

Effects of neighborhood trait composition on tree survival differ between drought and postdrought periods

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Abstract. Although direct tree demographic responses to drought are widely recognized, studies of drought-mediated changes in tree interactions are rare. We hypothesize that drought exacerbates soil-water limitation and intensifies competition for water, but reduces light limitation and competition for light. We predict that competition would be stronger for trees (1) consuming more water or more susceptible to water deficits during drought and (2) intercepting more light or more susceptible to shade during postdrought periods. We tested these predictions in a 50-ha tropical forest plot by quantifying the effects of neighborhood mean trait values on tree survival during versus after a severe drought. We used wood density (WD) and leaf mass per area (LMA) as proxies for water and light use strategies, respectively. Tree survival was lower, canopy loss was greater, and sapling recruitment was greater during the drought relative to postdrought census intervals. This suggests that drought pushed water deficits to lethal extremes and increased understory light availability. Relationships between survival and neighborhood WD were independent of drought, which is inconsistent with our first prediction. In contrast, relationships between survival and neighborhood LMA differed strongly with drought. Survival time was unaffected by neighborhood LMA during drought, but was longer for trees of all sizes in low-LMA neighborhoods in the postdrought census interval, consistent with the prediction of reduced competition for light during drought. Our results suggest that severe drought might increase light availability and reduce competition for light in moist tropical forests.

Key words: drought; functional traits; indirect effect; light; neighborhood; size classes; tree competition; tree survival; tropical forest.

INTRODUCTION

Drought is becoming more frequent and intense in many tropical regions (Feng et al. 2013, Duffy et al. 2015). Water stress can elevate tree mortality, which in turn alters forest structure, composition, and function (McDowell et al. 2008, Enquist and Enquist 2011, Anderegg et al. 2012, Fauset et al. 2012, Schlesinger et al. 2016). Thus, it is important to understand how forests respond to drought. Many studies have recognized the direct effects of drought on average tree growth and survival rates (reviewed by Bennett et al. 2015). However, how drought affects interactions among trees has rarely been investigated (but see Newbery and Stoll 2013, O'Brien et al. 2017). Understanding indirect responses to drought mediated by changing interactions

among species is crucial for forecasting ecosystem responses to climate change (Suttle et al. 2007, Clark et al. 2011).

Various environmental conditions can change during severe drought in forests. First, soil-water potential drops (Nepstad et al. 2007, Rowland et al. 2015). Second, temperature often increases (Condit et al. 1995, McDowell et al. 2008), which can intensify water loss from soil and leaves. Third, water deficits can lead to high levels of leaf abscission, wilting, and tree mortality (Wright and Cornejo 1990, Condit et al. 1992, Nepstad et al. 2007, Comita and Engelbrecht 2009, Bennett et al. 2015, Rowland et al. 2015), which together increases light penetration to the understory (Condit et al. 1992, 2017, Newbery and Stoll 2013). Over time, light levels will return to predrought levels as the canopy recovers (Condit et al. 1992, Newbery et al. 2011). In sum, drought may exacerbate water limitation but may also increase light levels in the forest understory.

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Drought may also modify interactions among neighboring individuals (Newbery and Stoll 2013, O'Brien et al. 2017). High soil-water deficits may intensify competition for water (O'Brien et al. 2017). The magnitude of this effect may vary among ontogenetic classes. Shallow root systems make seedlings and small saplings susceptible to drought (Cao 2000). Large numbers of sun-exposed leaves characterized by high vapor pressure deficits and transpirational demand make large trees particularly susceptible to drought (Bennett et al. 2015). At the same time, increased forest understory light levels may reduce the asymmetric competition for light between small, shaded trees and large, overtopping trees during drought (Newbery and Stoll 2013) without having much effect on large trees exposed to full sunlight.

Trait-based methods to detect trait-associated resource competition may allow us to disentangle the complex effects of drought on competition for water and light. Resource competition can be decomposed into processes associated with competitive impact on neighbors and competitive tolerance of neighbors (Goldberg 1990). Neighbors with traits associated with greater resource depletion rates may exert greater competitive impacts on focal trees (Goldberg 1990, Kunstler et al. 2015). Focal trees with traits associated with higher tolerance to resource deficits may be more tolerant of neighborhood competitive impact (Goldberg 1990, Kunstler et al. 2015, Fortunel et al. 2016). As an example, wood density (WD) is associated with whole-plant hydraulic function, with hydraulic conductivity and cavitation risk being inversely related to WD (Chave et al. 2009, Markesteijn et al. 2011, Poorter and Markesteijn 2008, Santiago et al. 2018, but see Zanne and Falster 2010 and Fortunel et al. 2014). Trees with lower WD tend to consume more water, to exert greater competitive pressure for water, and to be more susceptible to competitive impacts mediated by water availability. In contrast, trees with larger WD tend to consume less water, to exert lower competitive pressure for water, and to be more tolerant of neighborhood competitive impacts mediated by water availability. As a second example, leaf mass per area (LMA) is related to light use strategies (Wright et al. 2004). LMA measures the leaf dry mass per unit of light-capturing foliar area. Larger LMA is associated with lower photosynthetic rates per unit leaf mass and greater shade tolerance in interspecific comparisons within a single light environment (Osnas et al. 2018). Tree species with larger LMA often have longer leaf lifespan (Osnas et al. 2013), higher biomass allocation to leaves, and larger leaf area indices (Niinemets 2010), and may cast deeper shade on neighboring trees. Trees with larger LMA tend to exert greater competitive pressure for light, and to be more tolerant of neighborhood competitive impacts mediated by light availability.

Niche theory motivates predictions that trees with dissimilar traits compete less intensely (Uriarte et al. 2010, Chen et al. 2016). However, niche-based predictions can be inconsistent with predictions of the competitive

impact-tolerance framework described above. As an example, high-LMA species tend to intercept more light and exert larger impacts on neighbors than low-LMA species. From this impact-tolerance framework, focal species with high LMA will suffer greater competitive impacts from high-LMA neighbors (i.e., low LMA dissimilarity) than from low-LMA neighbors (i.e., high LMA dissimilarity), and focal species with low LMA will suffer greater competitive impacts from high-LMA neighbors (i.e., high LMA dissimilarity) than from low-LMA neighbors (i.e., low LMA dissimilarity). The competitive impact-tolerance framework suggests competition can increase as trait dissimilarity increases.

In this study, we assessed how drought modifies trait-based tree interactions in a 50-ha forest dynamics plot (FDP) in Panama, which suffered a severe drought during the 1982–1985 census interval (hereafter, the drought census interval; Condit et al. 1992, 1995, 2017). Previous studies found higher tree mortality during the drought census interval relative to the subsequent 1985–1990 census interval, which did not have a drought (hereafter, the postdrought census interval; Condit et al. 1992, 1995, 2017), indicating strong direct responses to the drought. We extend these studies by evaluating the indirect responses to the drought mediated by trait-based neighborhood interactions. We hypothesize that altered water and light availability during drought influence competitive interactions. To address the hypotheses, we conducted spatially explicit individual-based survival analyses for the 35 most abundant tree species in the 50-ha FDP. We quantified neighborhood composition using WD and LMA for all neighbors. We calculated neighborhood mean trait values to quantify potential trait-associated competitive impacts. We evaluated trait-associated tolerance of competitors by assessing relationships between traits of focal species and neighborhood competitive impacts. We predict that:

- 1) Greater competition for water in the drought census interval will increase the expression of
 - a) negative effects of low-WD neighbors on focal tree survival because of high water consumption by low-WD neighboring trees,
 - b) tolerance of high-WD focal species to low-WD neighbors, and
 - c) tolerance of high-WD species to overall neighborhood crowding.

We also predict these effects will be stronger among small and large focal trees than mid-size focal trees due to the higher vulnerability of small and large trees to drought.

- 2) Greater competition for light in the postdrought census interval will increase the expression of
 - a) negative effects of high-LMA neighbors on focal tree survival due to deep shading by high-LMA neighboring trees,

- b) tolerance of high-LMA focal species to high-LMA neighbors, and
- c) tolerance of high-LMA species to overall neighborhood crowding.

We also predict these effects will be stronger for small focal trees, which are in the understory and are often severely light limited.

MATERIALS AND METHODS

Study site

This study was conducted using the 1982, 1985, and 1990 censuses of a 50-ha plot of lowland moist tropical forest located on Barro Colorado Island (BCI), Panama (9°10' N, 79°51' W; Condit et al. 2012). Rainfall at the site is highly seasonal, and the dry season typically begins in mid-December and ends in April (Windsor 1990, Condit et al. 1995). The 1982–1983 dry season was extremely long and dry. It started about 1 month earlier than normal (Windsor 1990, Condit et al. 2004). Physical monitoring from two meteorological stations on BCI showed that rainfall and soil humidity were significantly lower during 1982–1983 dry season than during the average dry season (Appendix S1: Fig. S1). Tree mortality rates were significantly higher in the 1982–1985 than 1985–1990 census intervals (Condit et al. 1992, 1995, 2017). The 1997–1998 El Niño event also caused a harsh dry season (Appendix S1: Fig. S1). However, the 1997–1998 drought was not severe enough to increase tree wilting or mortality (Condit et al. 2004). Therefore, we focused this study on the first census interval (1982–1985) including the extreme 1982–1983 drought event and its closest postdrought census interval (1985–1990). To characterize the temporal variability in the drought environment, we categorized these two census intervals as the drought and postdrought census intervals. In each census, all freestanding woody stems ≥ 10 mm diameter at breast height (DBH) were tagged, mapped, identified to species, measured, and recorded with census dates and survival status using standardized methods (Condit et al. 2012). Tree measurement was taken at each 20×20 m quadrat, starting from the southwestern corner of the plot to the northeastern direction for the 1982 census and from the southeastern corner of the plot to the northwestern direction for the later censuses. Census intervals of the quadrats varied from 1.9 to 4.5 yr for the 1982–1985 census interval and from 4.9 to 5.6 yr for the 1985–1990 census interval (Condit et al. 1995).

Size classes

We selected the 35 most abundant species as focal species, which had $\geq 1,000$ individuals in both the 1982 and 1985 censuses. We used all individuals of the 35 species as focal trees in the analyses. These species accounted for ~45% of overall basal area, and represent broad ranges of

trait values and growth forms (Appendix S1: Fig. S2 and Table S1). We separated individuals of each species into three size classes according to their species-specific DBH distributions from 1982 to 1990. Individuals of each species with DBH $\leq 40\%$ quantile (mean \pm standard error: 19.0 ± 1.2 mm), $>90\%$ quantile (113.7 ± 16.4 mm), and between these two quantiles were grouped as small, large, and mid-size trees (Appendix S1: Table S1), respectively. We used these asymmetric quantile cutoffs because the tree size distributions of these species are right skewed, and trees above the 90% quantile should be approaching their species-specific maximum heights. Using these asymmetric size cutoffs, large trees of canopy and midstory species generally have larger sizes than those of understory and shrub species (Appendix S1: Table S1). The cutoffs also guarantee that each size class of each species includes ≥ 10 individuals. For the first census (1982), most trees (97.4%) of the 35 focal species were measured before the 1982–1983 drought event began (Appendix S1: Fig. S3).

Community structure change across census intervals

To explore direct tree responses to drought, we calculated median survival time (i.e., half-life or survival time with survival probability equal to 0.5) for each size class in the drought and postdrought census intervals. We calculated median survival time from Bayesian survival analysis (see Survival analyses). We chose survival analysis instead of logistic regression because of the large variation in census intervals of trees.

To infer changes in the understory light associated with drought, we calculated relative density change rates for large stems (≥ 100 mm in DBH) in each 20×20 -m quadrat (see Supplementary method in Appendix S1: Section S1). The relative density change rate of large stems reflects canopy change and thus, potential light availability in the forest understory. We also calculated relative sapling recruitment rates for each 20×20 m quadrat (see Supplementary method in Appendix S1: Section S1), which may reflect the changes in the understory light (Rüger et al. 2009). We defined sapling recruits as individuals that first reached the 10-mm DBH size threshold during a census interval (Rüger et al. 2009).

Neighborhood indices

We calculated two neighborhood indices to assess two potential neighborhood competitive processes: neighborhood mean trait value (MTV) and neighborhood crowding (NC) for processes associated with trait-mediated competitive impacts and trait-independent competitive impacts, respectively. We did not calculate trait dissimilarity to assess niche-associated processes because (1) the niche-based predictions can be inconsistent with the predictions from the competitive impact-tolerance framework, and (2) we found that the effects of trait dissimilarity on survival were much weaker than the effects of MTV in preliminary analysis (results not shown).

For every live tree of the 35 focal species at the start of each census interval, we identified all neighbors within a radius of 30 m. We chose the 30-m cutoff because previous research at this forest found that conspecific neighborhood effects were nonsignificant beyond this distance (Hubbell et al. 2001), and preliminary analyses using 25- and 35-m radius cutoffs showed qualitatively similar results. To avoid edge effects, we excluded individuals <30 m from the plot edge as focal trees.

We calculated MTV as the mean trait value of neighboring trees, weighted by basal area and inversely by spatial distance, because larger and spatially closer neighbors are expected to have a greater influence on focal trees (Uriarte et al. 2010). We calculated NC as the sum of the basal areas of neighbors with inverse weighting by spatial distance (Canham et al. 2006; see Supplementary method in Appendix S1: Section S1).

LMA was measured for shaded leaves taken from the tallest foliage of the smallest individuals of each species in the 50-ha plot. WD was determined for trees located outside of the plot but within 15 km of the plot edges. Wright et al. (2010) provides detailed descriptions of the trait measurements. WD and LMA were measured for all 35 focal species. For neighboring trees with missing trait information (<3% of all neighboring trees), we used the mean value of the next higher taxonomic level, because WD and LMA are phylogenetically conserved in this forest plot (Lebrija-Trejos et al. 2014).

We also performed an alternative analysis to characterize asymmetric competition for light better. We included neighbors larger than focal trees only (instead of all neighbors) when calculating neighborhood indices (Coomes and Allen 2007, Ruiz-Benito et al. 2013). The neighborhood indices based on larger neighbors had qualitatively similar effects on tree survival to the indices based on all neighbors (results not shown).

Survival analyses

We performed 12 Bayesian survival analyses (two census intervals \times three size classes \times two traits). We used Weibull regression (Kleinbaum and Klein 2012) to assess how the two neighborhood indices (neighborhood crowding ($NC_{i,j}$) and neighborhood mean trait value ($MTV_{i,j}$)) affect the time focal individual i of species j has survived:

$$\mu_{i,j} = \beta_{0,j} + \beta_{1,j} \log(\text{DBH}_{i,j}) + \beta_{2,j} \log(\text{NC}_{i,j}) + \beta_{3,j} \log(\text{MTV}_{i,j}) + \phi_{i,j}, \quad (1)$$

where $e^{\mu_{i,j}}$ equals to the scale parameter of the Weibull distribution and determines the expected survival time at a fixed survival probability (e.g., 0.5 corresponding to median survival time; see Supplementary method in Appendix S1: Section S1). $\text{DBH}_{i,j}$ is the initial tree size of the focal tree. $\beta_{1,j}$ represents the size dependence of survival. $\beta_{2,j}$ represents neighborhood crowding or trait-independent competitive impacts (predictions 1c and 2c).

$\beta_{3,j}$ represents species-specific trait-dependent competitive impacts (predictions 1a and 2a). The final term $\phi_{i,j}$ represents a normally distributed random effect for each 20×20 m quadrat, which was included to control variation in survival induced by spatial variation in the abiotic environment. We also set $\phi_{i,j}$ as a random effect for habitat type in preliminary analysis because trees might vary in their mortality risks in habitats with different soil moisture (Condit et al. 1995). The 1,250 20×20 m quadrats were assigned to seven habitat types (high plateau, low plateau, slope, swamp, stream, young forest, and mixed habitats) based on their topographic characteristics and forest ages (Harms et al. 2001). These alternative models produced qualitatively similar results (results not shown).

We log-transformed the explanatory variables before fitting the model because they had right-skewed distributions. We centered the initial size at its species-specific average value, and we centered the neighborhood indices at their community-wide average values. This centering enables predictions of survival time for species-specific average tree sizes and common competitive neighborhoods. We also divided all explanatory variables by their corresponding community-wide standard deviations to facilitate parameter interpretation and convergence (Gelman and Hill 2007).

Because sensitivity to drought and neighborhood competitive impacts may vary through effects mediated by traits, we modeled how traits of focal species j (Trait_j) affect species-specific average survival ($\beta_{0,j}$ in Eq. 1), crowding effects ($\beta_{2,j}$ in Eq. 1), and effects of neighborhood mean trait values ($\beta_{3,j}$ in Eq. 1) in a higher-level model as follows:

$$\beta_{m,j} = \beta_m + \gamma_m \text{Trait}_j + \varepsilon_{m,j} (m = 0, 2, 3 \text{ in Eq. 1}), \quad (2)$$

where β_m and γ_m represent intercepts and slopes, respectively, and $\varepsilon_{m,j}$ are normally distributed errors. γ_0 represents the relationship between survival and the trait value of the focal species. γ_2 represents the relationship between the effect of neighborhood crowding and the trait value of the focal species (i.e., tolerance of the focal species to trait-independent neighborhood competitive impacts, predictions 1c and 2c). γ_3 represents the relationship between the effect of neighborhood MTV and the trait value of the focal species (i.e., tolerance of the focal species to trait-mediated neighborhood competitive impacts, predictions 1b and 2b). We standardized Trait_j (mean zero and unit standard deviation) to facilitate parameter convergence (Gelman and Hill 2007). We modeled the species-level initial size effect ($\beta_{1,j}$ in Eq. 1) as the sum of the corresponding average effects across species (β_1) and a random effect for species ($\varepsilon_{1,j}$).

We fitted these models using Hamiltonian Monte Carlo implemented in Stan (Stan Development Team 2016). We used weakly informative priors as suggested by the Stan user guide (version 2.16.0; see Data S1 for Stan code). We ran three parallel chains with different initial values, and used the Gelman and Rubin

convergence diagnostics with a cutoff value of 1.05 to assess parameter convergence (Gelman and Rubin 1992).

Finally, we compared parameters from the drought and postdrought census intervals to assess how competitive processes associated with trait-mediated competitive impacts (β_3) and trait-mediated tolerances of focal species to competition (γ_2 and γ_3) vary between the two periods. We compared each pair of parameters for models using data from the drought versus postdrought census intervals, respectively. We randomly sampled the posteriors of each of these parameters estimated from the drought and postdrought census intervals, and calculated the 2.5% and 97.5% quantiles of the parameter difference. The parameters were significantly different for the drought and postdrought census intervals if the 95% intervals of the parameter difference excluded zero.

RESULTS

Temporal variation of community structure

Median survival time (i.e., survival time with survival probability equal to 0.5) decreased for all size classes during the drought relative to the postdrought intervals (Fig. 1; Appendix S1: Figs. S4–S6), with large trees exhibiting the most striking reduction of median survival time (averaging 8.15 yr, Fig. 1b; Appendix S1: Fig. S4), consistent with previous research in this forest. Most species also survived longer in the postdrought than drought census intervals (Appendix S1: Figs. S7–S8).

The density of large stems (>100 mm DBH) showed similar patterns as survival time. Large-stem density dropped during the drought interval but increased in the postdrought interval as smaller trees recruited to larger size classes (Fig. 2a). Sapling recruitment rates were greater during the drought interval and lower during the postdrought interval (Fig. 2b).

Effects of tree size and neighborhood crowding

Relationships between focal tree survival and initial tree size (β_1 in Eq. 1) differed among size classes (Appendix S1: Fig. S9). For the mid- and large-size classes, smaller individuals survived longer than larger individuals in both census intervals. For the small-size class, survival time increased with tree size in the postdrought but not the drought interval.

Focal trees of all sizes survived longer with greater neighborhood crowding, and the crowding effects were similar between the two census intervals (β_2 in Eqs. 1 and 2; Appendix S1: Fig. S10).

Relationships between WD and survival (predictions 1a–c)

Small trees of high-WD species survived longer than low-WD species in both census intervals (γ_0 in Eq. 2; Appendix S1: Fig. S11). Midsize trees of high-WD species survived longer than low-WD species in the drought but not postdrought intervals (Appendix S1: Fig. S11). The magnitudes of these effects were similar in the two census intervals (Appendix S1: Fig. S11).

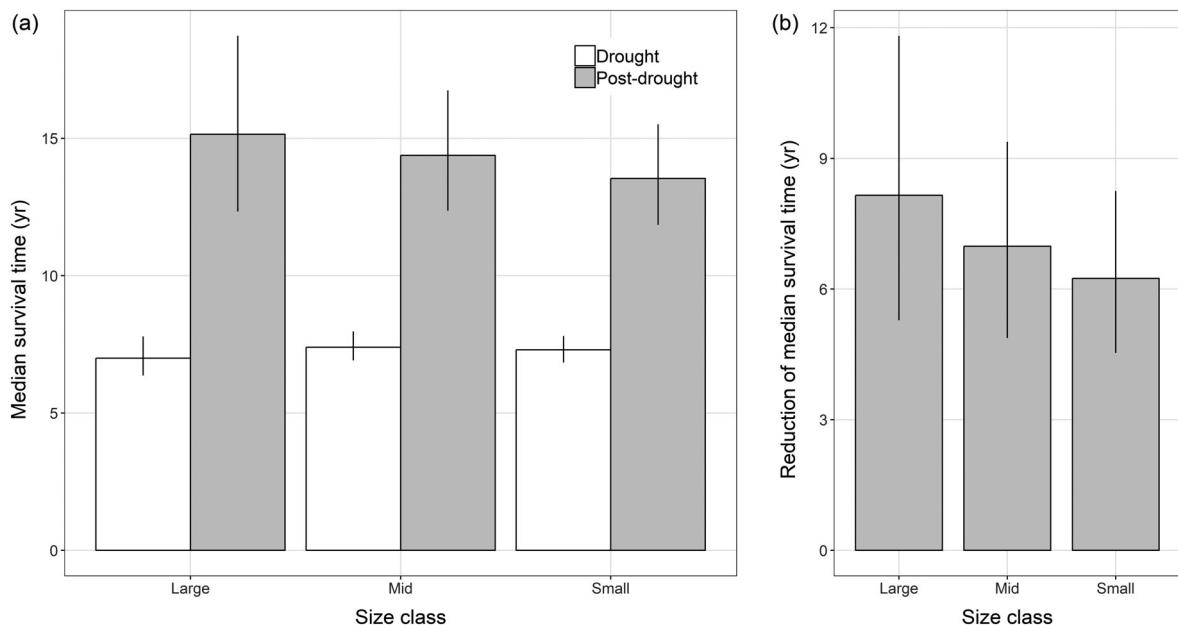


FIG. 1. Predicted median survival time for the drought [white bar in panel (a)] and postdrought [gray bar in panel (a)] census intervals and their difference [panel (b)] for large, midsize, and small trees. Vertical lines represent the 95% credible intervals. The reduction of median survival times is the difference in median survival between the postdrought and drought census intervals. These values are from the LMA-based models.

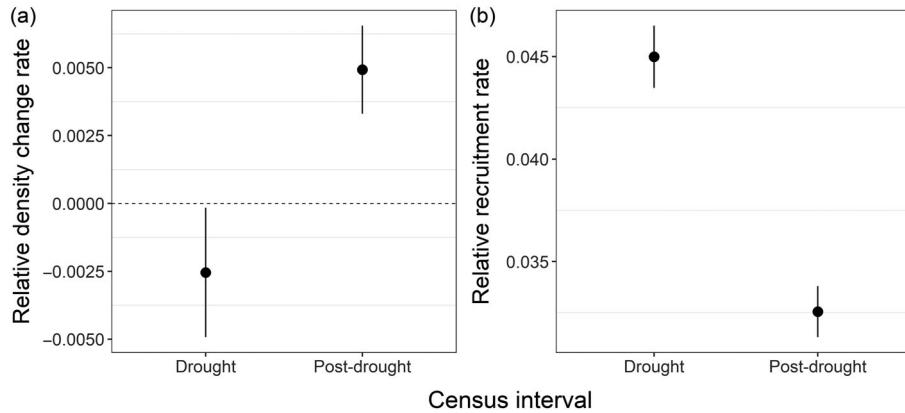


FIG. 2. (a) Relative rates of change in the densities of large stems (>100 mm DBH), and (b) relative sapling recruitment rates for the drought and postdrought census intervals. Circles and vertical lines represent the means and two times standard errors, respectively. The horizontal dashed line indicates a constant density of large stems across censuses.

Relationships between tree survival and WD-mediated neighborhood interactions were independent of drought. Trees in high-WD neighborhoods had reduced survival relative to individuals surrounded by low-WD neighbors in both census intervals (β_3 in Eqs. 1 and 2, prediction 1a, Fig. 3a–c). These negative effects of neighborhood mean WD on survival were similar in magnitude between the two census intervals and among size classes (Fig. 3a–c). Across all size classes, relationships between WD of the focal species and effects of neighborhood mean WD (γ_3 in Eq. 2, prediction 1b; Appendix S1: Fig. S12) or neighborhood crowding (γ_2 in Eq. 2, prediction 1c; Appendix S1: Fig. S13) did not vary significantly between the two census intervals.

Relationships between LMA and survival (predictions 2a–c)

Species with high LMA survived longer than species with low LMA for all size classes and both census intervals (γ_0 in Eq. 2; Appendix S1: Fig. S11).

Focal trees of all size classes had reduced survival when surrounded by high-LMA neighbors in the post-drought census interval (β_3 in Eqs. 1 and 2, prediction 2a; Fig. 3d–f). This was not the case in the drought census interval when neighborhood LMA did not influence focal tree survival (Fig. 3d–f).

Relationships between LMA of the focal species and effects of neighborhood mean LMA were nonsignificant for large and midsize trees in both census intervals (γ_3 in

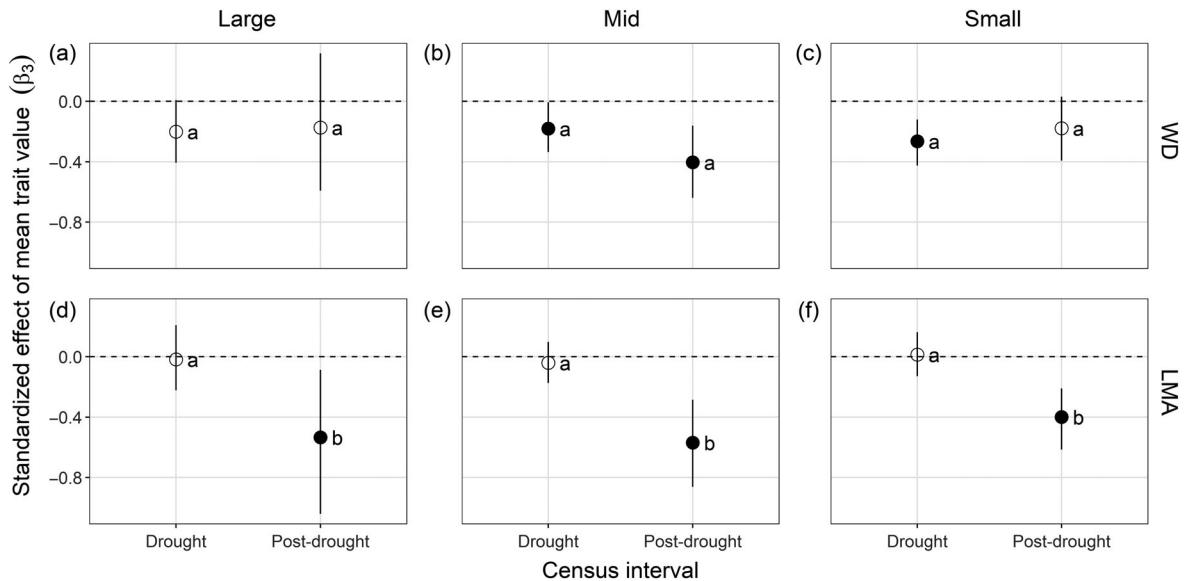


FIG. 3. Standardized effect of neighborhood mean trait value (β_3 in Eqs. 1 and 2) on tree survival during the drought and post-drought census intervals for large, midsize, and small focal trees. Neighborhood mean trait values were calculated using wood density [WD; panels (a), (b), and (c)] or leaf mass per area [LMA; panels (d), (e), and (f)]. Circles and vertical lines represent means and 95% credible intervals, respectively. Filled circles indicate significant results. Parameters were significant if their 95% credible intervals excluded zero. Effects were significantly different between the two census intervals if the letters beside circles were different in each panel.

Eq. 2, prediction 2b; Appendix S1: Fig. S12). For the small size class, focal species of low LMA were more tolerant of the negative impacts of high-LMA neighbors than focal species of high LMA in the drought census interval (γ_3 in Eq. 2; Appendix S1: Fig. S12). However, the relationship between LMA of the focal species and effects of neighborhood mean LMA did not differ significantly between the two census intervals for any size class (Appendix S1: Fig. S11). Focal species with different LMA showed similar responses to crowding in both census intervals (γ_2 in Eq. 2, prediction 2c; Appendix S1: Fig. S13).

DISCUSSION

We investigated how drought modified competition among trees and the consequences for survival. Tree survival was lower, canopy loss was greater, and sapling recruitment was greater during the drought relative to postdrought census intervals. This is consistent with the hypothesis that the 1982–1983 drought pushed water deficits to lethal extremes and increased tree mortality, understory light availability, and subsequent sapling recruitment (Condit et al. 1992, 1995, 2017). We hypothesized that drought intensifies competition for water but reduces competition for light. We predicted that competition (defined as the negative effects of neighboring trees on focal tree survival) would be stronger for trees (1) consuming more water or more susceptible to water deficits during drought and (2) intercepting more light or more susceptible to shade in the absence of drought. Using wood density (WD) as a proxy for water use strategies, we did not find evidence consistent with the first prediction. Using leaf mass per area (LMA) as a proxy for light use strategies, we found evidence consistent with the second prediction. For all tree size classes, survival was independent of neighborhood LMA during the drought interval when deciduousness and mortality reduced shading. But in the postdrought interval, survival decreased with neighborhood LMA as the canopy recovered and shading increased. These results suggest severe drought could indirectly impact forests by altering forest vertical structure and competition for light in moist tropical forests.

Drought-mediated changes in tree competition for light

Our results support the hypothesis that greater light availability in the forest understory reduced competition for light during the drought relative to the postdrought census intervals. The leaf-area index declined substantially during the warm, dry 2015–2016 El Niño dry season in this forest (Detto et al. 2018). Tree mortality was unaffected in 2015–2016; however, leaf fall increased substantially (Detto et al. 2018; S. J. Wright, *unpublished data*). This suggests that increased light availability in the understory might occur regularly during drought events. During the much more severe 1982–1983 El Niño dry season,

survival time of large trees decreased (Condit et al. 1992, 1995), the density of large stems declined, and these deaths opened tree fall gaps and further increased understory light availability. Increased sapling recruitment rates, together with increased tree growth rates during the drought interval documented by Condit et al. (1992) are also consistent with the hypothesis that death of large trees increased light at the forest understory during drought. The increased recruitment and growth rates in the 1982–1985 census interval might be because the positive effects of increased canopy gaps on recruitment and growth after the 1982–1983 drought overwhelmed the possible negative effects of water deficits during the 1982–1983 drought.

We also found evidence of reduced competition for light during the drought relative to postdrought intervals. Across size classes, trees had reduced survival when surrounded by high-LMA neighbors in the postdrought interval but not in the drought interval. These results suggest that light-associated neighborhood competitive impacts were reduced during the drought census interval. Our findings highlight the importance of considering indirect processes in predicting long-term impacts of drought on forests.

We speculate that drought-mediated changes in understory light availability and competition for light might occur in other tropical forests. In Amazon evergreen forests, canopy leaf abscission occurred in the late dry season and coincided with increased leaf area of the understory layer (Tang and Dubayah 2017), suggesting increased light penetration to forest understories in the dry season. In a Bornean forest, negative local conspecific density effects on tree growth were weaker during a severe drought relative to nondrought periods for small- to medium-sized trees (Newbery and Stoll 2013).

However, the degrees of drought-induced reduction in competition for light might depend on the characteristics of drought and forests. For example, drought-induced reduction of light competition would be strong if drought is extreme enough to kill large trees but also mild enough to keep small trees alive, and soil moisture availability could recover quickly in postdrought periods. Drought-induced reduction of light competition might not be important in Mediterranean forests, in which small trees are more vulnerable to drought than large trees and slow to recover in postdrought periods because of high water limitation (Lloret et al. 2004).

Drought-mediated changes in tree competition for water

We predicted that extreme soil-water deficits would reduce survival for large and small trees more than for midsize trees in the drought interval. Across all size classes, tree survival time decreased in the drought relative to postdrought intervals, suggesting intensified soil-water deficits during the drought interval. Large trees suffered the largest reduction of median survival time than midsize trees, consistent with the prediction and with experimental and observational findings in

other forests (Bennett et al. 2015, Rowland et al. 2015). However, small trees did not suffer greater mortality than midsize trees, counter to our prediction. This might be an artifact of the minimum size threshold (10 mm DBH). Saplings of this size might already have root systems well adapted to soil-water deficits relative to recently recruited seedlings. Increased understory light levels might also increase survival in the understory during the drought census interval, masking any negative effect of soil-water deficits.

Increased soil-water limitation during severe drought might intensify tree competition for water. Based on this hypothesis, we predicted longer tree survival in neighborhoods with greater mean WD, and higher tolerance of focal species with high WD to neighborhood competitive impacts during the drought relative to postdrought census intervals. Our results did not support these predictions. Relationships between focal tree survival and WD-mediated neighborhood interactions did not vary significantly between the two census intervals. There are several possible reasons. First, the positive effects of enriched light levels may overwhelm the negative effects of intensified soil-water deficits during the drought census interval. Second, WD may not be a good proxy trait for water use strategies in this forest. WD is a complex trait encompassing both vessel and fiber fractions, and a specific wood density can be achieved with different combinations of wood elements, and thus plant strategies (Zanne and Falster 2010, Fortunel et al. 2014). Future studies including traits more directly associated with water use (e.g., sapwood hydraulic conductivity; Markesteijn et al. 2011) may bring new insights. Third, the instantaneous soil-water limitation during the extreme dry season (1982–1983) included in the drought census interval (1982–1985) was severe, but we used multiple-year census data, which may not fully capture the drought effects over a much shorter timescale. Soil-water limitation in an extreme dry season is quickly alleviated in the following wet season in this forest (Wright and Cornejo 1990, Comita and Engelbrecht 2009).

Effects of neighborhood crowding on tree survival

We found that focal trees of all sizes survived longer in more crowded neighborhoods in both the drought and postdrought intervals. Greater survival in more crowded neighborhoods was independent of focal species identity in most cases, contrary to our prediction. A possible explanation is that large neighbor tree canopies might protect smaller trees from the high leaf-to-air vapor pressure deficits and evaporative losses during drought (Gómez-Aparicio et al. 2004). This possibility is unlikely to be an important cause for our findings because the positive crowding effects were present not only for small trees in the drought census interval but also for large and midsize trees in the postdrought census interval. Our previous study in this forest found the opposite crowding effects for growth rate in the absence of severe

drought (Chen et al. 2016). Focal trees grew more slowly in neighborhoods that were more crowded. These opposite results for growth and survival might result from the growth–survival trade-off observed in this and other forests (Pacala et al. 1996, Wright et al. 2010). Individuals growing rapidly in less crowded/shaded neighborhoods may allocate less to defense, and thus have higher mortality rates. Self-thinning might also raise mortality rates in less-crowded neighborhoods.

Changes of other environmental factors during drought

In addition to the changed water and light limitations, there could be other important factors leading to substantial indirect tree responses to droughts. For example, increased leaf abscission and tree mortality may provide an additional nutrient input into forest soil (Wieder and Wright 1995, Newbery et al. 2011, Anderegg et al. 2012, Schlesinger et al. 2016), which may modify tree competition for soil nutrients. Increased temperature and water deficit during severe drought may also change the population dynamics of insect herbivores (Bael et al. 2004, McDowell et al. 2008, Anderegg et al. 2015), which may in turn modify the tree–insect interactions. Finally, frequent droughts may induce shifts in functional compositions of forest communities (Enquist and Enquist 2011, Anderegg et al. 2012, Fauset et al. 2012), thus the compositions of competitors. Changes in competitor compositions may substantially shape forest responses to droughts (Suttle et al. 2007, Alexander et al. 2015).

Variation within census intervals

Our census intervals spanned 3 and 5 yr, and temporal variation within census intervals remains unknown. Outcomes over multiyear census intervals integrate net effects of multiple and potentially opposing processes operating at shorter timescales. For example, both sapling recruitment rates and survival might have varied among years within the drought census interval (1982–1985), with lower recruitment and survival during the 1982–1983 drought, and greater recruitment and survival in the 2 yr after the drought. Positive effects on recruitment rates associated with increased canopy gaps after the 1982–1983 drought might have overwhelmed a possible negative effect of water deficits during the drought, causing a net increase in the sapling recruitment rate over the 3-yr drought census interval. To disentangle these possibilities, future studies would benefit from censuses with higher temporal resolution.

CONCLUSIONS

Drought increases mortality rates for many tree species, and species-specific sensitivity to drought is often associated with traits (Poorter and Markesteijn 2008, Markesteijn et al. 2011, Ouédraogo et al. 2013, Greenwood et al. 2017). These direct responses to drought are widely

recognized as critical forces driving loss of carbon storage, shifts in community composition, and loss of biodiversity (Enquist and Enquist 2011, Fauset et al. 2012, Schlesinger et al. 2016). Our results illustrate that drought also has indirect effects on forests, which may modify these direct negative impacts. Loss of canopy trees opens light gaps, which facilitates sapling recruitment and reduces competition for light. Our study highlights the importance of considering indirect impacts of drought in predicting forest responses to drought and suggests that light, in addition to water, could be a crucial factor driving the impacts of drought on moist tropical forests.

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