few decades, and only a small minority includes annual data. Dendrochronology (tree-ring analysis) can provide longer datasets of annual growth, thus providing much more information on temporal variation in growth (Worbes 1995; Zuidema et al. 2012, 2013). Dendrochronological investigations in the tropics have mainly focused on areas with strong seasonality, specifically areas subjected to seasonal drought or flooding (Worbes 1995, 2002; Schöngart et al. 2004; Rozendaal and Zuidema 2011). Previous tree-ring studies in tropical forests found that interannual variation in growth was generally related to rainfall and/or temperature (Brienen and Zuidema 2005; Couralet et al. 2010; Mendivelso et al. 2013, 2014; Vlam et al. 2014).

Long-term datasets on tropical tree reproduction are sparse, mostly short, and noisy, and relatively less is known about how reproduction relates to climate (but see Wright and Calderón 2006). Given that tree growth and fruit production both represent carbon expenditures, we might expect them to have similar relationships to climate. Growth and reproduction might, however, show different patterns of variation reflecting year-to-year variation in carbon allocation and storage (LaDeau and Clark 2001; Rowland et al. 2014; Wagner et al. 2016). Negative interannual relationships between growth and fruit production may reflect allocation tradeoffs (Eis et al. 1965), or may simply

result from dependence on different climatic conditions (Knops et al. 2007). The production of large fruit crops is thought to be associated with decreased growth in masting tree species, which produce large crops at supra-annual intervals (Kelly and Sork 2002; Sakai et al. 2006). Relatively few Neotropical tree species show masting behavior (Wright et al. 2005, but see Norden et al. 2007), which opens the question of how growth, flower production, and fruit production are related in these species.

Here, we investigate how climate, radial growth, flower production, and fruit production are related using long-term records for three tree species from the moist tropical forests of the Barro Colorado Nature Monument (BCNM). We analyze 42–75 years of growth data reconstructed from tree rings, 28 years of flower and fruit production data obtained from litter traps, and local climate records. We address the following questions: (1) How is interannual variation in tree growth, flower production, and fruit production related to interannual variation in rainfall, temperature, and solar radiation? (2) Are climatic responses similar among species, and between growth and reproduction within species? (3) How are growth, flower production, and fruit production related to each other within species? Based on previous work, we expect that tree species will show positive growth responses to precipitation (Devall et al. 1995), positive responses of flower and fruit production to solar radiation (Wright and Calderón 2006), and thus no or possibly negative relationships of growth with flower and fruit production.

Methods

Study site and species

The study was carried out in the Barro Colorado Nature Monument (BCNM), a fully protected 5600-hectare reserve including Barro Colorado Island (BCI) and surrounding mainland peninsulas. The BCNM contains a mixture of old-growth and secondary wet tropical forest (Leigh 1999). Annual rainfall averages 2650 mm and is strongly seasonal, with just 10% falling from mid-December through mid-April.

We chose three abundant tree species known to form annual rings (Devall et al. 1995, 1996) and belonging to different families (see Table 1): *Jacaranda copaia* (Aubl.) D. Don (Bignoniaceae), *Tetragastris panamensis* (Engler) O. Kuntze (Burseraceae), and *Trichilia tuberculata* (Triana and Planch.) C. DC. (Meliaceae). *Jacaranda* is a light-demanding, deciduous species (up to 45 m height), whereas *Tetragastris* and *Trichilia* are shade-tolerant, evergreen species (up to 30 and 35 m height, respectively; Croat 1978). *Tetragastris* and *Trichilia* are dioecious, with sexes

Table 1 Species characteristics and dendrochronological statistics

	Jacaranda	*Tetragastris*	*Trichilia*
Shade tolerance	Light-demanding	Shade-tolerant	Shade-tolerant
Leaf phenology	Deciduous	Evergreen	Evergreen
Mean flowering date (day-of-year)	87	205	144
Mean fruiting date (day-of-year)	245	81	256
Dbh of sampled trees, mean ± SE (cm)	47.0 ± 2.9	38.8 ± 2.4	32.3 ± 1.6
Mean (range) tree-ring series length (years)	48 (23–106)	97 (63–125)	92 (56–153)
Best-replicated period	1972–2014	1939–2014	1939–2014
No. trees/no. radii	17/31	18/30	22/40
Tree-ring width, mean ± SE (mm)	3.49 ± 0.37	1.57 ± 0.12	1.39 ± 0.11
AC1[a]	0.30	0.42	0.37
MSx[a]	0.36	0.15	0.18
R-bar[a]	0.40	0.21	0.31

[a] AC1 is the first-order autocorrelation of ring-width indices, which measures the year-to-year growth similarity. MSx is the mean sensitivity of ring-width indices, which quantifies the year-to-year variability in width of consecutive rings. *R*-bar is the mean inter-series correlation between trees, which measures the internal coherence of tree-ring data within a species
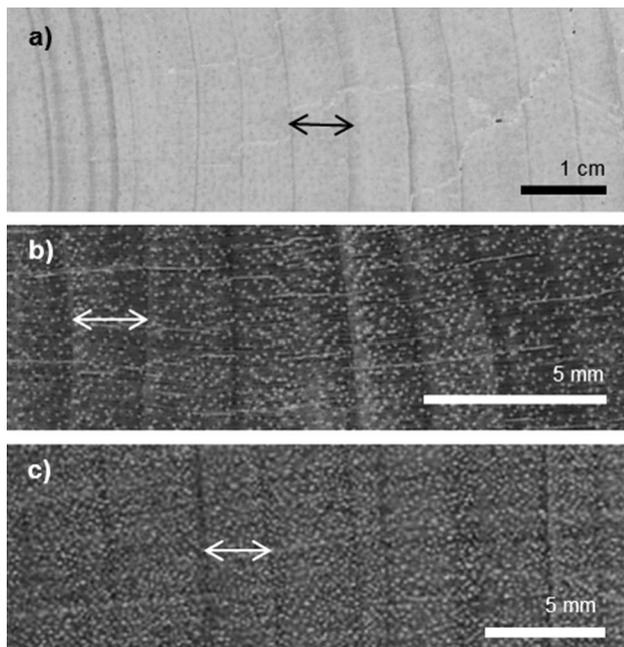

Fig. 1 Wood cross sections of *Jacaranda copaia* (**a**), *Tetragastris panamensis* (**b**), and *Trichilia tuberculata* (**c**). Each *double-headed arrow* indicates one annual tree ring. The growth direction is from *left* (pith) to *right* (bark)

almost equally represented within the BCNM (De Steven and Wright 2002). All three species have diffuse-porous wood and form tree-ring boundaries consisting of marginal parenchyma bands, albeit *Jacaranda* showed the most distinct increment zones (Fig. 1). *Jacaranda* flowers during the dry season and fruits during the wet season; *Tetragastris* flowers during the wet season and fruits at the end of the dry season and *Trichilia* flowers early in the wet season and fruits in the mid-wet season (Zimmerman et al. 2007) (Table 1; Fig. 2).

Climate data

Rainfall, air temperature, and solar radiation were collected on BCI since 1930, 1972, and 1984, respectively. Since 1972 data were collected in the Lutz stream catchment on the northeast slope of BCI by the Physical Monitoring Program of the Smithsonian Tropical Research Institute (http://biogeodb.stri.si.edu/physical_monitoring/research/barro-colorado). Daily rainfall data were recorded manually in a clearing with a rain gauge. Earlier rainfall data were provided by the Panama Canal Authority (ACP) station located approximately 360 m to the NNW of the BCI rainfall monitoring station. We compared precipitation data between ACP and BCI for the overlapped period 1972–2014, and found a very high correlation ($r = 0.91$, $P < 0.001$, Fig. S1). Temperature was recorded with a Taylor max–min thermometer in the understory (1 m above ground) at the Lutz meteorological tower. Solar radiation was recorded at the top of the tower with a pyranometer (Li-Cor Silicon Pyranometer, Lincoln, NE, USA). The tower was originally 42 m in height, and was raised to 48 m in 2001 to keep it above the surrounding canopy as nearby trees grew.

The timing and length of the growing seasons of trees are not as neatly defined in tropical as in temperate and boreal forests (Worbes 1995; Borchert 1999). This makes it tricky to construct appropriate climate metrics with which to relate annual growth, much less flower and seed production, which follow species-specific phenological years (Fig. 2). We used rainfall data to define the first and last
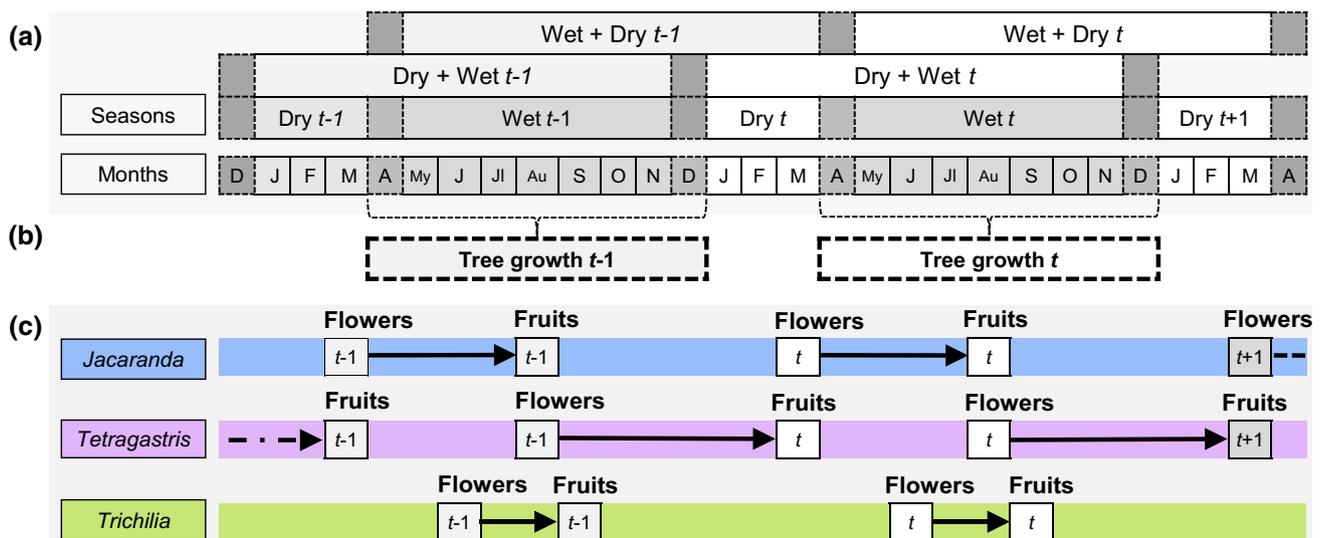
Fig. 2 Relationship of seasonal climate variation in the moist tropical forest of the Barro Colorado Nature Monument (**a**), with inferred annual growth in the focal ring-forming tree species at this site (**b**), and species-specific flower and fruit production in the focal species (**c**). Annual climate variables are computed by combining a wet-season value with the previous or following dry season value, with these two alternate annual metrics denoted Dry + Wet and Wet + Dry, respectively

dates of the dry season for every year from 1930 through 2014 (Supplementary Methods, Table S1). We calculated climate metrics for each dry season, each wet season, each dry season and following wet season combined, and each wet season and following dry season combined (Fig. 2a). The climate metrics we calculated were total precipitation, average daily solar radiation, average daily maximum, minimum and mean temperatures (as the average between the daily maximum and minimum temperatures), and dry- and wet-season lengths in days (Electronic Supplementary Material 2, Table S1).

We excluded highly correlated ($r > 0.70$) climate variables. Thus, we retained dry- and wet-season rainfall (R_D and R_W, respectively) and excluded annual rainfall metrics (R_{DW} and R_{WD}) because they were highly correlated with R_W (Table S2a). We retained both annual mean temperature metrics (T_{DW} and T_{WD}) and the annual minimum temperature $Tmin_{WD}$ (Table S2a). We retained average wet-season solar radiation (Sr_W) while dry-season solar radiation was not considered, because light is unlikely to be limiting in the dry season when there are few clouds (Wright and Calderón 2006). We also included dry- and wet-season lengths (DSL and WSL, respectively).

To characterize ENSO events, we used the Southern Oscillation Index (SOI) and three related sea-surface temperature indices (ENSO3, ENSO1.2 and ENSO3.4) obtained from the KNMI Climate Explorer webpage (http://climexp.knmi.nl). The SOI is based on air pressure differences between Tahiti and Darwin, Australia and is inversely related to the strength of ENSO events (Trenberth

and Caron 2000). The sea-surface temperature indices cover different areas of the equatorial Pacific. ENSO3 corresponds to 90°–150°W and 5°N–5°S, ENSO1.2 corresponds to 80°–90°W and 0°–10°S, and ENSO3.4 corresponds to 120°W–170°W and 5°N–5°S. The ENSO3 and ENSO1.2 regions are closest to the BCNM. Strong "El Niño" events were defined as those with at least eight consecutive months of sea-surface temperature anomalies in the ENSO3.4 region exceeding +0.5 °C that bring anomalous high temperatures, low cloud cover, low rainfall, and high solar irradiance to the BCNM (Wright and Calderón 2006) (Electronic Supplementary Material 2).

Dendrochronological sampling and analyses

We sampled 57 trees in January–April 2015 (Table 1). We used Pressler increment borers (Haglöf, Sweden) to collect cores at 1.3 m height from mature trees reaching the canopy in the Gigante Peninsula, one of the mainland areas of the BCNM. We also used chain saws to collect cross sections (disks) from recently, naturally fallen trees on BCI. Cores and disks were air dried and carefully polished with increasingly fine sandpaper until rings were clearly visible and then scanned at 3200 dpi resolution using a flatbed scanner (Epson Expression 10,000 XL). Tree rings were assigned to a calendar year through visual cross-dating. We measured ring widths to 0.01 mm resolution using the software CDendro-CoRecorder (Cybis Elektronik 2013). We verified the visual cross-dating using the program

COFECHA (Holmes 1983) (Electronic Supplementary Material 2).

Following standard practices for analyses of interannual variation in radial growth, we removed size-dependent growth changes to obtain a detrended and standardized chronology of ring-width indices for each species using the program ARSTAN (Cook 1985). Each tree-ring width series was detrended using negative exponential or linear functions to preserve the high-frequency variation in tree growth. Detrended series were standardized and averaged within species using a bi-weight robust mean (Cook and Holmes 1996). The resulting standardized indexed ring-width series, which still preserved first-order autocorrelation, were used to analyze relationships of growth with climate, flower production, and fruit production. We calculated three standard dendrochronological statistics to characterize the growth features of each species. AC1 is the first-order autocorrelation of ring-width data, which measures year-to-year growth similarity. MSx is the mean sensitivity of ring-width indices, which quantifies the relative year-to-year variability in growth. R-bar is the mean inter-series correlation, which measures the internal coherence of ring-width indices among individuals within species (Cook and Kairiukstis 1990). To check that our results were robust to the details of our detrending methods, we also repeated all analyses using a different detrending method based on cubic smoothing splines. Results based on this alternative detrending method are shown in the Electronic Supplementary Material 1.

Flowering and fruiting data

Flowering and fruiting data were obtained from weekly censuses of flower, seed, and fruit rain at two sites located on BCI from January 1987 through December 2014. The first site is the 50-ha Forest Dynamics Plot, where we censused 200 traps (0.5 m^2 per trap) and recorded counts for seeds and fruits and the presence of flowers (Electronic Supplementary Material 2). The second site is located on Poacher's Peninsula, the southernmost extension of BCI, where we censused 59 traps (0.25 m^2 per trap) and recorded dry masses of all flowers, seed, and fruits captured (g m^{-2} $year^{-1}$) (Electronic Supplementary Material 2). We standardized flower data sets to standard normal deviates for each species using annual numbers of flower presences and flower dry mass for the 50-ha plot and Poacher's Peninsula, respectively. We also standardized fruit data sets to standard normal deviates but first had to combine counts of simple seeds and fruits for the 50-ha plot. To do this, we multiplied seed and fruit counts by species-specific mean dry masses and summed to obtain annual values. We also *log* transformed both fruit dry mass

data sets to achieve normality before converting to standard normal deviates. Finally, we combined the standardized data sets for each phenophase using weights proportional to relative sampling area (100 and 14.75 m^2 for the 50-ha plot and Poacher's Peninsula, respectively).

Statistical analyses

We calculated Pearson correlation coefficients to evaluate associations of climate variables (R_D, R_W, T_{DW}, T_{WD}, $Tmin_{WD}$, Sr_W, DSL, WSL) with: (1) ENSO indices; (2) ring-width indices; (3) flower and fruit production. Correlations involving standardized ring-width indices were calculated for the best-replicated period (i.e., 1972–2014 for *Jacaranda* and 1939–2014 for *Tetragastris* and *Trichilia*). Correlations involving flower and fruit production were restricted to the 1987–2014 period. We included current and prior-year climate variables because a lagged effect of climate on tree growth and reproduction has frequently been found for tropical tree species (Brienen and Zuidema 2005; Wright and Calderón 2006, respectively). Thus, we calculated 16 correlation coefficients to evaluate climate–growth, climate–flowering and climate–fruiting relationships for each species (eight climate variables for the current and prior years) and used species-wise, Bonferroni-corrected (α') significance levels to protect against Type I errors ($\alpha' = 0.05/16 = 0.0031$). We calculated Pearson correlation coefficients to evaluate associations of ENSO indices with (1) ring-width indices and (2) flower and fruit production. We calculated four correlation coefficients to evaluate ENSO-growth, ENSO-flowering and climate-fruiting relationships for each species and used species-wise, Bonferroni-corrected (α') significance levels to protect against Type I errors ($\alpha' = 0.05/4 = 0.0125$). Finally, we calculated Pearson correlation coefficients of tree-ring indices with flower and fruit production, and between flower and fruit production, within each species. To test whether any relationships of flower and fruit production with tree growth were driven by both being dependent on climate variables, we also calculated partial correlations while controlling for the effects of individual climate variables.

Results

Tree growth

The species-specific ring-width chronologies ranged from 23 to 153 years in length, with a mean of 79 years. Mean tree-ring widths were 3.49, 1.57, and 1.39 mm for *Jacaranda, Tetragastris*, *and Trichilia*, respectively (Fig. 1).

The first-order autocorrelation was largest for *Tetragastris*, and year-to-year variability was highest in *Jacaranda* (Table 1). The R-bar values were 0.40, 0.21, and 0.31 for *Jacaranda*, *Tetragastris*, and *Trichilia*, respectively, which indicates relatively synchronous growth among conspecific individuals.

ENSO indices and climate

The ENSO3, ENSO1.2, and ENSO3.4 indices were significantly and negatively correlated with annual and wet-season rainfall and positively associated with mean, minimum, and maximum temperatures. ENSO1.2 was also significantly positively correlated with solar radiation. ENSO3 and ENSO1.2 were significantly and positively correlated with DSL (Table S2a). SOI was significantly and positively associated with annual and wet-season rainfall and significantly negatively correlated with annual and maximum temperatures.

Relationships of climate and ENSO indices to growth, flower and fruit production

The three tree species exhibited significant positive correlations between ring-width indices and current-year wet-season rainfall for the period 1972–2014 in *Jacaranda* and 1939–2014 in *Tetragastris* and *Trichilia* (Table 2; Table S3; Fig. S2a). These climate–tree growth relationships varied with the length of the data analyzed. For the 1987–2014 period (during which flower and fruit production data were available), *Jacaranda* exhibited significant positive correlations of ring-width index with current-year wet-season rainfall as well as significant negative correlations with $Tmin_{WD}$. This species also exhibited significant negative associations of current-year dry-season rainfall with flower production and significant positive associations of previous-year dry-season rainfall with fruit production. *Tetragastris* exhibited a significant positive correlation between current-year annual temperature (T_{DW}) and flower production (Table 2; Table S3). *Trichilia* showed a significant

Table 2 Pearson correlation coefficients calculated by relating tree growth (standardized ring-width indices), flower production, and fruit production with climate variables in the current and previous years for *Jacaranda* (a), *Tetragastris* (b), and *Trichilia* (c)

	Climatic period	R_D	R_W	T_{DW}	T_{WD}	$Tmin_{WD}$	Sr_W	DSL	WSL
(a) *Jacaranda*									
Tree growth	Current year	0.00	**0.63**	0.02	−0.05	−0.02	−0.47	0.01	0.11
	Previous year	−0.04	−0.16	0.10	0.05	0.10	0.30	−0.01	0.04
Flowers	Current year	−0.59	−0.11	0.35	0.30	0.21	−0.02	−0.06	−0.23
	Previous year	0.38	−0.06	−0.00	0.09	0.02	−0.07	−0.29	0.16
Fruits	Current year	−0.44	0.00	0.15	0.10	0.12	0.08	−0.16	−0.23
	Previous year	**0.55**	0.01	−0.14	−0.07	−0.02	0.03	0.07	0.17
(b) *Tetragastris*									
Tree growth	Current year	0.12	**0.39**	−0.17	−0.20	−0.22	−0.26	−0.09	0.13
	Previous year	−0.07	−0.25	0.14	0.02	0.04	0.45	0.23	−0.02
Flowers	Current year	−0.18	−0.17	**0.56**	0.26	0.09	0.04	−0.19	0.05
	Previous year	0.28	0.12	0.31	0.44	0.06	0.07	−0.41	0.24
Fruits	Current year	0.03	−0.14	0.02	0.02	0.30	0.45	0.20	−0.03
	Previous year	−0.11	−0.2	−0.01	−0.04	0.23	0.16	0.40	−0.47
(c) *Trichilia*									
Tree growth	Current year	−0.08	**0.39**	−0.32	−0.39	−0.35	−0.37	−0.05	0.14
	Previous year	0.00	−0.26	−0.18	−0.21	−0.18	0.12	0.26	−0.06
Flowers	Current year	−0.08	−0.16	−0.02	0.25	0.46	0.26	0.18	−0.07
	Previous year	0.21	−0.31	0.03	0.02	0.23	0.24	−0.25	−0.19
Fruits	Current year	−0.38	−0.17	0.06	0.17	0.03	0.09	0.22	−0.19
	Previous year	0.28	−0.13	−0.24	−0.11	−0.27	−0.10	−0.44	−0.09

Correlations of tree growth with total dry season rainfall (R_D), total wet-season rainfall (R_W), dry season length (DSL) and wet-season length (WSL) were calculated for 1972–2014 in *Jacaranda* and for 1939–2014 in *Tetragastris* and *Trichilia*. In all species, correlations of growth with annual mean and minimum temperatures (T_{DW}, T_{WD}, $Tmin_{WD}$, see Fig. 2) were calculated for 1972–2014 and with average daily wet-season solar radiation (Srw) were calculated for 1984–2014. Correlations of flower and fruit production with climate variables were calculated for 1987–2014. Bold indicates values that are statistically significant after applying species-wise Bonferroni corrections to protect against Type I errors, $\alpha' = 0.05/16 = 0.0031$. Tree growth results for the period 1987–2014 alone (paralleling the flowering and fruiting time series) and results based on an alternative detrending methods are given in Table S3

Table 3 Pearson correlation coefficients calculated by relating tree growth (standardized ring-width indices), flower production, and fruit production with SOI and ENSO indices for *Jacaranda* (a), *Tetragastris* (b), and *Trichilia* (c)

	SOI	ENSO3	ENSO1.2	ENSO3.4
(a) *Jacaranda*				
Tree growth	0.22	−0.25	−0.23	−0.24
Flowers	−0.10	0.15	0.10	0.16
Fruits	−0.04	−0.01	−0.01	0.02
(b) *Tetragastris*				
Tree growth	0.05	−0.13	−0.20	−0.06
Flowers	0.14	−0.03	−0.03	−0.06
Fruits	−0.38	0.36	0.40	0.32
(c) *Trichilia*				
Tree growth	0.23	**−0.33**	**−0.37**	−0.23
Flowers	−0.44	0.42	0.43	0.39
Fruits	−0.05	0.16	0.20	0.12

Correlations of flower and fruit production were calculated for 1987–2014. Correlations of tree growth were calculated for 1972–2014 in *Jacaranda* and for 1939–2014 in *Tetragastris* and *Trichilia*. Significant values are indicated in bold after applying species-wise Bonferroni corrections to protect against Type I errors, $\alpha' = 0.05/4 = 0.0125$. Additional tree growth results for correlations with prior-year indices, for the period 1987–2014, and for tree-ring indices calculated using an alternative detrending method are given in Table S4

negative correlation between ring-width index and ENSO3 and ENSO 1.2 indices (Table 3; Table S4).

Relationships among growth, flower, and fruit production

Flower and fruit production were significantly positively correlated in *Jacaranda* ($r = 0.68$, $P < 0.0001$) and *Trichilia* ($r = 0.53$, $P < 0.001$), but not in *Tetragastris* (Fig. 3). A significant negative correlation was found between previous- and current-year flower production in *Jacaranda* ($r = -0.46$, $P < 0.05$, Fig. S3). In addition, significant negative correlations were also detected between previous- and current-year fruiting in *Jacaranda* ($r = -0.66$, $P < 0.001$) and *Trichilia* ($r = -0.38$, $P < 0.05$), but again not in *Tetragastris* (Fig. S3).

Neither *Jacaranda* nor *Trichilia* exhibited significant relationships of tree growth with prior or current year flower or fruit production. Interannual variation in *Tetragastris* tree growth was positively correlated with prior-year fruit production ($r = 0.69$, $P < 0.001$), and negatively correlated with current-year flower production ($r = -0.39$, $P < 0.05$) (Table 4). The association with prior-year fruit production remained highly significant after controlling for prior-year wet-season rainfall ($r = 0.69$ partial correlation), prior-year minimum temperature ($r = 0.66$) or prior-year dry-season length ($r = 0.69$) ($P < 0.001$ in all cases).
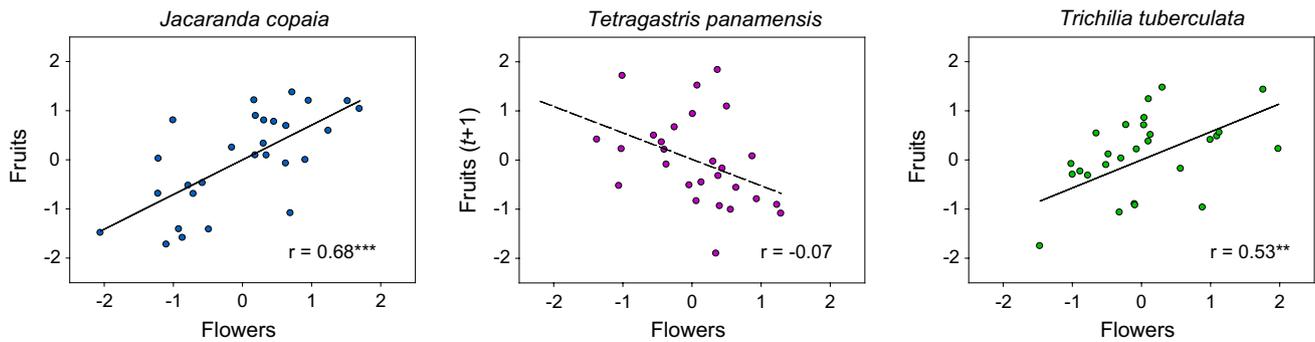

Fig. 3 Relationships of annual flower production with the corresponding annual fruit production for each of the three focal species for 1987–2014, with linear regressions (*black lines*) and associated Pearson correlations and their significance levels (**$P < 0.01$; ***$P < 0.001$). In *Tetragastris*, flower production in year t correlated with fruit production in year $t + 1$, in accordance with the phenology of this species (see Fig. 2)

Table 4 Pearson correlation coefficients of tree growth indices with prior year (t-1) and current (t) flowering and fruiting data for the period 1987–2014

	Flowers t-1	Fruits t-1	Flowers t	Fruits t
Jacaranda	−0.17 ($P = 0.407$)	−0.27 ($P = 0.180$)	−0.12 ($P = 0.531$)	−0.10 ($P = 0.598$)
Tetragastris	−0.06 ($P = 0.749$)	**0.69** ($P = 0.001$)	**−0.39** ($P = 0.041$)	0.02 ($P = 0.913$)
Trichilia	0.29 ($P = 0.137$)	−0.04 ($P = 0.825$)	0.24 ($P = 0.226$)	−0.02 ($P = 0.921$)

Significance levels (P) are given in parentheses and cases with $P < 0.05$ are highlighted in bold

However, the association with current-year flower production ceased to be significant after controlling for wet-season rainfall ($r = -0.33$, $P = 0.10$).

Discussion

Here, we evaluated how rainfall, temperature, solar radiation, and dry- and wet-season length impacted year-to-year variation in tree radial growth, flower production, and fruit production in three Neotropical tree species common at the BCNM, Panama, using long-term datasets. Multi-year census intervals provide limited power to assess how interannual climatic variation affects tree growth (e.g., Feeley et al. 2007; Dong et al. 2012), and there are very few long-term datasets of annual tree growth. We found different results when testing responses on tree growth–climate over the short (27 years) and long terms (43–75 years). These outcomes highlight the importance of carrying out long-term studies to obtain robust conclusions about effects of climate variation on tropical forest productivity and reproductive performance. Our analyses are also strengthened by the use of local meteorological data, in comparison with other studies using gridded climatic data or data from stations located further from the study sites which may underestimate climate–growth correlations (e.g., Vlam et al. 2014).

All three species exhibited some synchrony in interannual growth among conspecific individuals, with *Jacaranda* showing the highest within-species coherence (R-bar = 0.40). Given that the other two species had R-bar values below 0.4, cross-dating uncertainty is a distinct concern (Black et al. 2016). This is consistent with life history differences among the three species. *Jacaranda* is a light-demanding species whose individuals are almost always in high-light environments even as juveniles (Wright et al. 2003), and thus have fairly consistent growing conditions over time and across individuals. In contrast, *Tetragastris* and *Trichilia* are shade-tolerant species that can be found in highly variable light environments which modify their growth and confound their responses to climate (Wright et al. 2010; Worbes 1995). Similar coherence values have been reported for other tropical studies (Brienen and Zuidema 2005). *Jacaranda* also exhibited the most distinct tree-ring boundaries (Fig. 1), which combined with its high between-tree coherence, suggests that uncertainty is lowest in this species.

Wood formation showed a common response to climate in all three species, increasing with wet-season rainfall. This could indicate that stem radial growth is limited by water availability, since drought stress constrains wood formation in tropical forests probably through shorter growing seasons and stomatal closure (Phillips et al. 2009; Wagner et al. 2016). The importance of rainfall to growth is consistent with previous dendrochronological studies in Panama and other moist and dry tropical forests (Devall et al. 1995; Worbes 1999; Brienen and Zuidema 2005; Rozendaal and Zuidema 2011; Mendivelso et al. 2013, 2014), as well as with analyses of census data for multi-year intervals in permanent plots in Panama (Feeley et al. 2007). This suggests that growth occurs primarily in the wet season for the focal species in the BCNM (Fig. 2). Consistent with this idea, weekly measurements of radial stem increments in several *Trichilia* trees using dendrometers revealed that stems enlarged fairly steadily throughout the wet season, but did not increase or even shrank in the dry season (Fig. S4; C. Tribble and H. Muller-Landau, *unpublished data*). This provides further indirect evidence for the annual character of ring formation in this species (Worbes 1999). Significant correlations between chronologies and climate variables themselves comprise evidence that tree-ring widths are annual and respond to climate (Groenendijk et al. 2014).

Woody productivity in tropical forests depends on multiple climatic factors and, therefore, different growth responses to climate are expected depending on the most limiting factor for wood formation (Wagner et al. 2016). Here, tree growth increased with precipitation and decreased with current-year wet-season solar radiation (Fig. S2b), consistent with long-term tree census measurements (Clark et al. 2003, 2013; Dong et al. 2012) but inconsistent with experimental and observational studies suggesting that higher solar radiation (related to decreased cloud cover) increases tropical productivity (Graham et al. 2003 and Nemani et al. 2003, respectively). Solar radiation and rainfall were not significantly negatively correlated in our study site during the time period for which both were available, though there was a negative trend (Table S2). We conclude that growth mainly responded to precipitation variability (Table 2), while the association with radiation was an indirect output.

Reproductive patterns showed disparate responses to climate across species, consistent with their different reproductive phenologies (Fig. 2). Multispecies analyses of the BCI flower production data set indicate that flower production increases with warmer temperatures (Pau et al. 2013). Our findings are consistent with this positive relationship between temperature and flower production, but also reveal differences regarding climate sensitivity to flowering and fruiting among species. In *Tetragastris*, positive associations between flower production and T_{DW} and trends for positive associations between fruit production and Sr_W (Table 2b) suggest that flowering and fruiting were favored by sunnier and warmer conditions. In *Jacaranda*, negative associations of flower and fruit production with current dry-season rainfall (Table 2a) suggest that rainy dry seasons reduce current year flower and fruit production (albeit

the correlation is not statistically significant for fruiting). There were trends for similar responses in *Trichilia*, but correlations were not statistically significant for this species (Table 2c).

### How ENSO affects climate and tree growth, flowering, and fruiting in the BCNM

El Niño events tend to bring higher temperature and solar radiation and lower rainfall to the BCNM (Wright and Calderón 2006). Many BCI species have high levels of fruit production associated with El Niño events (Wright et al. 1999, Wright and Calderón 2006). Our analyses suggest that El Niño has consistent negative effects on radial growth across all study species and positive effects on reproduction in *Tetragastris* and *Trichilia*. These effects on radial growth and reproduction were most pronounced during the record-hot 1997–1998 El Niño (Fig. 4; Fig. S2; Howe 1990; Leigh

1999). Similar effects on tree growth were observed in the Costa Rican forest of La Selva (Clark et al. 2003) and in other tropical forests (e.g., Schöngart et al. 2004; Brienen et al. 2010).

Relationships between growth, flowering, and fruiting

The negative 1-year lagged correlations in *Jacaranda* flowering, *Jacaranda* fruiting, and *Trichilia* fruiting suggest year-to-year alternating patterns in reproductive effort (Fig. S3), consistent with previous reports for *Jacaranda* (Jones and Comita 2010). This could be explained because a high fruit yield could consume part of stored reserves (Wright et al. 1999), or alter primary-growth patterns (e.g., the formation of reproductive buds), thus affecting reproduction in the following year (Camarero et al. 2010). In addition, unfavorable climate conditions for flowering and fruit set in one year could lead to

Fig. 4 Time series of tree growth (*solid lines*), flower production (*dashed lines*), and fruit production (*dotted lines*) in the three focal tree species. Tree growth, fruit production, and flower production are standardized within each species. Strong El Niño events are indicated with *vertical gray bars*
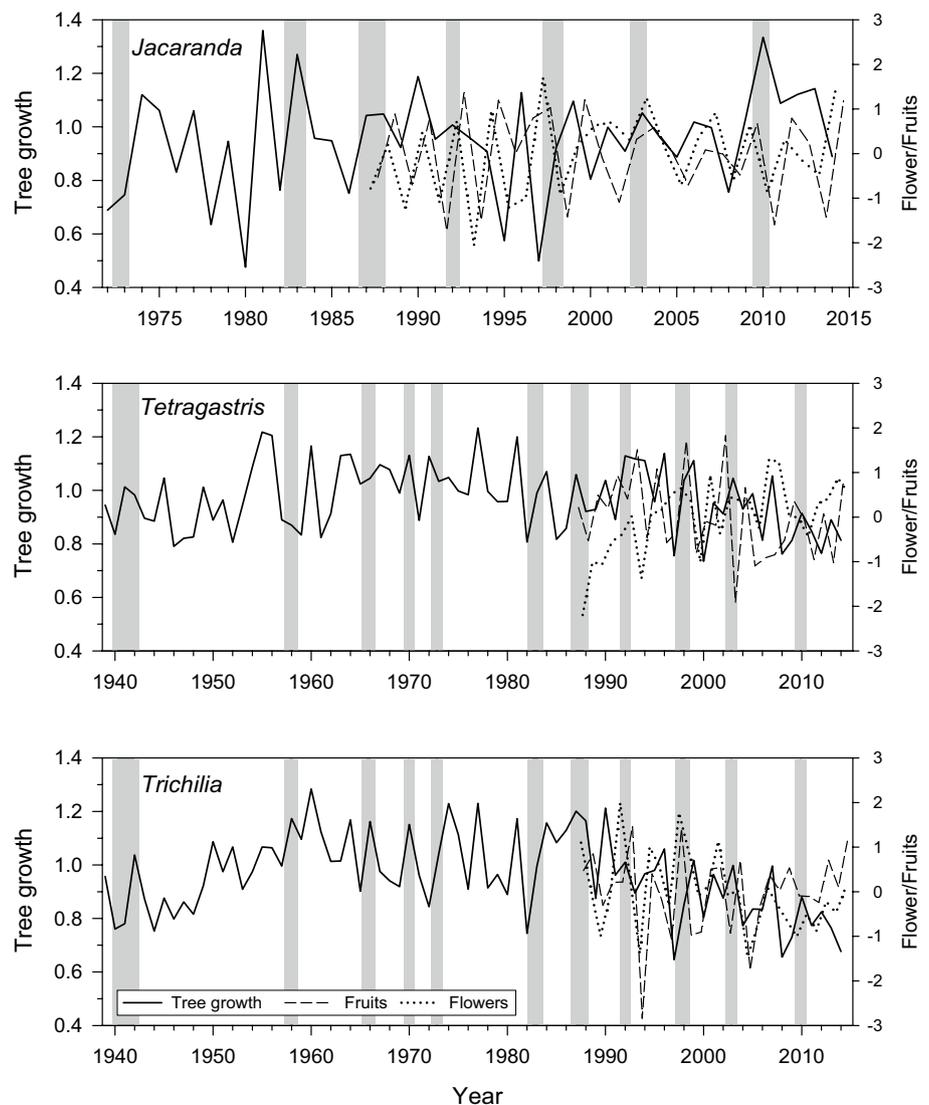
increases in stored reserves and thus enhance reproduction in the following year (Ichie et al. 2013).

Our results were not consistent with the tradeoff hypothesis (Knops et al. 2007) that allocational tradeoffs should result in negative correlations between growth and reproductive effort among years. Two of three species showed no significant correlations of growth with current or prior-year fruit or flower production. *Tetragastris* exhibited a significant positive correlation of growth with previous-year fruit production that persisted even after controlling for individual climate variables. The significant negative correlation of growth with current-year flower production in *Tetragastris* disappeared after controlling for climate. This last result is consistent with the weather hypothesis (Knops et al. 2007) that negative correlations of growth with reproduction are driven by both being independently influenced by the same environmental variables.

To conclude, radial growth of three tree species was positively related to precipitation in BCNM, whereas flower and fruit production showed different and species-specific responses to climate. Strong ENSO events and associated drier and sunnier conditions reduced growth but not reproduction. These results show that climate effects on growth may differ from those on reproduction, contrary to what would be expected if both simply vary in concert with total plant carbon gain, as assumed in vegetation models (Cramer et al. 2001). At the same time, growth and reproduction were not negatively correlated as one might assume if interannual variation were driven primarily by allocational shifts (tradeoff hypothesis; Knops et al. 2007). Our results further highlight that climate may differentially affect coexisting tree species with similar functional traits (here shade-tolerance and deciduousness), presenting a clear challenge for vegetation models in which the diversity of tropical trees is commonly reduced to at most a handful of functional types (Scheiter et al. 2013). Finally, the fairly modest relationships of growth and reproduction to climate in these tropical tree species, and their heterogeneity across species, highlight the importance of acquiring and analyzing similar data sets in other tropical forests and species.

Author contribution statement RAS conceived and led the study. All authors contributed research ideas, participated in manuscript writing, and approved the final manuscript.

References

Black BA, Griffin D, Van der Sleen P, Wanamaker AD, Speer JH, Frank DC, Stahle DW, Pederson N, Copenheaver CA, Trouet V, Griffin S, Gillanders BM (2016) The value of crossdating to retain high-frequency variability, climate signals, and extreme events in environmental proxies. Glob Change Biol 22:2582–2595

Borchert R (1999) Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. IAWA J 20:239–247

Brienen RJW, Zuidema PA (2005) Relating tree growth to rainfall in Bolivian rainforests: a test for six species using tree ring analysis. Oecologia 146:1–12

Brienen RJW, Lebrija-Trejos E, Zuidema PA, Martínez-Ramos M (2010) Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. Glob Change Biol 16:2001–2012

Camarero JJ, Albuixech J, López-Lozano R, Casterad MA, Montserrat-Martí G (2010) An increase in canopy cover leads to masting in *Quercus ilex*. Trees-Struct Funct 24:909–918

Cheesman AW, Winter K (2013) Elevated night-time temperatures increase growth in seedlings of two tropical pioneer tree species. New Phytol 197:1185–1192

Clark DA, Clark DB (2010) Assessing tropical forests' climatic sensitivities with long-term data. Biotropica 43:31–40

Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to inter-annual temperature variation during 1984–2000. Proc Natl Acad Sci USA 100:5852–5857

Clark DA, Clark DB, Oberbauer SF (2013) Field-quantified responses of tropical rainforest aboveground productivity to increasing CO_2 and climatic stress, 1997–2009. J Geophys Res Biogeosci 118:783–794

Cook ER (1985) A time series analysis approach to tree ring standardization. Tucson, University of Arizona, Arizona, USA

Cook ER, Holmes RL (1996) Guide for computer program ARSTAN. In: Grissino-Mayer HD, Holmes RL, Fritts HC (eds) The International Tree-Ring Data Bank Program Library version 2.0, user's manual. University of Arizona, Tucson, AZ, USA, pp 75–87

Cook ER, Kairiukstis LA (1990) Methods of dendrochronology: applications in the environmental sciences. Kluwer, Dordrecht

Couralet C, Sterck FJ, Sass-Klaassen U, Van Acker J, Beeckman H (2010) Species-specific growth responses to climate variations in understory trees of a central African rain forest. Biotropica 42:503–511

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Glob Change Biol 7:357–373

Croat TR (1978) Flora of Barro Colorado Island. Stanford University Press, Stanford

Cybis Elektronik (2013) CDendro and CooRecorder. http://www.cybis.se/forfun/dendro/index.htm. Accessed 15 May 2015

De Steven D, Wright SJ (2002) Consequences of variable reproduction for seedling recruitment in three neotropical tree species. Ecology 83:2315–2327

Devall MS, Parresol BR, Wright JS (1995) Dendroecological analysis of *Cordia alliodora, Pseudobombaxseptenatum* and *Annona spraguei* in Central Panama. IAWA J 16:411–424

Devall MS, Parresol BR, Lê K (1996) Dendroecological analysis of Laurel (*Cordia alliodora*) and other species from a lowland moist Tropical Forest in Panama. In: Dean JS, Meko DM, Swetnam TW (eds), Proc. international conference of tree rings, environment, and humanity, May 17–21, 1994, Tucson, AZ

Dong SX, Davies SJ, Ashton PS, Bunyavejchewin S, Supardi MNN, Kassim AR, Tan S, Moorcroft PR (2012) Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. Proc Biol Sci 279:3923–3931

Eis S, Garman EH, Ebell LF (1965) Relation between cone production and diameter increment of douglas fir (*Pseudotsugamenziesii*(Mirb.) Franco), grand fir *Abiesgrandis*(Dougl.)Lindl) and western white pine (*Pinusmonticola* Dougl.). Can J Bot 43:1553–1559

Feeley KJ, Wright SJ, Supardi MNN, Kassim AR, Davies SJ (2007) Decelerating growth in tropical forest trees. Ecology 10:461–469

Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. PNAS 100:572–576

Groenendijk P, Sass-Klaassen U, Bongers F, Zuidema PA (2014) Potential of tree-ring analysis in a wet tropical forest: a case study on 22 commercial tree species in Central Africa. For Ecol Manag 323:65–78

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull 43:69–75

Howe HF (1990) Seed dispersal by birds and mammals: implications for seedling demography. In: Bawa KS, Hadley M (eds) Reproductive biology of tropical forest plants. Man and the Biosphere Series, Parthenon/United National Educational Scientific and Cultural Organization (UNESCO). Paris and Parthenon Publishing, Carnforth, pp 191–218

Ichie T, Igarashi S, Yoshida S, Kenzo T, Masaki T, Tayasu I (2013) Are stored carbohydrates necessary for seed production in temperate deciduous trees? J Ecol 101:525–531

Jones FA, Comita LS (2010) Density-dependent pre-dispersal seed predation and fruit set in a tropical tree. Oikos 119:1841–1847

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447

Knops JMH, Koenig WD, Carmen WJ (2007) Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. PNAS 104:16982–16985

LaDeau SL, Clark JS (2001) Rising CO_2 levels and the fecundity of forest trees. Science 292:95–98

Leigh EG Jr (1999) Tropical forest ecology. A View from Barro Colorado Island. Oxford University Press, Oxford

Mendivelso HA, Camarero JJ, Royo O, Gutiérrez E, Toledo M (2013) Differential growth responses to water balance of coexisting deciduous tree species are linked to wood density in a Bolivian tropical dry forest. PLoS One 8:e73855. doi:10.1371/journal.pone.0073855

Mendivelso HA, Camarero JJ, Gutiérrez E, Zuidema PA (2014) Time-dependent effects of climate and drought on tree growth in a Neotropical dry forest: short-term tolerance vs. long-term sensitivity. Agric For Meteorol 188:13–23

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563

Norden N, Chave J, Belbenoit P, Caubère A, Châtelet P, Forget PM, Thébaud C (2007) Mast fruiting is a frequent strategy in woody species of eastern South America. PLoS One 2(10):e1079. doi:10.1371/journal.pone.0001079

Pau S, Wolkovich EM, Regetz J, Cook BI, Nytch C, Zimmerman J, Wright J (2013) Clouds and temperature drive dynamic changes in tropical flower production. Nat Clim Change 3:838–842

Philander SGH (1990) El Niño, La Niña and the Southern Oscillation. Academic PressCA, San Diego

Phillips OL et al (2009) Drought sensitivity of the amazon rainforest. Science 323:1344–1347

Roderick M, Farquhar G, Berry S, Noble I (2001) On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129:21–30

Ropelewski CF, Halpert MS (1987) Global and regional scale precipitation patterns associated with the El Nino/Southern Oscillation. Mon Weather Rev 115:1606–1626

Rowland L, Malhi Y, Silva-Espejo JE, Farfán-Amézquita F, Halladay K, Doughty CE, Meir P, Phillips OL (2014) The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest. Oecologia 174:295–306

Rozendaal DMA, Zuidema PA (2011) Dendroecology in the tropics: a review. Trees Struct Funct 25:3–16

Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yasunari T, Chong L, Nakashizuka T (2006) Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. Am J Bot 93:1134–1139

Scheiter S, Langan L, Higgins SI (2013) Next-generation dynamic global vegetation models: learning from community ecology. New Phytol 198:957–969

Schöngart J, Junk WJ, Piedade MTF, Ayres JM, Hüttermann A, Worbes M (2004) Teleconnection between tree growth in the Amazonian floodplains and the El Niño-Southern Oscillation Effect. Glob Change Biol 10:683–692

Trenberth KE, Caron JM (2000) The southern oscillation revisited: sea level pressures, surface temperatures, and precipitation. J Clim 13:4358–4365

Vlam M, Baker PJ, Bunyavejchewin S, Zuidema PA (2014) Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. Oecologia 174:1449–1461

Wagner FH, Hérault B, Bonal D, Stahl C, Anderson LO, Baker TR et al (2016) Climate seasonality limits carbon assimilation and storage in tropical forests. Biogeosciences 13:2537–2562

Worbes M (1995) How to measure growth dynamics in tropical trees. A review. IAWA J 16:337–351

Worbes M (1999) Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J Ecol 87:391–403

Worbes M (2002) One hundred years of tree-ring research in the tropics—a brief history and an outlook to future challenges. Dendrochronologia 20:217–231

Wright SJ, Calderón O (2006) Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. Ecol Lett 9:35–44

Wright SJ, Carrasco C, Calderón O, Paton S (1999) The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. Ecology 80:1632–1647

Wright SJ, Muller-Landau HC, Condit R, Hubbell SP (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology 84:3174–3185

Wright SJ, Muller-Landau HC, Calderón O, Hernandéz A (2005) Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. Ecology 86:848–860

Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Díaz S, Engelbrecht BMJ, Harms KE, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE (2010) Functional traits and the growth–mortality trade-off in tropical trees. Ecology 91:3664–3674

Zimmerman JK, Wright SJ, Calderón O, Pagan MA, Paton S (2007) Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. J Trop Ecol 23:231–251

Zuidema PA, Brienen RJ, Schöngart J (2012) Tropical forest warming: looking backwards for more insights. Trends Ecol Evol 27:193–194

Zuidema PA, Baker PJ, Groenendijk P, Schippers P, van der Sleen JP, Vlam M, Sterck FJ (2013) Tropical forests and global change: filling knowledge gaps. Trends Plant Sci 18:413–419