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Title: Drought and the interannual variability of stem growth in an aseasonal, everwet forest

Running head: drought and tree growth at Luquillo

List of authors (ORCID IDs in parentheses)**:**

J. Aaron Hogan[1,8] (0000-0001-9806-3074),

Sean M. McMahon[2] (0000-0001-8302-6908),

Vanessa Buzzard[3] (0000-0003-2929-0833),

Sean T. Michaletz[3,4,5] (0000-0003-2158-6525),

Brian J. Enquist[3] (0000-0002-6124-7096),

Jill Thompson[6] (0000-0002-4370-2593),

Nathan G. Swenson[7] (0000-0003-3819-9767),

Jess K. Zimmerman[8]

Institutional affiliations:

[1] International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL, USA 33199

[2] Smithsonian Environmental Research Center, Edgewater, MD, USA 21037

[3] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA 85721

[4] Biosphere 2, University of Arizona, Tucson, Arizona 85721

[5] Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

[6] Centre for Ecology & Hydrology, Edinburgh, Midlothian EH26 0QB, United Kingdom

[7] Department of Ecology and Evolutionary Biology, University of Maryland, College Park, MD, USA 20742

[8] Department of Environmental Sciences, University of Puerto Rico – Río Piedras, San Juan, PR, USA 00925

Corresponding author information:

J. Aaron Hogan, email: jhogan@fiu.edu, telephone: (970) 485-1412

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Abstract

Linking drought to the timing of physiological processes governing tree growth remains one limitation in forecasting climate change effects on tropical trees. Using dendrometers, we measured fine-scale growth for 96 trees of 25 species from 2013-2016 in an everwet forest in Puerto Rico. Rainfall over this timespan varied, including an unusual, severe El Niño drought in 2015. We assessed how growing season onset, median day, conclusion, and length varied with absolute growth rate and tree size over time. Stem growth was seasonal, beginning in February, peaking in July and ending in November. Species growth rates varied between 0 and 8 mm/yr and correlated weakly with specific leaf area, leaf Phosphorus and leaf Nitrogen, and to a lesser degree with wood specific gravity and plant height. Drought and tree growth were decoupled, and drought lengthened and increased variation in growing season length. During the 2015 drought, many trees terminated growth early but did not necessarily grow less. In the year following drought, trees grew more over a shorter growing season, with many smaller trees showing a post-drought increase in growth. We attribute the increased growth of smaller trees to release from light limitation as the canopy thinned because of the drought, and less inferred hydraulic stress than larger trees during drought. Soil type accounted for interannual and interspecific differences, with the finest Zarzal clays reducing tree growth. We conclude that drought affects the phenological timing of tree growth, and favors the post-drought growth of smaller, sub-canopy trees in this everwet forest.

Keywords: interannual, tree growth, drought, dendrometers, allocation, phenology, Luquillo, aseasonal, tropical forest

ACCURATELY QUANTIFYING TROPICAL TREE GROWTH AT INTERANNUAL SCALES IS DIFFICULT (Chambers *et al.* 1998). Variation remains problematic, in even the most-precise stem diameter measurements over time, for two main reasons. First, while differences in growth rates are often linked to variation in abiotic conditions including climate (Chapin *et al.* 1990, Clark *et al.* 2003, Clark *et al.* 2010, Wagner *et al.* 2016, Michaletz *et al.* 2018), it is less clear how tree growth is both influenced by resource supply and allocation at the organismal level (Körner 2006, Würth *et al.* 2005), and how these may interact (Sala *et al.* 2010). Moreover, it is methodologically difficult and painstaking to continuously monitor carbon stocks (i.e., non-structural carbohydrates) of individual trees (Körner 2015, Adams *et al.* 2017, but see Dickman *et al.* 2018). Our lack of knowledge of physiology and resource allocation is particularly acute in long-lived trees due, in part, to the impracticality of experimental manipulations (but see da Costa *et al.* 2010, Meir *et al.* 2015, Roland *et al.* 2015). Second, organism size is a primary factor underlying variability in growth and species life-history strategy (Calder 1984, Niklas 1994), and trees are no exception (Samson & Werk 1986). Studies documenting the size dependency of life-history traits in tropical trees are numerous (Hubbell 1980, Peters *et al.* 1988, Wheelwright & Logan 2004, Iida *et al.* 2014, Visser *et al.* 2016, Rüger *et al.* 2018), yet understanding how these relate to growth and contribute to tropical forest dynamics in a changing climate is vital.

Size-effects aside, tropical trees differ in growth rates across species and within individuals of the same species (Lieberman & Lieberman 1987, Poorter 1989, Clark & Clark 1992). For example, annual diameter increment for six species of adult trees in lowland tropical forest at La Selva, Costa Rica varied up to 14 mm/yr (Clark *et al.* 2003). Within sites, growth rates are greatly influenced by climate (i.e., temperature, precipitation, solar radiation) (Vlam *et* *al.* 2014, Wagner *et al.* 2016), global-scale climate drivers (i.e., the El Niño Southern Oscillation, the North Atlantic Oscillation) (Enquist & Leffler 2001, Schöngart *et al.* 2004) and environment (e.g., light, nutrients, soil moisture) (Wagner *et al.* 2012, Lambers & Poorter 1992, Brienen *et al.* 2010). The degree to and exact nature by which climate controls ecosystem productivity and tree stem growth are a topic of current debate (Chu *et al.* 2016, Michaletz *et al.* 2014, 2018). But from a climate perspective, the best single predictor of wood production in tropical trees is precipitation, explaining nearly half of the variation among 68 tropical forests (Wagner *et al.* 2016). Significant variation in growth exists among individual trees and across years, because individual-based allocation of carbon to radial stem growth is a physiological process that competes with carbon-investment in leaf, root, branch, and reproductive organ production (Chapin *et al.* 1990, Lacointe 2000, McMurtrie & Dewar 2013) and has a set phenology depending on the environment and individual performance (Alvim 1964, Shiel 1997, Baker *et al.* 2002). In tropical forests, an estimated >60% of carbon is allocated to leaves (37%) and roots (24%) (Malhi *et al.* 2011), further confounding relationships between tree stem-growth and climate (Doughty *et al.* 2014).

There is serious potential for climate change to affect tropical tree growth through the increasing concentration of atmospheric carbon-dioxide, shifting precipitation regimes and the increased frequency of drought (Malhi & Wright 2004, Choat *et al.* 2012, Feng *et al.* 2013, Wagner *et al.* 2014, Pachauri *et al.* 2014). Increased atmospheric concentrations of carbon dioxide have been hypothesized to enhance the carbon-use efficiency of plants (i.e., the ratio of carbon assimilation via photosynthesis to water loss through transpiration) (Chaves *et al.* 2003), resulting in increased growth rates. However, the degree to which an increase in carbon-use efficiency translates to changes in biomass production (i.e., stem growth) remains unclear

(Feeley *et al.* 2007, McMahon *et al.* 2010, Peñuelas *et al.* 2011, Zuidema *et al.* 2013, Van Der Sleen *et al.* 2015, Slot & Winter 2016). Conversely, there is mounting evidence that growth rates of mature tropical trees are slowing, with decreases in stem growth being attributed to an increase in temperature and drought frequency and severity (Clark *et al.* 2003, Clark *et al.* 2010, Brienen *et al.* 2015).

Droughts, and severe El Niño-related drought events in particular, decrease the physiological functioning of tropical trees through hydraulic stress (Choat *et al.* 2012, Körner 2015, Wolfe *et al.* 2016, Adams *et al.* 2017, Santiago *et al.* 2016). This can increase tree mortality (Phillips *et al.* 2010, Condit *et al.* 2013), reduce tree growth (da Costa *et al.* 2010, Rowland *et al.* 2015) and decrease forest ecosystem processes such as carbon uptake (Doughty *et al.* 2015, McDowell *et al.* 2018a). Hydraulic stress interacts with the abiotic environment (Santiago *et al.* 2016, Adams *et al.* 2017, McDowell *et al.* 2018a), making it very difficult to separate from other drivers (e.g., carbon deficit, nutrient limitation, liana load) that reduce tree physiological functioning and increase risk of mortality (Sala *et al.* 2010, Adams *et al.* 2017, McDowell *et al.* 2018a). Ultimately, the interaction of drought and tree growth is of interest because it may translate to changes in community composition of tropical forests based on the relative drought tolerance of tropical tree species, and their performance in dry years (Engelbrecht *et al.* 2007, Uriarte *et al.* 2016, Zuleta *et al.* 2017, Bartlett *et al.* 2018).

Additionally, drought effects vary with plant size, disproportionately affecting the largest individuals in the forest (Bennett *et al.* 2015, McDowell et al. 2018b). Using data from the Caxiuanã throughfall-exclusion experiment in the Amazon, Rowland *et al.* (2015) showed that xylem vulnerability to embolism increased with tree size (i.e., the stem water potential values at 50% loss of xylem connectivity, P_{50}, decreased). Although the largest trees may not necessarily dominate the carbon uptake of the forest (Meakem *et al.* 2017), they are still very important for understanding and predicting climate effects on forest structure and function, because they represent the upper bound on size distributions that determine total stocks and fluxes (Enquist *et al.* 2016, Meakem *et al.* 2017, McDowell *et al.* 2018b). Recent research has shown that taller forests in the Amazon were more photosynthetically-resistant to the 2015 El Niño drought, showing less of a decrease in remotely-sensed canopy fluorescence than shorter forests (Giardina *et al.* 2018), evidencing that they potentially access deeper, more stable sources of soil water (Brando 2018), and that hydraulic stress may not correlate directly with photosynthesis (Saleska *et al.* 2007). Therefore, drought may prove to be an increasingly important driver of ecological change in moist tropical forests through its potentially-differential size effects on tree performance (Choat *et al.* 2012, Allen *et al.* 2015, Corlett 2016, Mier *et al.* 2015, McDowell *et al.* 2018a). However, relatively less is known about how smaller trees might respond to droughts and climate change, and the potential they hold to offset the negative effects of drought on large trees (Uriarte *et al.* 2016, McDowell *et al.* 2018a).

The predictions of downscaled global climate change models for the island of Puerto Rico are: a) a 4.6-9°C warming, b) an average precipitation decline between 313 and 511 mm/yr depending on slope and aspect, and c) an 18-21% increase in the total number of dry days by 2100, depending on the IPCC emission scenario and locale (Khalyani *et al.* 2016). These projected changes are expected to disproportionately affect wetter areas of the island (i.e., El Yunque in the northeast) and at the landscape-scale are forecast to result in the loss of the subtropical rainforest and a major diminution of the subtropical wet forest Holdridge life zone by the end of the century (Khalyani *et al.* 2016). Furthermore, the Ecosystem Demography model parametrized using physiological data from trees in El Yunque was projected to 2050, forecasting forest productivity to go negative by 2036 assuming a 1.2 °C warming and 30% drought frequency (Feng *et al.* 2017). Given these predictions, it is critical to understand and validate the effects of drought through *in situ* measurements of tree growth.

We monitored fine-scale tree growth patterns for 96 tropical trees over four years (2013-2016), a period that included a severe meteorological drought. Our first objective was to characterize the seasonal phenology of tree growth. We asked:

1) What is the phenology of stem growth in this everwet forest? We hypothesized that tree growth would be greatest between May and November when temperatures are slightly warmer and total solar irradiation peaks (Zimmerman *et al.* 2007).

2) How did a sharp decrease in annual rainfall in 2016 affect the seasonality of tree growth, overall and among species? We expected that resultant hydraulic stress from drought would decrease tree stem growth and alter any seasonal patterns in growth evident under normal rainfall conditions, shortening the duration of the growing season.

3) What abiotic factors exacerbate or mediate drought susceptibility for 12 common tree species in the tree community? Ridge areas generally have less ability to retain soil water than slopes or bottoms, and soils with coarser textures drain more readily. We, therefore, anticipated topographic position and soil type to interact to determine drought susceptibility as both have been shown to influence soil water storage capacity.

As a second objective, we were interested in whether phenological patterns in growth or the effects of drought differed by tree size.

Methods

SITE DESCRIPTION & THE 2016 EL NIÑO DROUGHT. — The forest at Luquillo is a broadleaf subtropical wet forest (Ewel & Whitmore 1973) with a history of some land-use (Thompson *et* *al.* 2002) that is subject to infrequent hurricanes (Zimmerman *et al.* 1994, Hogan *et al.* 2016). The landscape is mountainous with a rugged topography dissected by several low-order freshwater streams and rivers (Scatena 1989). Soils are highly weathered, volcanically-derived clays that differ in the water permeability and occurrence; the three main soils types from most to least permeable and most common to rarest, are Zarzal (78% clay, 19% silt, 3% sand), Cristal (75% clay, 19% silt, 6% sand), and Prieto (52% clay, 29% silt, 15% sand) (Thompson *et al.* 2002, Mount & Lynn 2004). The study site was the 16 -Ha Luquillo Forest Dynamics Plot (LFDP, Latitude: 18°20'N, Longitude: 62°49'W) of Northeastern Puerto Rico. The LFDP is in the Tabonuco forest, which is dominated by *Dacryodes excelsa* Vahl and *Prestoea acuminata* (Wild.) H.E. Moore var. *montana* (Graham) A.J. Hend & Galeano. In the Tabonuco forest, a uniform canopy reaches an average height of 20 m (Brokaw & Grear 1991).

In the greater El Yunque area, precipitation ranges from 2216 mm/yr on the western, leeward side of the mountains (Guarbo watershed) to 4447 mm/yr on the southeastern, windward slopes (Icacos watershed) (Murphy *et al.* 2017), and always exceeds 100 mm/m, technically classifying the forest as aseasonal (i.e., lacking a dry season; Walter *et al.* 1975) or everwet (McGregor & Nieuwold 1998), although some seasonality in temperature exists (Fig 1a) . A severe meteorological drought started in April 2015, triggered by the unusual lack of May rains (Fig. 1b). The meteorological drought developed into a hydrological drought throughout the summer as streamflow and soil moisture decreased (Clark *et al.* 2017, O'Connell *et al.* 2018), until late August when Tropical Storms Danny and Erika passed over the forest. Danny and Erika combined dropped over 200 mm of rain in 9 d. However, rainfall at El Verde Field Station (300m adjacent to the LFDP, in northwestern El Yunque), for 2015 totaled 2036 mm, well below the annual average of 3655 mm (Fig. 1b). The light environment from 2013-2016 was constant.

Photosynthetic photon flux density and total solar infrared radiation oscillated with season, averaging about 17,000 millimoles/m^2, and 834 Watts/m^2, respectively (Fig. S1). Similarly, there was no notable change in cloud cover or minimum cloud base height from 2013-2016 (Fig. S2).

DENDROMETER BANDS. — In November 2012, spring-tensioned dendrometer bands were placed on 96 mature trees (>10 cm diameter at 1.4m from the ground) of 25 species in the LFDP. Dendrometer bands were constructed individually for each tree from 20 mm width, 150 μm thickness, hard tempered aluminum and fastened with a stainless-steel spring. The species and number of individuals fit with dendrometer bands per species are given in Table S1 (also see supplement 1).

Each dendrometer band was revisited 54 times during the 4-yr span, measuring dendrometer gap-openings using a digital Vernier caliper (Mitutoyo Digimatic 500, Mitutoyo America, USA) precise to the hundredth of a millimeter. For the first year and a half, measurements were taken every other month, then sampling was intensified to roughly every two weeks. Of 96 trees that were initially fit with dendrometer bands in November 2012, measurements were discontinued on five trees that died or were severely damaged at some point during the 4-yr monitoring period.

DATA TRANSLATION, THE FITTING OF TREE GROWTH MODELS. — Fine-scale fluctuations in dendrometer gap-openings were translated to incremental changes in stem diameter using:

$$D_{t+1} = D_t + \frac{x_{t+1} - x_t}{\pi} \qquad \text{(eq. 1)},$$

Where *x* is the dendrometer band gap, *D* is stem diameter, *t*+1 is the time at which the stem is being measured and *t* is the previous time the stem was measured (i.e., the last known diameter). This approach assumes the tree's main stem is circular. Richards 5-parameter logistic growth model (Richards 1959) was then fit to time series of tree stem diameter measurements (Fig. 2) using the workflow and functions developed by McMahon and Parker (2015).

The model gives daily tree growth, dbh_{doy}, as:

$$dbh_{doy} = \frac{L+(K-L)}{1+\left({}^{1}/_{\theta}\right)\cdot e^{(-r\,(doy-doy_{ip})/\theta)^{\theta}}}\,, \qquad \text{(eq. 2)}$$

where doy_{ip} is the day of the year where the inflection point in tree growth occurs, L and K are the upper and lower asymptotes of the logistic growth curve, respectively, r is the slope of the growth curve at the inflection point, and θ allows for asymmetrical fits (McMahon & Parker 2015). The inverse of the logistic function (see equation 3 in McMahon & Parker, 2015) was then used to estimate secondary metrics that characterize the phenology of growth of that individual: day of first growth, day of last growth, median day of growth, 80th and 90th percentiles of growing season length, and the day of the year (i.e. ordinal date) at 5, 10, 90, and 95 percent of total annual growth. Annual and relative growth rates (AGR, RGR) are also calculated from Richard's curve fits by taking the absolute and difference between the log-transformed upper and lower bounds of the growth curve (i.e. the modeled change in diameter) (McMahon & Parker, 2015)

PHENOLOGICAL INTERPRETATION OF TREE GROWTH FROM MODEL FITS & CIRCULAR STATISTICS. — We looked at relationships (i.e., paired correlations) between all secondary metrics from the Richards curve fits, including AGRs and RGRs to understand how all the parameters were related. We decided to use four of the secondary metrics from the Richards curves, which are conservative estimates of key phenological events in stem growth that correspond to biological cues related to allocation of resources to woody biomass production. They are: 1) the number of days to grow 80% of the total annual growth (growing season length), 2) the ordinal date at 10% of total annual growth (start of growing season), 3) the median ordinal date of growth (middle of growing season), and 4) the ordinal date at 90% of total annual growth (end of growing season). Because of low sampling effort in 2013, we refrained from fitting models for 42 of the individuals that had less than five measurements for the year, and we removed 16 trees from the data set due to unacceptable model fits or erratic data, because they did not grow sufficiently, or because the data had measurement error. We checked for points exerting high leverage on model fits and re-fit the models excluding them where necessary. This resulted in a total of 283 tree-yrs from 80 individuals, that we used Richards curve fit metrics from (see supplement 1) in histograms of phenological metrics.

To examine the overall seasonality and interannual differences between secondarily-derived metrics following model fitting, we used circular statistics. The circular nature of the ordinal calendar means that classical linear approaches are not adequate to statistically test the phenological timing of events against independent variables, because, for example, a tree with an ordinal date of 359 (December 25th) and tree with an ordinal date of 7 (January 7th) for middle of growing season, are equidistant from the start of the calendar year (ordinal date 1) and are not treated so in a classical linear regression. We plotted circular histograms for three of the four chosen metrics: start, middle, and end of growing season. Circular plots were not necessary for growing season length because it is measured as the number of days rather than an ordinal date. We statistically tested whether the density distributions of these phenological metrics differed from circular uniformity using the Rayleigh, Kuiper's, Watson's and Rao's tests. Circular uniformity in our case represents a lack of seasonality in growing season onset, midpoint, or conclusion. The Rayleigh test tests for any single peak departure from circular uniformity, while the other three tests have greater ability to detect more complex deviations from circular uniformity (Pewsey *et al.* 2013). Kuiper's test is a rotation-invariant Kolmogorov-type test statistic that tests whether the circular uniform distribution is contradicted by the sample distribution. Watson's test performs a goodness of fit test between the sample distribution and a circular uniform (Mardia & Jupp 2009). Lastly, Rao's test relies on the assumption that if data are circularly uniform then they ought to be roughly evenly spaced about the unit circle, and tests for deviations from even spacing as evidence for directionality (i.e. seasonality) in the data (Levitin & Russell 1999).

To examine how the seasonality of stem growth was influenced by tree performance (i.e. AGR) and tree size, we used nonparametric circular regression. The response variables: growing season length, start of growing season, middle of growing season, and end of growing season were circular-transformed and regressed against AGR and tree size. This is akin to doing classical regression with the y-axis wrapped as a cylinder, where the absolute maximum and minimum values are adjacent in the wrapped cylindrical y-axis space. The regression line is then fit through the cylindrical plane, minimizing the mean squared error. These analyses were conducted in R v. 3.4.2 (R Core Team 2017) using the 'circular' (Agostinelli & Lund 2017) and 'NPCirc' packages (Oliveira *et al.* 2014).

SPECIES DIFFERENCES & SIZE EFFECTS. —We correlated AGR and RGR with eight functional traits from the tree community. We used species-level traits collected from canopy trees of the same species in this study (Swenson *et al.* 2012), including leaf area, specific leaf area (SLA), leaf Carbon (C), leaf Nitrogen (N), leaf Phosphorus (P), wood specific gravity, plant height, and seed mass, to understand and generalize how growth rates varied among species. We limited analyses of the individual and interannual growth responses trees that had at least one annual RGR > 0.0025 %, a criterion we determined from the data to signify tree-yrs with greater than poor growth. Implementing that criterion for RGR left 195 tree-yrs from 69 individuals.

We enumerated growth from each of these individuals into categories of growth or no growth and conducted Chi-Squared tests for independence to see whether growth across years differed, whether growth between drought years (2014, 2015) differed from non-drought years (2013, 2016) and whether growth in the severe drought year of 2015 differed from the other years. Next, we classified individual growth patterns into 6 growth classifications based on the shape of the Richards curve fits over time (see supplement 1). The classifications were: 1) unaffected by drought, no post-drought growth response, 2) unaffected by drought, post-drought growth response, 3) negatively affected by drought, no post-drought growth response, 4) negatively affected by drought, post-drought growth response, 5) positively affected by drought, and 6) dying (see Table 3). We employed homoscedastic, single-factor analysis of variance with a post-hoc Tukey HSD test and eight t-tests on tree size (i.e., annual starting diameter) data of the individuals in these six classifications to examine the interplay between drought susceptibility and recovery with tree size. The eight t-tests evaluated size-differences between trees unaffected and negatively affected by drought, but with differing post-drought growth trajectories (classifications 1 vs. 2, 2 vs. 4, and 3 vs. 4), those unaffected, negatively affected and positively affected by drought (in several combinations of classifications: 1 vs. 3, 1 and 2 vs. 5, 3 and 4 vs. 5, 1 and 2 vs. 3 and 4), , and those positively affected by drought and others (classifications 1, 2, 3, and 4 vs. 5).

LINEAR MIXED MODELING. — Lastly, tree absolute growth rate was modeled using a linear mixed effect model with gamma-distributed error and an inverse link function. We implemented the same criterion characterizing trees with greater than poor growth, RGR > 0.0025 %, for 12 species (with the largest sample sizes), leaving growth data for 72 individuals comprising 180 tree-yr. We explored the use of Lidar-derived topographic variables (slope and curvature at a

23m spatial scale) from a May 2011 Lidar flight by the National Center for Airborne Laser Mapping (http://calm.geo.berkeley.edu/ncalm/ddc.html; see Wolf *et al.* 2016 for further details), as fixed effects in the model, but they did not perform as well as soil type. Soil type (as described above; Zarzal vs. Prieto vs. Coloso), tree size, and year were used as fixed covariates. Interannual and interspecific differences in growth were modeled using a random effect of year with species nested within. All independent covariates were scaled and centered prior to model building, and model selection was performed using AICc. Best Unbiased Linear Predictors (BULP) for the random factors were explored to look at year and species effects in relation to drought. Analyses were performed using 'lme4' and 'sjPlot' packages in R v.3.4.4 (R Core Team, 2017).

Results

TREE STEM GROWTH: SPECIES AND INTERANNUAL VARIATION. — Measured individual tree growth was variable over the 4-yr study period, with estimated AGRs ranging from -51 to 13 mm/yr, being negative for 26 of the 283 tree-yr, but mostly ranging from -2 to 2 mm/yr (Table S1). Absolute tree growth was not statistically different among years (ANOVA, F= 1.70, df = 3, p = .17). Early successional species, such as *Inga laurina*, tended to grow slightly faster than shade-tolerant species, such as *Dacryodes excelsa* or *Maniklara bidentata* (Table 1). When correlated with functional traits, four-year AGRs were weakly and positively correlated with SLA (r = 0.23), leaf P (r = 0.16), leaf N (r = 0.12). Pearson correlations with RGRs were very similar, however in addition to SLA, leaf P and leaf N, leaf C (r = 0.16) and total plant height (r = -0.14) were significantly correlated (all p values < .05). Within years, AGR-functional trait correlations differed slightly, with SLA being correlated in 2013 (r = 0.32) and 2015 (r = 0.28), and leaf P being correlated only in 2015 (r = 0.27); 2014 and 2016 had no significant correlations between any functional traits and AGR. Despite being statistically significant these traits explained very little of the variation in growth among individual trees. For example, the strongest correlated trait over all four years was SLA with a Pearson correlation coefficient of 0.23, and thus only explained 5% of the variation in growth. Absolute growth was marginally greater for large trees than for smaller trees in non-drought years but leveled out when precipitation declined in 2014 and 2015 (Fig. S3). Generally, absolute and relative growth rates were idiosyncratic with respect to species and tree size (Fig. S4)

Our analysis of the secondary metrics from Richards growth model fits across all 4 years show that the average growing season length (± standard error) was 160 ± 6 d. From 2013 to 2016, it was 137 ± 11, 161 ± 12, 178 ± 13, and 156 ± 8 d, respectively (Fig. 3a). Regarding the hypotheses that the length of the growing season varied with fluctuations in rainfall, we found that the length of growing season did not vary significantly across years (F = 2.32, df =3, *p* = .76). Trees in the LFDP began their annual growth cycles in the first quarter of the calendar year (Fig. 3b). Watson's test found that the distribution of the start of the growing season differed significantly from normal (Table 2). The middle of the growing season peaked between the first week in June and the first week in July (Fig. 3c) and was slightly more normally distributed (i.e., circularly uniform) than the distributions of the other either the start or end of the growing season. The end of the growing season occurred most frequently from October to early November, with about 5% of trees growing into December (Fig. 3d).

SEASONALITY, GROWTH AND TREE SIZE. — The circular regressions (Fig. 4) further clarified the seasonal pattern in stem growth in relation to absolute growth (panels a-d) and tree size (panels e-h). Over the four years for which we collected data, the average day of median growth for all individuals was June 18 (ordinal date 169, Fig. 4b,f). The average ordinal date for the start and end of the growing season were March 7 (ordinal date 66, Fig. 4c,g) and October 17 (ordinal date 290, Fig. 4d,h), respectively. Length of growing season was positively related to tree AGR up to an AGR of 2.5 mm/yr, wherein the length of the growing season reached an asymptote and oscillated noisily around a growing season length of 240 d (Fig. 4a). Trees that grew more did not necessarily tend to begin growth earlier in each calendar year, or grow later into the calendar year (Fig. 4c,d). In fact, trees with a median day of growth values closer to June 18th tended to perform better (i.e., have greater growth rates) (Fig. 4c; notice how points converge toward the 4-yr trend with increasing AGR). Tree size showed virtually no relationships with the model-derived metrics for seasonality; that is seasonal trends were consistent across trees of varying diameter (Fig. 4e-h).

INTERANNUAL VARIABILITY. — Due to the large interannual variation on rainfall during from 2013-2016 (i.e., the dry year in 2014, and the severe drought in 2015), the data were well suited to examine how tree growth varied among years in relation to climate, and we did so by plotting histograms of the metrics of seasonality. The circular histogram for start of growing season had an even annual distribution within the two-week bins, illustrating little interannual variability in the start of the growing season (Fig. 3b). The day at median growth peaked between the first week in June and the first week in July and was dominated by the growth pattern of trees in 2013 and 2014. The bins from April to May are almost exclusively driven by growth pattern of trees in 2015 and 2016 (Fig. 3c). Similarly, during these years, the distribution for the end of growing season was shifted earlier in the calendar year. In fact, there is a clear division at the end of growing season for the severe drought year of 2015, with some trees terminating growth between June and August, and others growing to the end of the growing season in November (Fig. 3d).

The circular regressions depict some interannual differences in the seasonal phenology of stem growth. For example, in 2016, the start of the growing season began slightly earlier, with the middle of the growing season occurring more than 38 d earlier than the 4-yr average, and the end of the growing season being nearly two months (59 d) premature (Fig. 4a-d). Many of the larger trees tracked seasonal growth phenology more closely (Fig. 4e-h). In the case of the two drought years (2014 and 2015 more so), the phenological timing of growth events tended to be delayed, tracking the cessation of drought conditions. The tree size-seasonal metric relationships differed in nature among years (Fig. 4e-h). For 2013 and 2014, the start of the growing season had a more-fluctuating relationship with tree size, whereas variation in end of the growing season was more consistent across tree size in the other years. Additionally, in 2016, 56 of 79 (70% of) trees completed 90% of their total annual growth earlier than October 19th, the four-yr average for end of growing season. This took place about eighty days sooner for many of the smaller individuals (dbh < 350 mm), however, the circular regression fit for 2016 more closely resembles the four-yr average for larger trees (dbh > 350mm) (Fig. 4h).

Of the 195 tree-yrs where individuals grew well (RGR > 0.0025 mm/yr), 55% (105) occurred during the drought. Of the remaining tree-yrs where individuals grew poorly, 40% occurred in non-drought years. Results from the Chi-Squared tests showed that the number of trees that grew well (RGR > 0.0025 mm/yr) was not statistically different across all years ($X^2 = 2.13$, df = 3, $p = .54$), between drought (2014, 2015) and non-drought (2013, 2016) years ($X^2 = 1.03$, df = 1, $p = .35$), or for the severe drought year of 2015 and the other three ($X^2 = 0.011$, df = 1, $p = 1$). Therefore, the drought did not impact the trees consistently (i.e., tree growth and drought were decoupled). Some trees grew during drought years, and some did not; the same occurred for non-drought years.

Based on the visual assessment of the Richard curves over time for the 65 individuals that registered at least one year with an RGR > 0.0025 mm, 22 were unaffected by the drought with no post-drought growth response, 14 were unaffected by the drought but had increased growth following the drought, 10 were negatively affected by the drought with no post-drought growth response, 11 were negatively affected by drought and had a post-drought increase in growth, six were positively affected by drought (i.e., had increased growth during the drought), and two were dying (Table 3). Analysis of variance followed by a Tukey HSD test showed no statistical difference between tree size for the six groups (F = 1.25, df = 6, *p* = .29). We conducted eight t-tests to assess size differences between trees unaffected, negatively affected, and positively affected by drought and trees with or without a growth response. The only statistical difference detected was between trees unaffected by drought, either with or without a post-drought growth response (i.e., between growth classifications 1 and 2, see Table 3). Trees that grew more post-drought were smaller (t = 2.25, df = 34, *p* = .015), however trees that were larger were not more-negatively affected by drought (t = 0.37, df = 55, *p* = .35).

SPECIES-RESPONSES. —Results from the linear mixed-effects model confirmed that in 2016 trees that grew, grew slightly more than in the previous years (*p* < .05, Table S1, Fig. 5). Furthermore, large trees tended to grow less across all years (tree size effect on AGR = -0.05, *p* < .01, Fig. 5, Table S1). Growth rates of trees that grew in 2014 and those that grew in 2015 were comparable. Growth on Prieto soil was highly variable, but the Zarzal soil type had a negative effect on tree growth (*p* < .01, Fig. 5, Table S1). Within the above described interannual dynamics of tree growth, slight intraspecific differences in AGR over the four-yr period were observed along species life-histories. The 2015 drought affected species consistently, in terms of their stem growth (Fig.6). However, the two species with most negative BULP for the random intercept for species in normal years (i.e., *Inga laurina*, and *Guarea Guidonia*), exhibited the most positive effect in 2016, the year post-drought (Fig. 6). In other words, species that grew well in 2013 and 2014, grew more poorly following drought in 2016 and vice versa. These trends are subtle and rarely statistically significant (i.e., most of the BLUP confidence intervals intersect the zero-effect line, Fig. 6).

Discussion

Patterns of tree growth at Luquillo are seasonal and vary inter-annually with rainfall, with drought increasing seasonal variability. We frame our discussion on interannual trends in the tree growth of the Luquillo everwet forest in relation to the timing of stem growth, the variability in that dynamic attributable to environmental differences and growth difference by tree size. Wagner *et al.* (2016) found that sites lacking a dry season, like Luquillo, were outliers in their analyses of precipitation controls on wood production in tropical forests. In very wet tropical forests, stems can be subject to waterlogging, which results in cambial dormancy during the wettest periods of the year when the soil is water-saturated (Schöngart *et al.* 2002). Absolute growth rates of trees measured were comparable to other Caribbean montane forests (Bellingham & Tanner 2000), and lower than typical Neotropical lowland forest (Lieberman & Lieberman 1987, Clark *et al.* 2003).

A significant limitation of the use of dendrometer bands is the inability to separate wood production from incremental increases in stem diameter (Keeland & Sharitz 1993, Stahl *et al.* 2010). At the scale of our dendrometer measurements, diurnal fluctuations in stem water potential were consistent and thus negligible (Baker *et al.* 2003). However, several trees showed significant stem shrinkage in response to dry environmental conditions (see table S1, supplement 1), reflecting atmospheric and soil moisture deficit (Stahl *et al.* 2010, Uriarte *et al.* 2016, Bretfield *et al.* 2018). The degree to which individual stems shrunk during drought varied, and was greatest for *Manilkara bidentata*, a Sapotaceae with thick bark and a corky periderm (Keeland & Sharitz 1993, Table S1). We are still confident that we have measured variation in stem wood production because changes in stem diameter of angiosperm trees can be compared to that of a tree fern *Cyathea arborea* (see tree 74, CYAARB in supplement 1), which decreased in stem diameter 0.4 mm over the 4-yr study period. Thus, in the absence of wood production, stem shrinkage due to decreases in stem water potential for these data are estimated to occur at a maximum rate of 0.1 mm/yr.

THE TIMING OF STEM GROWTH AT LUQUILLO. — From 2013 to 2016, eighty percent of tree growth occurred in two-thirds (66.8% or 244 d) of the calendar year between March 7 and October 16 (Figs. 3 & 4). Stem growth increased in the summer months, peaking at June 15th (Fig.3), which corresponds to the temporal onset of sap flow increase in the trees (Warren 2009), slightly warmer temperatures, the maximum of total solar irradiance in the environment (Fig. S1, Zimmerman *et al.* 2007), the peak in leaf flush (Angulo-Sandoval & Aide 2000) and total forest litterfall (Zalamea & González 2008). Therefore, like the reproductive phenology of the forest (Zimmerman *et al.* 2007), the allocation of resources to stem growth by trees is mildly seasonal. Rainfall at Luquillo is uniformly distributed throughout the year (Fig.1), so seasonal patterns in stem growth cannot be explained by variation in precipitation.

The circular statistical tests (Table 2) showed that the onset of the growing season in February was the most-synchronous among trees in the community, differing statistically from circular uniformity. This is probably due to the peak in total solar radiation (Zimmerman 2007) at the site which cues allocation to radial mainstem growth. Growing season midpoint and conclusion were marginally statistically different from circular uniformity and had greater variability among individuals and years. Thus, trees in the forest synchronize when they start growing, but when they stop growing and how much they grow is related to tree size, access to resources, and the allocation of resources to other needs (e.g., defense, root and leaf production, or storage) (Chapin *et al.* 1990, Mahli *et al.* 2011, McMurtrie & Dewar 2013, Doughty *et al.* 2014). Tree growth and net primary production have been shown to have a seasonal dynamic in other aseasonal, wet tropical forests, with total production varying with soil type, moisture, and fertility (Koh *et al.* 2013).

DROUGHT EFFECTS ON STEM GROWTH & INTERSPECIFIC VARIABILITY. — Across and within years, not all trees grew; many individuals had no change in stem diameter or had stem shrinkage (see Fig. S4, supplement 1). Contrary to the hypothesis that drought would shorten the growing season, drought increased the variability in growing season length (Figs. 3, 4, 5). Hulshof *et al.* (2012) reported comparable results for a common tree in the dry forests of Costa Rica, where precipitation was decoupled from stem growth. The species at Luquillo that did not grow or had stem shrinkage tended to have conservative leaf traits associated with shade-tolerant species, (i.e., low leaf N, low SLA). Species with conservative leaf traits also grew slower (Table 1) (Poorter 1989) and experienced less of a post-drought increase in growth (Fig. 5), although these effects were weak and rarely statistically significant, because differences in data are at most a few mms in stem growth/yr.

Growing season metrics estimated from the Richards growth curves varied across years and tended to be less consistent during drought, with increased variability in growing season length during 2015 (Fig. 3a). However, in 2016, most individuals had a shortened growing season (Fig. 4d,h), and experienced more overall growth as illustrated by the positive effect of 2016 in the mixed-effect model (Fig 5, Table S1). This suggests that the effects of drought can continue after drought conditions have subsided, with the frequency and severity of drought being important determinants of longer-term tree growth and ecosystem functioning (Anderegg *et al.* 2013, McDowell et al. 2018b). The drought of 2015 was the first severe drought since 1994 (Larsen, 2000), provoking the question of species resiliency to drought and whether the trees studied herein were adapted to drought (see Mitchell *et al.* 2016)

DROUGHT AND THE ABIOTIC ENVIRONMENT. — We tested for topographic effects using landscape slope and curvature (at the 23m scale), but results were inconclusive, most likely because of a small sample size (<100 trees). The three soil main soil types within the plot at Luquillo, Zarzal, Cristal, and Prieto (Mount & Lynn 2004 Thompson *et al.* 2002), represent a gradient from greatest to least water storage capacity, increasing amounts of available soil oxygen, and are weakly correlated with topography (Silver *et al.* 1999). Therefore, the fine Zarzal clays likely hold the available soil water more tightly, requiring a more negative plant water potential to extract a given quantity of water from the soil, which is one explanation for the negative effect of Zarzal soils in the linear mixed-effects model (Fig. 5). Future research directions could investigate the interaction of soil type (i.e., soil particle size) and drought to reveal if trees growing on Zarzal soils at Luquillo experience greater degrees of drought stress. During the roughly five-month drought in 2015, soils dried substantially (a 63% decline from >0.4 to <0.2 soil moisture fraction) in ridge and slope habitats, and recovery of soil moisture took an additional 3 months following rewetting (O'Connell *et al.* 2018). A negative effect for tree size was also observed in the linear mixed-effects model (Fig. 5). In general, assessing how absolute growth rates of trees vary with tree size is complicated and depends on the metrics and statistical methods used (Das 2012, Stephenson et al 2014). Over four-years at Luquillo, our modeling approach shows that tree growth rates slowed as trees became larger. We had insufficient data to fit a model with a year times size interaction term because we had very few large individuals and not for all species, so we could not directly model whether larger trees grew less during the 2015-16 El Niño drought than in the previous years.

A 350% increase in litterfall was recorded as the drought intensified (i.e., mid-May 2015, Fig. 1) (Fig. S5), and 30% decrease in the annual growth of the 1000 largest trees in the LFDP (Feng *et al.* 2017). As a drought avoidance strategy (Santiago *et al.* 2016, Wolfe *et al.* 2016), the litterfall event occurred in two stages, first with canopy trees abscising leaves in May and later shedding branches and portions of the canopy in September (Fig. S5). Shedding branches and portions of the canopy was observed during the 2015-16 extreme El Niño drought in the Amazon, as well (Leitold *et al.* 2018). Considering this, the early termination of stem growth in 2016 likely reflects investment in other physiological processes such as the production of new branches, leaves, and roots (Mahli *et al.* 2011, Doughty *et al.* 2014) or replenishment of stored carbohydrate reserves (Würth *et al.* 2005, Sala *et al.* 2010). These processes occur to a greater degree in larger trees that are more affected by drought (Bennett *et al.* 2015, Rowland *et al.* 2015).

DIFFERENTIAL DROUGHT EFFECTS BY TREE SIZE: THE ROLE OF SMALLER TREES IN TROPICAL FOREST DROUGHT RESILIENCE. — What is arguably more important for predicting dynamics of tree growth in tropical forests under climate change is how tropical trees respond to increased precipitation variability and drought (Feng *et al.* 2013, Adams *et al.* 2017, McDowell *et al.* 2018a, 2018b). Interestingly, several small trees (dbh < 200mm) showed increased growth during drought, which points to a release from light limitation, due to thinning in the canopy as a result of drought. The only significant t-test of the eight conducted that comparted tree sizes among the six growth classifications (Table 3) was between trees with no visible effect of drought in their diameter timeseries, and with differing growth trajectories following drought. This result should be interpreted with caution because of the multiple comparisons being made. Yet, Uriarte *et al.* (2016) found that drought reduced the growth of large trees and favored the growth of smaller trees in 8 plots of varying forest age in Costa Rica using 15-years of data. This dynamic was meditated by functional differences among species, where greater wood specific gravity improved drought survival in large trees, while species with lower wood specific gravity had higher growth potential during drier conditions (Uriarte *et al.* 2016, Zuleta *et al.* 2017). It can be explained by a trade-off in hydraulic efficiency and hydraulic safety, in that species with less-dense wood have higher rates of transpiration and smaller hydraulic safety margins (Santiago *et al.* 2004, Santiago *et al.* 2010, Choat *et al.* 2012, Bartlett *et al.* 2018). Furthermore, in response to the 2015 El Niño drought, Bretfield *et al.* (2018) showed that, in Panamian forests, forest successional status (i.e., forest age) does, indeed, influence forest-wide drought tolerance. They measured greater sap flow velocities increases in older forests than younger ones under drought conditions, leading them to conclude that the physiological-transpiration interface, under drought, shifts from the plant-soil boundary to the canopy-atmosphere boundary with forest succession.

The lower evapotranspirative demand of smaller, sub-canopy trees also means they are generally less affected by the drought in the first place (Santiago *et al.* 2004, Kempes *et al.* 2011, McDowell & Allen 2015, Wolfe *et al.* 2016, McDowell *et al*. 2018b, Xu *et al.* 2018) allowing them to take advantage of an increase in light and grow well in the year following the drought. Such ontogenetic differences illustrate the need to better understand the interplay between individuals, ontogenies, and physiology in terms of resource allocation and growth for tropical trees in the context of drought and global change (Uriarte *et al.* 2016, McDowell *et al.* 2018b).

A recent study that measured non-structural carbohydrate stocks in leaves and stems of 23 tree species along a rainfall gradient in Panama during the 2015-16 El Niño drought (Dickman *et al.* 2018), found them to be largely unrelated to metrics of drought stress (e.g., differences in pre-dawn and mid-day water potentials) leading them to conclude that a high degree of homeostatic regulation exists. They did find interspecific variation in leaf and stem non-structural carbohydrate stocks along axes of life history variation (i.e., leaf and wood carbon investment), and an increase in starch content relative to soluble sugar contents with increasing dry period length. Taken in context, our results suggest that drought potentially acts as a mechanism alleviating growth suppression of juveniles, which is strong in moist tropical forests (Brienen *et al.* 2010). This could be due to the ability of smaller trees to continue to produce and use soluble sugars during dry periods. Lastly, the drier year of 2015 interacted subtly with species life-histories (Fig. 6). More resource-acquisitive species tended to grow slightly better after the drought year of 2015, while resource-conservative species grew more poorly, a reversal from the wetter years of 2013 and 2014 (Poorter 1989, Santiago *et al.* 2004). These effects were confounded by the size effects because many of the intermediate-sized trees in this study were on the resource-acquisitive end of the plant economics spectrum (Table 1).

Conclusion

We used fine-scale tree growth measurements to shed new light on variability in growth and shifts in phenology during and following drought in a wet tropical forest. These results are consistent with the predicted effects on vegetation and the projections of a regionally-downscaled climate model for the El Yunque. Khalyani *et al.* (2016) predict an upslope migration of the wet forest life zone, given increasing frequency of drought. This could potentially be a consequence of decreased growth and reproduction of individuals in the wet forest life zone given an increase in the frequency and intensity of drought stress. We show that drought increased the variability in stem growth cycles for the wet forest tree community, and this may preferentially affect shade-tolerant, dense-wooded species with low growth rates. Secondly, in the Ecosystem Demography model parameterized by Feng *et al.* (2017), a 30% drought frequency interacted with the climate warming scenario as a key determinant of the positive to negative switch in forest productivity. Over the twentieth century, droughts have occurred at a tenth of that frequency, with three severe droughts similar to the 2015 El Niño event affecting Puerto Rico (Larsen 2000). If droughts do occur more frequently in the near future, reduced growth of many dense-wooded species coupled with a major increase in leaf litterfall (including coarse woody material), could potentially drive the modeled flip in the total forest carbon balance (Feng *et al.* 2017).

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Data accessibility: Dendrometer measurements for the trees in this study at the Luquillo Forest Dynamics plot are archived on the Luquillo LTER data portal (dataset #203): http://luq.lter.network/data/luqmetadata203

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Tables:

Table 1: Average tree size (dbh: diameter at breast height) and growth (AGR: absolute growth rate, RGR: relative growth rate), for 72 individuals of 12 species that grew (AGR > 0) in the Luquillo Forest Dynamics Plot from November 2012 to November 2016.

Code	Species	Tree-yr	Mean dbh (± SE) (mm)	Mean AGR (± SE) (mm/yr)	Mean RGR(± SE) (%/yr)
ALCFLO	*Alchorneopsis floribunda* (Benth.) Müll	6	185 ± 18	2.55 ± 0.70	0.0162 ± 0.0049
ALCLAT	*Alchornea latifolia* Sw.	8	217 ± 47	2.75 ± 0.66	0.0156 ± 0.0055
CALCAL	*Calophyllum antillanum* Britton	5	342 ± 28	1.59 ± 0.48	0.0049 ± 0.0016
CASARB	*Caseria arborea* (Rich.) Urb.	33	145 ± 8	1.95 ± 0.22	0.0143 ± 0.0017
DACEXC	*Dacryodes excelsa* Vahl	47	290 ± 12	1.52 ± 0.12	0.0056 ± 0.0005
DENARB	*Dendropanax arboreus* (L.) Decne. & Planch.	4	192 ± 2	3.67 ± 0.54	0.0189 ± 0.0028
GUAGUI	*Guarea guidonia* (L.) Sleumer	16	289 ± 21	3.49 ± 0.71	0.0125 ± 0.0024
GUTCAR	*Guatteria caribaea* Urb.	6	166 ± 24	3.54 ± 0.87	0.0199 ± 0.0028
INGLAU	*Inga laurina* (Sw.) Willd.	19	171 ± 12	4.25 ± 0.87	0.0234 ± 0.0044
MANBID	*Manilkara bidentata* (A. DC.) A.Chev.	18	170 ± 14	1.70 ± 0.29	0.0115 ± 0.0022
MELHER	*Meliosma herbertii* Rolfe	5	149 ± 11	1.00 ± 0.34	0.0062 ± 0.0020
SLOBER	*Sloanea beteroana* Choisy ex DC.	13	220 ± 27	2.76 ± 0.59	0.0126 ± 0.0023

Table 2: Circular statistical tests for the seasonal metrics derived from Richards curve fits for 80 trees from 2013-2016 at Luquillo, Puerto Rico. See Fig. 2 for seasonal metric descriptions and circular distributions of data. Statistically significant p-values are bolded.

metric	Rayleigh's Z		Kuiper's V		Watson's U^2		Rao's U	
	Test Statistic	p-value	Test Statistic[₳]	p-value	Test Statistic[£]	p-value	Test Statistic[₡]	p-value
Start of growing season	0.110	**0.039**	1.745	$0.05 < x < 0.10$	0.201	**$0.025 < x < 0.05$**	185.774	**< 0.001**
Middle of growing season	0.103	0.060	1.743	$0.05 < x < 0.10$	0.173	< 0.10	168.089	**< 0.001**
End of growing season	0.094	0.098	1.425	> 0.15	0.156	$0.05 < x < 0.10$	160.420	**< 0.001**

[₳] Kuiper's V critical value for $\alpha = .05$ is 1.747
[£] Watson's U^2 critical value for $\alpha = .05$ is 0.187
[₡] Rao's U critical value for $\alpha = .05$ is 140.57

Table 3: Table of growth classifications for 65 individual trees from the Luquillo Forest Dynamics Plot, Puerto Rico, which grew in at least one year (AGR > 0). Tags are listed for reference and comparison to supplement 1, which contains tree diameter time series and Richards curve fits. An average of individual tree size using the starting diameter for each of the 4-years of measurements was used for the average size by growth classification. Letters following average sizes denote no statistical differences among groups using a single-factor two-way ANOVA with post-hoc Tukey HSD test.

Growth classification	N	Tree tag numbers†	Average size (mean dbh ± standard error, mm)
1) unaffected by drought, no post-drought growth response	22	105159, 123839, 125584, 12997, 16345, 16348, 16826, 17456, 18385, 18621, 19012, 24120, 28638, 3502, 37823, 43232, 4531, 4548, 4953, 5507, 61542, 78229	257 ± 20^{a*}
2) unaffected by drought, post-drought growth response	14	105170, 106782, 106792, 12961, 1470, 1476, 16330, 19011, 42889, 4970, 68013, 79274, 79307, 96326	187 ± 22^{a*}
3) negatively affected by drought, no post-drought growth response	10	103861, 14699, 16761, 17284, 17310, 28364, 29003, 4502, 48829, 68097	220 ± 38^{a}
4) negatively affected by drought, post-drought growth response	11	16827, 16828, 17317, 21970, 3956, 4557, 5516, 5555, 68005, 68585, 69190	218 ± 33^{a}
5) positively affected by drought	6	111812, 112715, 13906, 17901, 17903, 4934	179 ± 24^{a}
6) dying	2	1512, 4954	186 ± 6^{a}

†see supplement 1

[*] statistical difference 2-tailed T-test between groups

Figure Legends

Figure 1: a) Walter climate diagram for El Verde, Puerto Rico, using temperature and precipitation data from 1990-2016. The temperature curve is shown in red, and the precipitation curve in blue. The shaded blue areas show months of precipitation surplus (i.e., exceeds 100mm). b) Monthly precipitation matrix plot for the years when fine-scale tree growth data were collected (2013-2016). Color shade corresponds to total monthly precipitation with red boxes indicating drier months. The mean monthly precipitation from 1990-2016 was 305 mm; months with 281-313 mm of precipitation are colored gray.

Figure 2: Two examples of tree diameter time series: tree diameter a breast height (DBH) in millimeters over time, with annual Richards curve fits (green lines). a) a *Dacryodes excelsa* Vahl (Burseraceae), shows no change in stem diameter under meteorological drought, whereas the bottom tree, a *Calophyllum brasiliense* Cambess (Calophyllaceae), experiences drought-related stem shrinkage. Stem diameter time series plots along with model fits for all individuals can be found in supplement 1.

Figure 3. Distributions of tree growth metrics. (a) Histogram of the 80th percentile of growing season length. Circular histograms of (b) the ordinal date at 10% annual growth (start of growing season), (c) the ordinal date at median annual growth (middle of growing season), and (d) the ordinal date at 90% annual growth (end of growing season). Data are derived from Richards curve fits for 94 trees in the Luquillo Forest Dynamics Plot measured for a total of 316 tree-yrs. Histogram bins are 7 d for (a) and 14 d for (b-d).

Figure 4: Nonparametric circular regression plots for the four seasonality metrics derived from growth model fits; growing season length (a,e), start of growing season (c,g), median day of growth (b,f) and end of growing season (d,h). Circular response variables (y-axis) are in ordinal

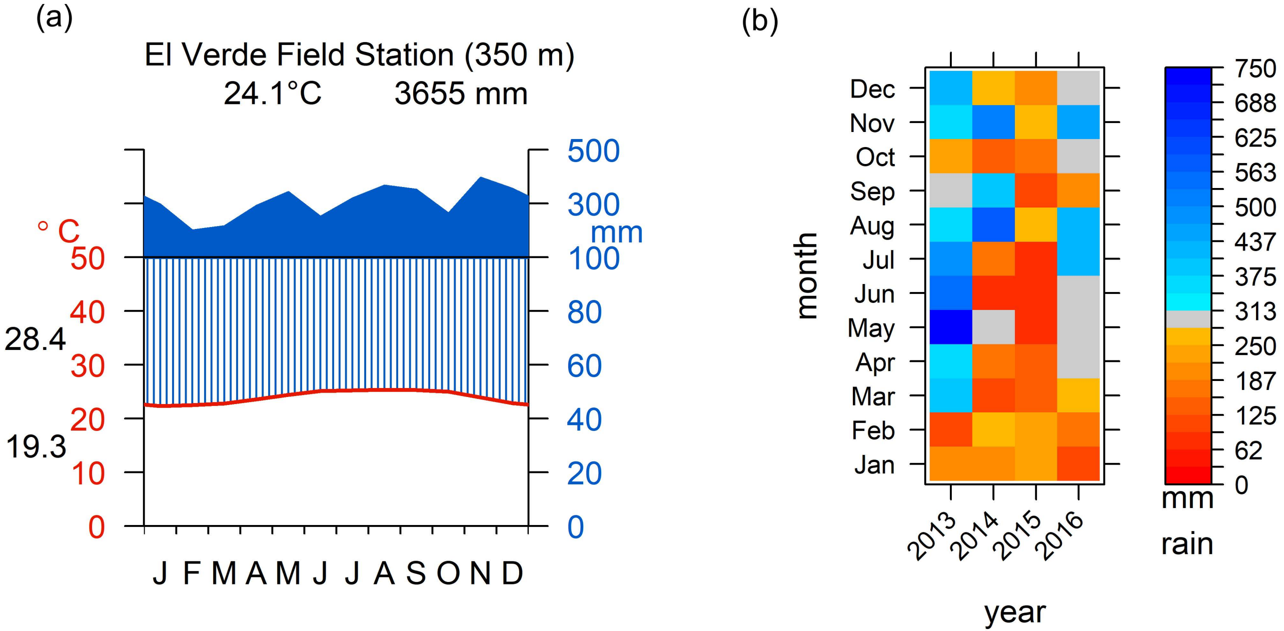
date (b-d and f-h), or the number of ordinal days in the case of growing season length (a,e). Absolute growth rate (AGR) (a-d) and tree size (e-h) are the linear covariates (x-axes).

Figure 5: Standardized effect size for fixed-covariate relationships with absolute growth rate of 72 trees from 2013-2016. Points are mean parameter values and lines are 95% confidence intervals. Effect magnitude is printed above the points with asterisks denoting statistical significant (one for $\alpha = .05$ and two for $\alpha = .01$). The first level of factors, in this case, Cristal soil and 2013, correspond to the model Intercept term. See Table S2 for model statistics.

Figure 6: Standardized effect size (dots are means and lines are 95% confidence intervals) of year on tree growth. Best Unbiased Linear Predictors (BULP) for random slopes for species with year as random intercept, demonstrating in the interspecific variability in absolute growth rate across years. Species code abbreviations correspond to Table 1. See Table S2 for a complete table of model coefficients and a statistical summary.

SUPPLEMENTS (1):

Supplement 1: Dendrometer time series and Richards curve fits for all 96 individuals fit with dendrometer bands in the Luquillo Forest Dynamics Plot and measured from 2013-2016. Red shading delimits the 2015 El Niño drought (May-December).


(a)
El Verde Field Station (350 m)
24.1°C 3655 mm
° C
50
40
30
20
10
0
28.4
19.3
500
300
mm
100
80
60
40
20
0
J F M A M J J A S O N D
(b)
month
Dec
Nov
Oct
Sep
Aug
Jul
Jun
May
Apr
Mar
Feb
Jan
2013
2014
2015
2016
year
750
688
625
563
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437
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313
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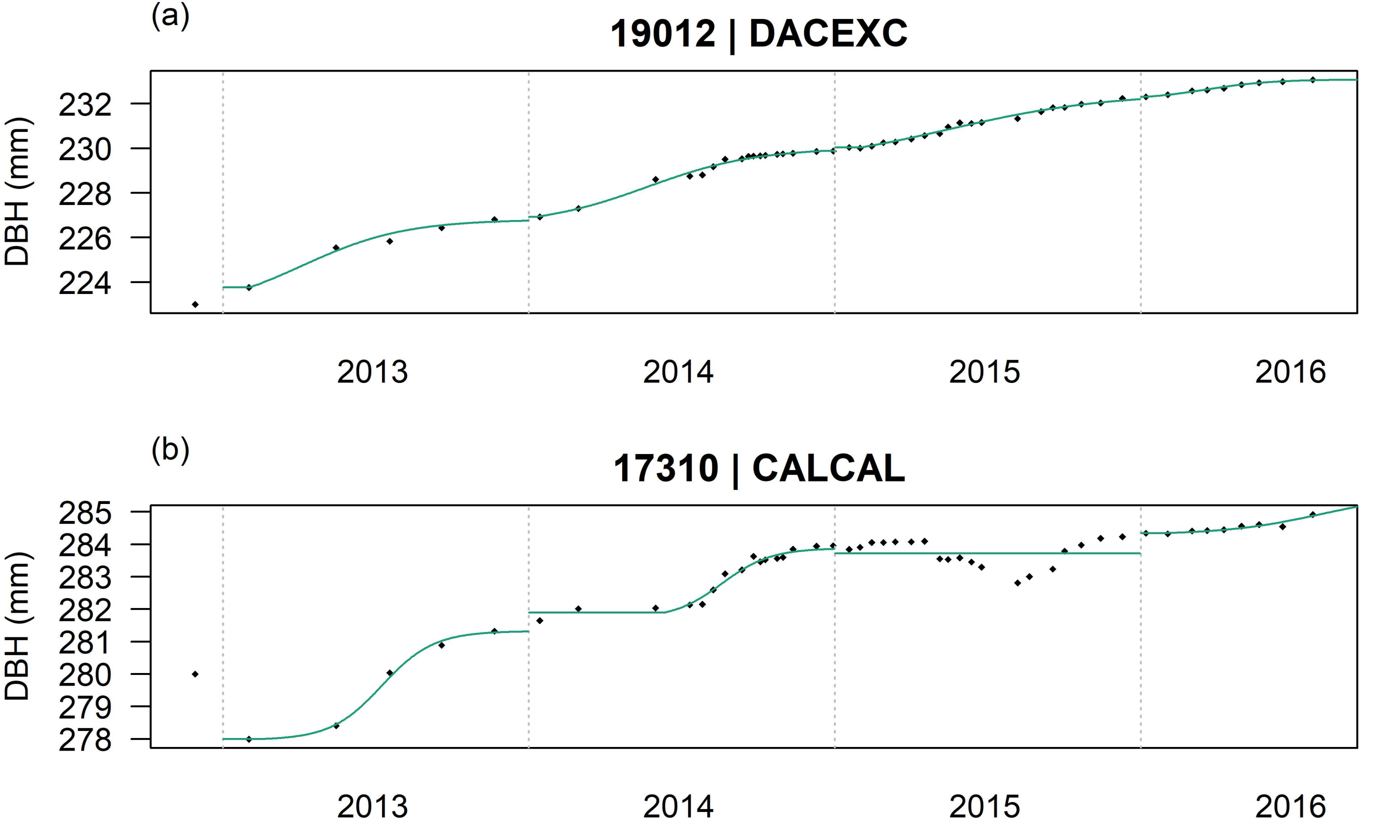
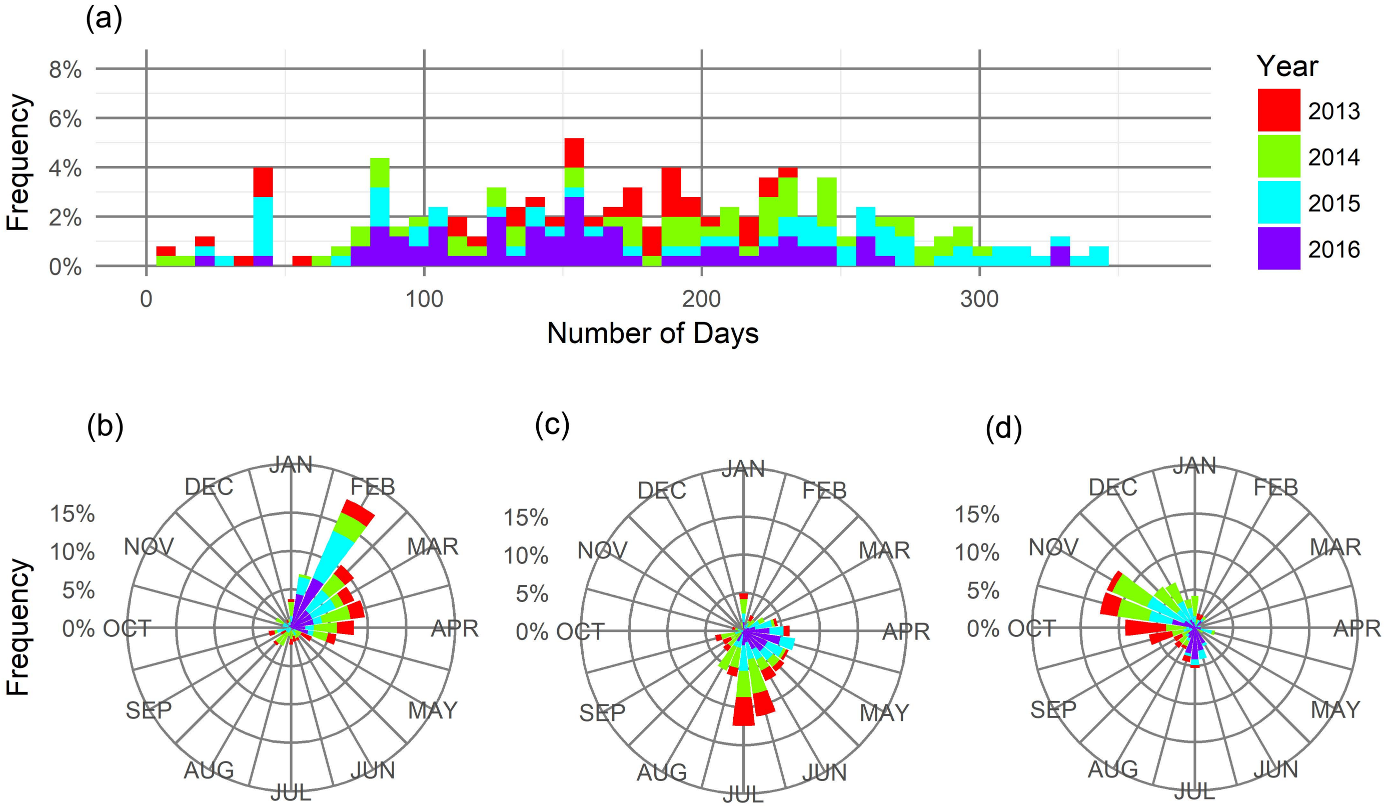
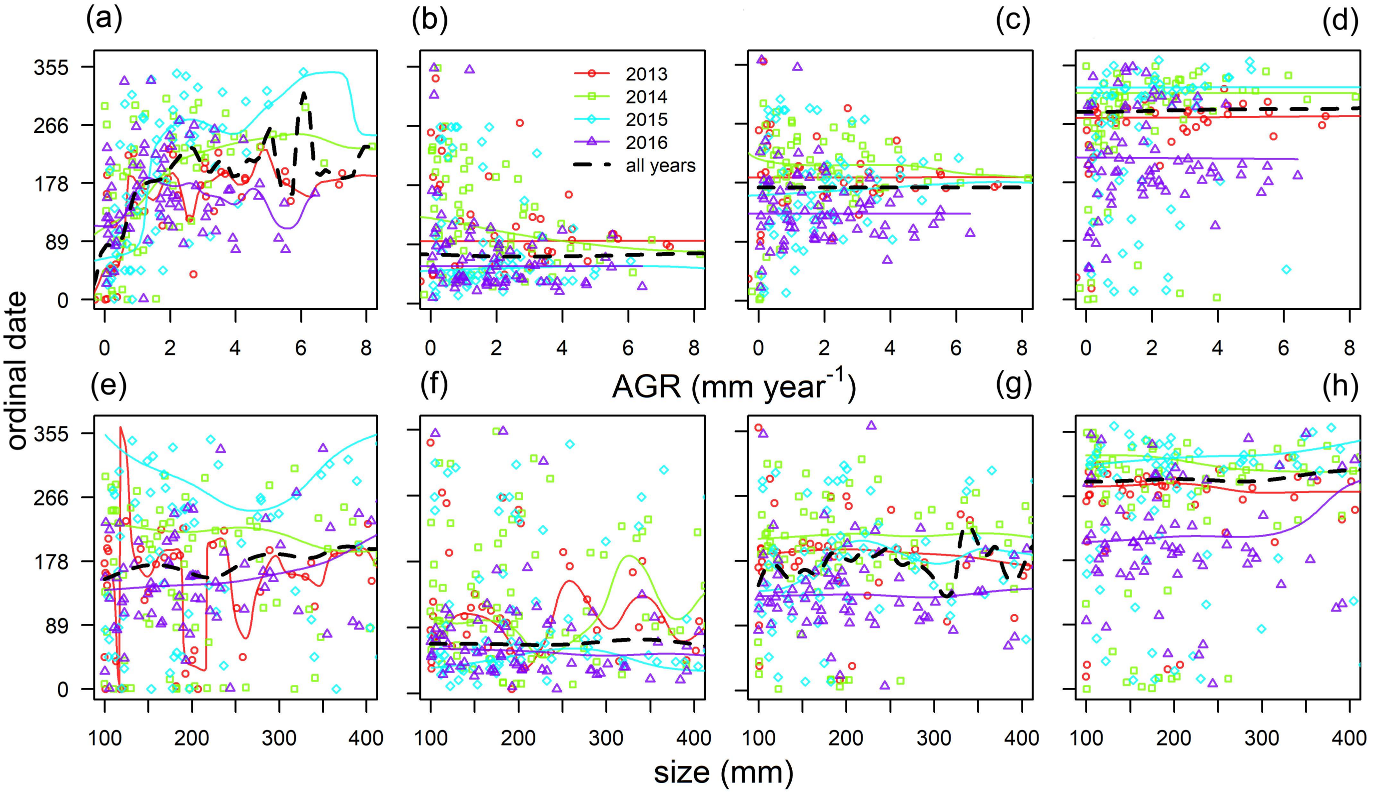
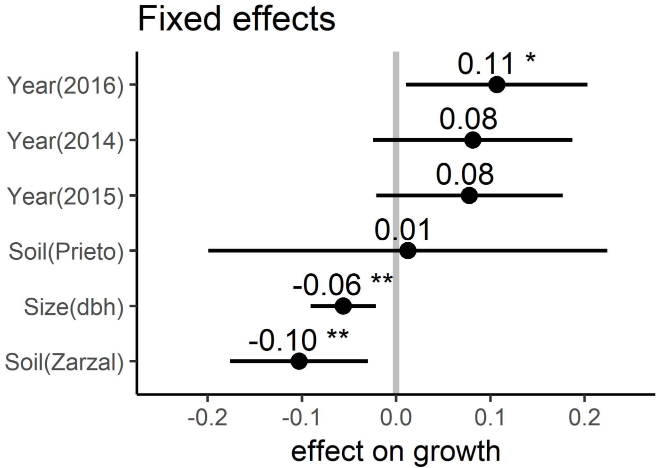
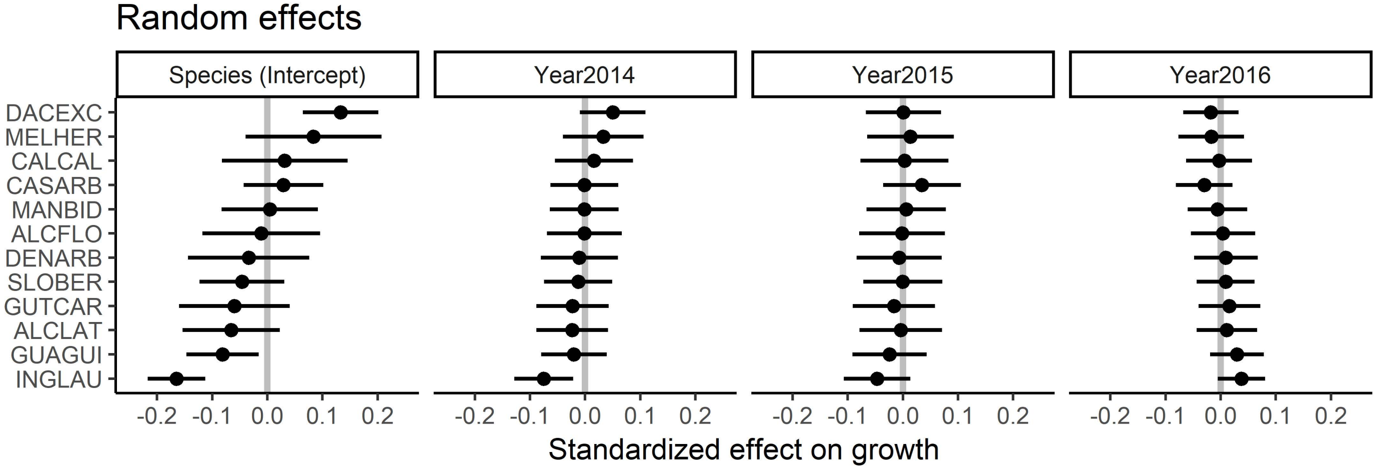
187
125
62
0
mm
rain


(a)
19012 | DACEXC
DBH (mm)
224
226
228
230
232
2013
2014
2015
2016
(b)
17310 | CALCAL
DBH (mm)
278
279
280
281
282
283
284
285
2013
2014
2015
2016


(a)
Frequency
8%
6%
4%
2%
0%
0
100
200
300
Number of Days
Year
2013
2014
2015
2016
(b)
(c)
(d)
Frequency
15%
10%
5%
0%
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
2013
2014
2015
2016
all years
ordinal date
0
89
178
266
355
AGR (mm year^{-1})
0
2
4
6
8
size (mm)
100
200
300
400


Fixed effects
Year(2016)
Year(2014)
Year(2015)
Soil(Prieto)
Size(dbh)
Soil(Zarzal)
0.11 *
0.08
0.08
0.01
-0.06 **
-0.10 **
-0.2
-0.1
0.0
0.1
0.2
effect on growth


Random effects
Species (Intercept)
Year2014
Year2015
Year2016
DACEXC
MELHER
CALCAL
CASARB
MANBID
ALCFLO
DENARB
SLOBER
GUTCAR
ALCLAT
GUAGUI
INGLAU
-0.2
-0.1
0.0
0.1
0.2
Standardized effect on growth