Lianas have a seasonal growth advantage over co-occurring trees

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Abstract. The seasonal growth advantage hypothesis posits that plant species that grow well during seasonal drought will increase in abundance in forests with increasing seasonality of rainfall both in absolute numbers and also relative to co-occurring plant species that grow poorly during seasonal drought. That is, seasonal drought will give some plant species a growth advantage that they lack in aseasonal forests, thus allowing them attain higher abundance. For tropical forest plants, the seasonal growth advantage hypothesis may explain the distribution of drought-adapted species across large-scale gradients of rainfall and seasonality. We tested the seasonal growth advantage hypothesis with lianas and trees in a seasonal tropical forest in central Panama. We measured the dry-season and wet-season diameter growth of 1,117 canopy trees and 648 canopy lianas from 2011 to 2016. We also evaluated how lianas and trees responded to the 2015–2016 El Niño, which was the third strongest el Niño drought on record in Panama. We found that liana growth rate was considerably higher during the dry-season months than the wet-season months in each of the five years. Lianas achieved one-half of their annual growth during the 4-month dry season. By contrast, trees grew far more during the wet season; they realized only one-quarter of their annual growth during the dry season. During the strong 2015–2016 El Niño dry season, trees essentially stopped growing, whereas lianas grew unimpeded and as well as during any of the previous four dry seasons. Our findings support the hypothesis that seasonal growth gives lianas a decided growth advantage over trees in seasonal forests compared to aseasonal forests, and may explain why lianas peak in both absolute and relative abundance in highly seasonal tropical forests. Furthermore, the ability of lianas to grow during a strong el Niño drought suggests that lianas will benefit from the predicted increasing drought severity, whereas trees will suffer, and thus lianas are predicted to increase in relative abundance in seasonal tropical forests.

Key words: El Niño; lianas; Panama; plant distribution; seasonal growth advantage; tropical forests.

INTRODUCTION

Determining the mechanisms responsible for the abundance and distribution of organisms is one of the central goals in ecology (Krebs 1972, Brown 1984). Within the tropics, the abundance (density) of most plant groups (e.g., trees, palms, herbs, and epiphytes) tends to increase with increasing mean annual precipitation (Gentry 1991, Schnitzer 2005). By contrast, the abundance of lianas, a common tropical plant group that is both taxonomically and functionally diverse (Schnitzer and Bongers 2002, Wyka et al. 2013, Gianoli 2015, Schnitzer et al. 2015), deviates from this common trend. Specifically, the density of lianas in tropical forests, both in absolute terms and relative to trees, increases with the strength of seasonal drought and

decreases with increasing mean annual precipitation and the availability of soil moisture (e.g., Schnitzer 2005, DeWalt et al. 2010, 2015, Manzané-Pinzón et al. 2018).

The seasonal growth advantage hypothesis may explain the unique distribution of lianas and other species that increase in abundance with the intensity of seasonal drought. The seasonal growth advantage hypothesis states that species that grow best during seasonal drought, when solar radiation is high (due to the absence of thick cloud cover) and water availability is low, will realize more annual growth than those same species in aseasonal areas, where they lack a season of high growth (Schnitzer 2005, 2015a, 2018). In interspecific comparisons, there is a trade-off between growth rate and survivorship (e.g., Wright et al. 2010); however, intraspecific variation in growth rate is positively correlated with higher survivorship (e.g., Camac et al. 2018) and presumably fecundity, which we hypothesize culminates in higher densities. For liana species, the period of high dry-season growth in seasonal tropical forests (commonly ranging from two to six months) is

hypothesized to increase liana size and survival, ultimately resulting in higher density (in both absolute terms and relative to co-occurring tree species that grow poorly during seasonal drought) compared to aseasonal forests (Schnitzer 2005, 2015a, 2018). Even a slight seasonal growth advantage could, over decades, allow liana species to increase in relative abundance with increasing forest seasonality. Thus, the seasonal growth advantage hypothesis may explain the increase in liana density (both in absolute terms and relative to trees) in forests with increasing seasonality across the tropics (Schnitzer 2005, 2018).

The seasonal growth advantage hypothesis has been tested primarily in studies that measured the physiological responses of lianas and trees during wet and dry seasons. These studies reported that lianas generally have better access to water, experience less water stress, have higher levels of photosynthesis, and have greater water-use efficiency and osmotic adjustment than do co-occurring trees during the dry season relative to the wet season (Cai et al. 2009, Chen et al. 2015, Maréchaux et al. 2017). For example, in a common garden study with six replicated tree species and six replicated liana species in central Panama, C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data* found that, compared to trees, lianas had 44% higher predawn leaf water potential, 61% higher intrinsic water-use efficiency, and 28% higher photosynthesis in the dry season compared to the wet season. In an examination of physiological traits of liana and tree saplings that were growing along roadsides in wet and seasonal forests in Panama, van der Sande et al. (2019) reported that trees had the expected trade-off between hydraulic conductance and hydraulic safety, whereas lianas did not, suggesting that lianas had the capacity to maintain high conductivity and thus high growth rates while resisting embolism. Collectively, these studies suggest that lianas are better able to grow during the dry season than co-occurring trees, and thus are able to capitalize on high dry season light availability. In addition, one study (Schnitzer 2005) measured the height growth of liana and tree saplings in the understory during a wet and a dry season of a seasonal forest in Panama and found that lianas grew proportionally more than trees during the dry season than the wet season, supporting the hypothesis that lianas had a seasonal growth advantage.

Previous studies, however, were limited in their ability to test the seasonal growth advantage hypothesis for two main reasons. *First*, although studies on plant water status and the physiological responses of lianas and trees to low water availability were consistent with underlying physiological mechanisms that could confer a dry season growth advantage to lianas over trees (e.g., Cai et al. 2009, Chen et al. 2015, Maréchaux et al. 2017; Smith-Martin et al., *unpublished*), none of the physiology-oriented studies actually demonstrated that lianas had higher growth during the dry season. Less negative water potential during the dry season (e.g., Cai et al. 2009, Chen et al. 2015, 2017)

could indicate that lianas limit carbon assimilation during the day to avoid water loss. Alternatively, to remain physiologically active during periods of low water availability, it is possible that lianas allocate much of their extra carbon to non-structural carbohydrates (NSC) rather than to growth, because NSC can help plants maintain a healthy water balance during periods of water stress (Würth et al. 2005, Körner 2015, Martinez-Vilalta et al. 2016, De Baerdemaeker et al. 2017). If so, then higher dry-season photosynthesis may not translate directly into higher growth. *Second*, in the one study that measured seasonal growth of lianas and trees, the author measured height growth for juvenile plants in the forest understory (Schnitzer 2005). However, the responses of juvenile understory plants may not accurately reflect the growth of canopy individuals, which may be a stronger contributor to population demographic rates. Further, many liana species grow like tree saplings in the understory (Manzané-Pinzón et al. 2018), and thus sapling physiology and growth (e.g., van der Sande et al.) may not accurately represent the liana-tree comparison for canopy individuals. Also, Schnitzer (2005) sampled liana and tree growth during one wet and one dry season, and thus they could not remove the effects of that particular year on seasonal growth. Therefore, while there is some evidence supporting the fundamental premise of the seasonal growth advantage hypothesis, direct evidence that canopy lianas grow more than canopy trees across multiple dry seasons relative to multiple wet seasons is lacking.

We tested the seasonal growth advantage hypothesis by comparing annual wet- and dry-season growth of canopy lianas and canopy trees over a consecutive 5-yr period (2011–2016). Each year we measured the seasonal diameter growth of 1,117 large trees (≥10 cm diameter) and 648 large lianas (≥5 cm) in eight m plots in central Panama (1,765 total canopy plants). During the final year of the study (2015–2016), Panama experienced the third-strongest el Niño drought on record (S. Paton, *personal communication*), and we predicted that the intense drought would elicit an even stronger disparity in the ratio of dry to wet season growth between lianas and trees, with trees suffering more during the dry season than lianas. This study is the most comprehensive test of the seasonal growth advantage hypothesis to date, and the first to use multi-year seasonal diameter growth of adult lianas and trees.

Methods

We conducted the study on Gigante Peninsula, a 60-yr-old secondary forest that is part of the Barro Colorado Natural Monument (BCNM) in the Republic of Panama. The forest on Gigante Peninsula is classified as a semideciduous, seasonally moist forest (Leigh 1999). The Gigante forest receives a mean annual rainfall of ~2,600 mm and has a strong dry season from January until May in which rainfall is less than 100 mm per month (Schnitzer and Carson 2010). During the period

of the experiment (from 2011 until 2016), annual rainfall on the BCNM varied from 1,807 to 3,262 mm/yr (S. Paton, *personal communication*). The 2016 El Niño drought in year 5 of the experiment resulted in the third driest year in the 90-yr continuous record, and the BCNM received only ~1,480 mm of rain during the wet season, followed by a long and strong dry season (S. Paton, *personal communication*).

In 2008, we established eight 80 × 80 m plots, which initially served as controls for an ongoing liana removal experiment (e.g., Alvarez-Cansino et al. 2015, van der Heijden et al. 2015, Reid et al. 2015, Martinez-Izquierdo et al. 2016, Rodriguez-Ronderos et al. 2016, Garcia-Leon et al. 2018). Because lianas were not experimentally removed and no other manipulations were conducted in these plots, they were well suited to test the seasonal growth advantage hypothesis. In each plot, we permanently tagged, mapped, measured the diameter (1.3 m along the stem from the roots), and identified to species all trees and lianas ≥1 cm diameter within the center 60 × 60 m portion of the plot. Plant surveys followed sampling protocols established by Gerwing et al. (2006) and Schnitzer et al. (2008) for lianas and Condit (1998) for trees.

For canopy lianas ≥5 cm diameter and canopy trees ≥10 cm diameter, which were the focus of this study, we used a fabric diameter tape to precisely measure the stem diameter of each individual 1.3 m along the stem from the roots (where we painted an orange mark on each stem to facilitate repeated measurements) at the beginning and end of the wet and dry seasons. For the canopy trees, we also installed manual dendrometer bands in mid-November 2010, prior to the 2011 dry season, and allowed the bands to settle on the trees for at least four months before collecting measurements (follows Alvarez-Cansino et al. 2015). We used the dendrometer bands to determine the seasonal diameter increment for trees; however, dendrometer bands did not work well for the smaller liana stems, and thus seasonal diameter increment was based on diameter tape measurements (van der Heijden et al. 2015). The patterns of tree diameter growth were the same regardless of the measurement method (dendrometer band or diameter tape); however, dendrometer measurements had lower variability than diameter tape measurements.

Tree and liana diameters were calculated seasonally each year from the beginning of the 2011 wet season (May 2011) until the end of the 2016 dry season (May 2016). Each year, we started the wet season census in late April/early May, immediately after the dry season trade winds had stopped and there was rain for at least five consecutive days. In central Panama, the beginning of the wet season is marked by a tapering of the trade winds and the onset of rains, which correspond to the northward movement of the intertropical convergence zone in mid-April. We conducted a second census at the start of the dry season (and end of the wet season) in late December/early January, after the dry season trade winds had gained strength and there was no rainfall for at least five consecutive days. In central Panama, the onset of the dry season can occur abruptly, often in a single day, changing from cloudy and rainy to sunny and windy with no rain. Thus, we were able to quantify dry season (January–May) and wet season (May–January) diameter growth for canopy lianas and trees over five consecutive years (2011–2016).

Data analyses

We calculated mean seasonal growth for lianas and trees as both a percentage of the initial stem diameter (relative growth) and also as absolute diameter increase. Because the wet season in Panama is twice as long as the dry season, we also annualized the data to compare a seasonal growth rate for both the wet and dry seasons. We included individuals that were alive during the entire 5-yr census period to avoid aberrant growth rates attributed to dying or dead individuals. To test whether seasonal growth patterns were driven primary by common species, we compared the growth trends of the most common and the rare liana and tree species. For trees, there was a total of 128 species, with 7 that we defined as common ($n > 30$ individuals) and 96 that we defined as rare ($n < 5$ individuals). For lianas, there was a total of 54 species, with 4 that we defined as common ($n > 30$ individuals) and 30 that we defined as rare ($n < 5$ individuals). On nearby Barro Colorado Island, only 6.3% of the canopy trees are deciduous during the peak of the dry season (Condit et al. 2000), indicating that relatively few of the canopy trees in this area were deciduous, and none of the common tree or liana species in our study were deciduous (Croat 1978).

We tested for differences in the mean growth rates between seasons in each year of the study for all measures of liana and tree growth (absolute, relative and annualized growth) using a Monte Carlo bootstrapping approach. This method allowed us to compare liana and tree growth between seasons in each year using a single analysis, without the need for post hoc testing. The Monte Carlo bootstrapping approach also allowed us to integrate measurement error into the confidence intervals and the analyses (cf. van der Heijden et al. 2015). For this approach, we varied the initial diameter of each tree in each plot at random using a normal distribution with a standard deviation of 5%. Tree diameters in subsequent censuses were calculated by adding a randomly selected value from the normal distribution of dendrometer increment measurements with a standard deviation of 3% to the tree diameter of the previous census. For lianas, we varied the diameter measurements in each census by adding a randomly value selected from a normal distribution with a standard deviation of 5% (cf. van der Heijden et al. 2015). We used this approach to calculate 100,000 realizations of mean liana and tree growth for each season and the differences in growth between seasons. These data were then used to calculate the mean

seasonal growth for lianas and trees, as well as the mean difference in liana and tree growth between the wet and dry season for each year of the study and their 90% and 95% confidence intervals. The confidence intervals for the difference between mean wet and dry season growth for each of the growth forms were used to determine whether these differences were significant for each year of study. Differences in tree or liana growth between seasons were considered significant or marginally significant when the 95% confidence interval ($P \leq 0.05$) or 90% confidence interval ($0.05 < P \leq 0.10$), respectively, did not overlap with zero. The actual and modeled mean growth values per season were nearly identical.

Results

Lianas grew as much or more during the 4-month dry season than they did during the entire 8-month wet season (Fig. 1a). Liana growth rate (controlling for the length of the season) was far higher during the dry season months than the wet season months (Fig. 1c). By contrast, trees had the opposite pattern. Trees realized the vast majority of their growth during the wet season (Fig. 1b), and tree growth rate was more than two times higher during the wet season than the dry season (Fig. 1d). The 2015–2016 El Niño dry season was particularly devastating for trees, and they essentially stopped growing during this period (Fig. 1b, d). Lianas, however, maintained their growth during the strong El Niño dry season, growing as well as the previous four dry seasons (Fig. 1a, c).

For both lianas and trees, the seasonal growth patterns of the most common species were similar to that of the least common species (Figs. 2 and 3). Therefore, the patterns of vigorous dry season growth for lianas and vigorous wet season growth for trees were not driven solely by the common species, but they was also shared, on average, by the rare species. For one common liana species (*Bauhinia guianensis*), dry and wet season relative growth were similar (Fig. 2). Nonetheless, the seasonal growth of *B. guianensis* was not weighted as heavily towards wet season growth as was the majority of the tree species (Fig. 3). The seasonal growth responses of lianas and trees were the same regardless of whether we examined growth relative to the initial stem size (Figs. 1–3) or absolute growth over time (Appendix S1: Figs. S1 and S2).

Discussion

Evidence for the seasonal growth advantage hypothesis

Our data strongly support the hypothesis that lianas have a growth advantage in seasonal forests. Canopy lianas achieved more than half of their annual growth during the 4-month dry season, with the rest of their growth occurring during the remaining 8-month wet season. By contrast, canopy trees grew two to three times more during the 8-month wet season than during the 4-month dry season. The ability of lianas to maintain higher growth rates during the dry season than during the wet season gives them approximately four months of relatively high growth in this forest, a growth advantage that would be lacking in ever-wet forests. The seasonal growth advantage for lianas is even greater relative to co-occurring trees, since trees grew relatively poorly during the dry season and, instead, concentrated their growth during the wet season. Presumably, lianas would benefit even more relative to co-occurring trees in forests with an even stronger dry season, which was the case for the extremely dry El Niño dry season, when lianas grew well and trees essentially stopped growing.

Over decades, high dry-season growth could result in greater annual liana growth and survival, with a greater number of liana stems accumulating in seasonal forests compared to aseasonal forests (Schnitzer 2005, 2015a, 2018). This phenomenon could explain why liana density tends to increase in tropical forests with relatively high seasonality and low annual rainfall and soil moisture availability (e.g., Schnitzer 2005, Swaine and Grace 2007, DeWalt et al. 2010, 2015, Manzané-Pinzón et al. 2018). By contrast, trees should be favored over lianas in forests that lack a dry season, since trees grow well during rainy periods. Further, the ability of canopy lianas to grow well even during a strong el Niño dry season, while canopy trees largely stopped growing, indicates that stronger droughts, which are both now observed and predicted to increase in the future (e.g., Fu et al. 2013), may further favor lianas over trees in seasonal forests.

Our findings were similar to those of Schnitzer (2005), who measured juvenile lianas and trees (<2 m tall) in a seasonal forest in Panama for one year. In that study, both lianas and trees grew better during the wet season than the dry season, but lianas grew relatively more during the dry season than the wet season compared to trees. In the current study, we found a far higher growth rates for canopy lianas during the dry season than during the wet season, with canopy trees displaying the opposite growth pattern. The slight disparity between the two studies may be due to the focus on canopy lianas and trees in the current study vs. juvenile plants in the previous study. Another difference is the much longer duration of the current study (5 yr vs. 1 yr), along with the larger sample size in this study (1,765 canopy lianas and trees vs. 384 juvenile lianas and trees in the previous study). Collectively, these studies indicate that both canopy and understory lianas have a seasonal growth advantage compared to co-occurring trees, thus explaining why liana density peaks in seasonal forests.

Why lianas grow more than trees during season drought

High seasonal growth for lianas may be due to their ability to capitalize on the high-light conditions that are present during seasonal drought (Schnitzer 2005, 2018). During the dry season, the lack of clouds results in intense solar radiation that is less common during the rest of the year. For example, in Central Panama, light
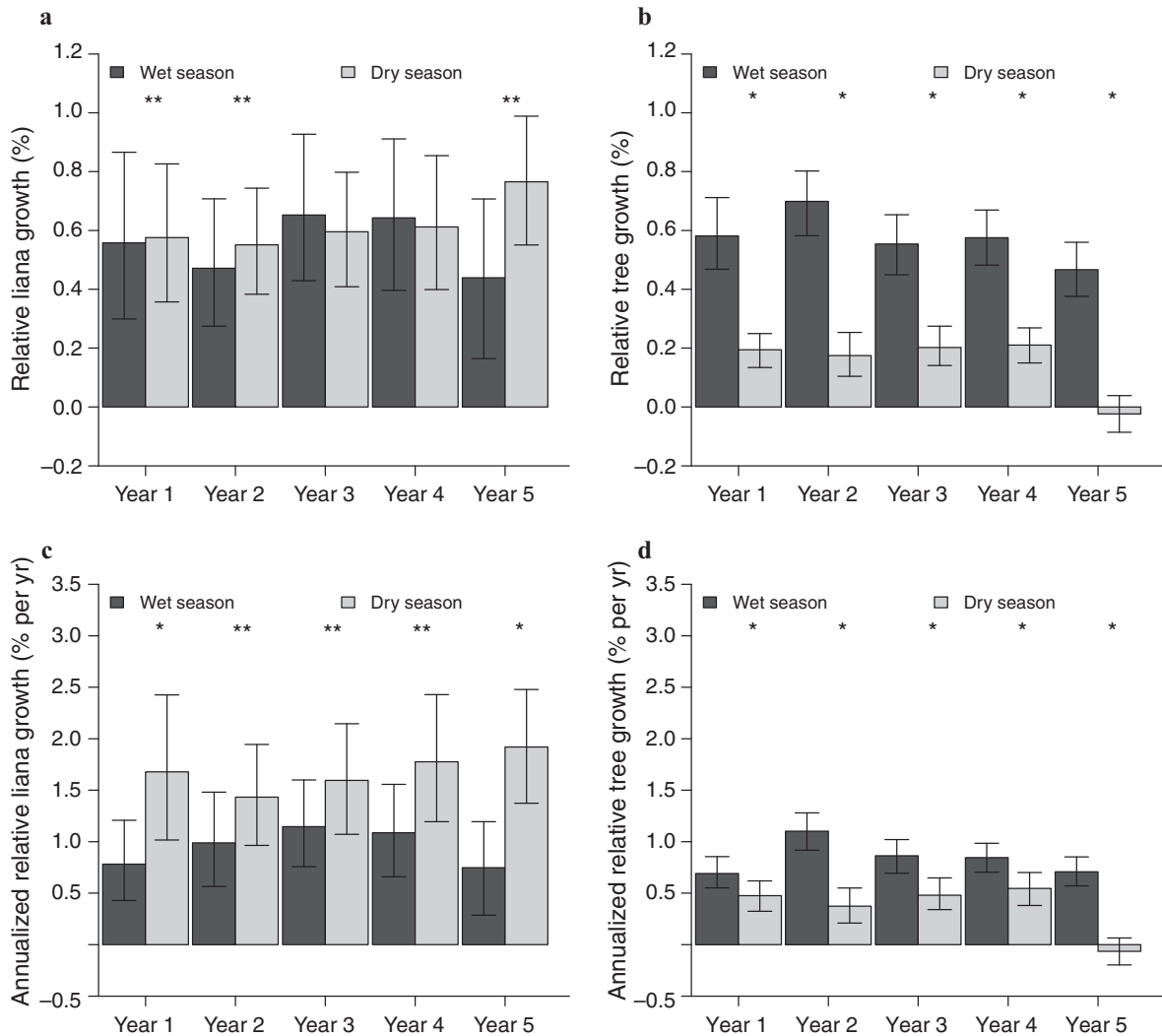
FIG. 1. Mean bootstrapped relative growth (based on initial size) and annualized relative growth for lianas (first column, $N = 648$ individuals and 54 species) and trees (second column, $N = 1,117$ individuals and 128 species) over a five-year period (2011–2016) on Gigante Peninsula in central Panama. Error bars represent 95% confidence intervals based on 100,000 bootstrap iterations; * indicates $P < 0.05$, ** indicates $0.05 \leq P \leq 0.10$.

availability above the forest canopy can increase 50% from dry season to wet season (Wright and van Schaik 1994, Graham et al. 2003). Plants that can manage water and avoid severe water stress can capitalize on high dry-season light availability through increased photosynthesis and carbon fixation. Furthermore, lianas appear to have a higher photosynthetic capacity than trees (Cai et al. 2009, Chen et al. 2015; C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data*), and by maintaining healthy water status and maintaining high hydraulic conductivity during the dry season (e.g., van der Sande et al., 2019), lianas are particularly well suited to take advantage of high dry-season light availability. By contrast, trees appear to suffer more water stress (C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data*) and have a more

conservative hydraulic conductivity strategy than lianas (van der Sande et al., 2019), and thus trees may not be able to capitalize as well as lianas on the high dry season light. The ability of lianas to capitalize on high solar radiation while maintaining healthy water status may also explain their extremely high abundance in such high-light areas as treefall gaps, forest edges, and young tropical forests (reviewed by Schnitzer 2018).

The ability to maximize photosynthesis and carbon fixation with high light availability requires some combination of access to sufficient quantities of water and the ability to use water efficiently. Several studies have shown that lianas have access to water during the dry season, which may allow them to maintain healthy water status during seasonal drought (e.g., Cai et al. 2009, Chen et al. 2015, 2017; C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data*). Lianas may
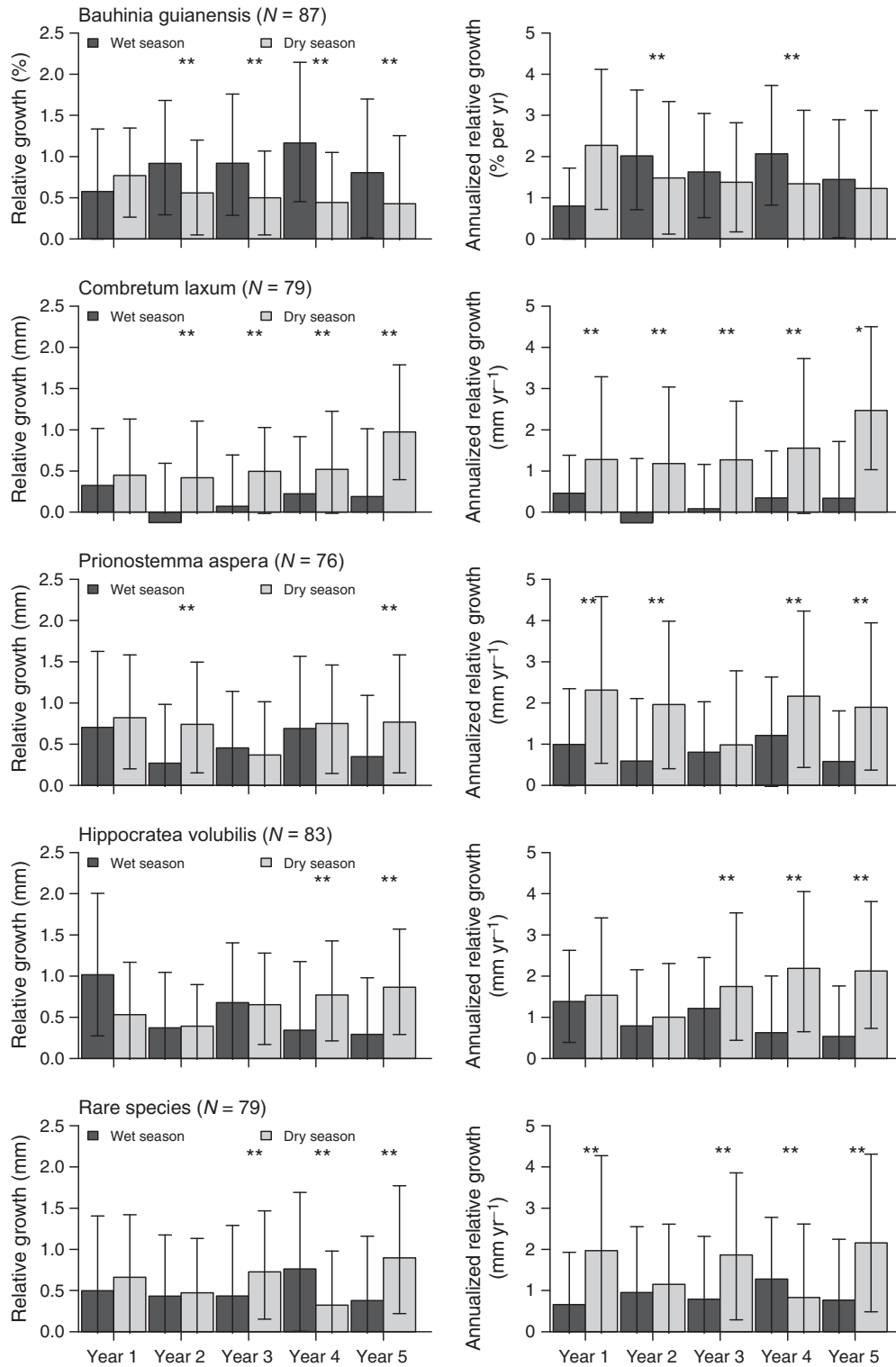
Fig. 2.   Mean bootstrapped relative growth (based on initial size) and annualized relative growth for common and rare liana species over a five-year period (2011–2016) on Gigante Peninsula in central Panama. Common species were those with more than 30 replicate individuals among the eight plots. Rare species were those with fewer than five individuals, and each individual was used as a replicate to calculate a mean response. There were four common and 30 rare liana species. Error bars indicate 95% confidence intervals based on 100,000 bootstrap iterations; * indicates $P < 0.05$, ** indicates $0.05 \leq P \leq 0.10$.

be able to further maintain healthy water status by minimizing the trade-off between photosynthesis and water loss (Schnitzer 2018). C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data* found that during the dry season in Panama, lianas had 63% higher intrinsic water-use efficiency than co-occurring trees. During the wet season, however, water-use efficiency between trees and lianas was similar. Also in Panama, van der Sande et al. (2019) suggested that lianas, but not trees, could maintain high vascular conductivity and presumably growth under dry conditions while resisting vascular cavitation and embolism. Studies in southwest China also reported that lianas used water and nitrogen more efficiently than did trees during the dry season (e.g., Cai et al. 2009, Chen et al. 2015). Therefore, lianas appear to be able to acquire and efficiently use soil moisture, which allows them to capitalize on the high-light environment that is present during the dry season while simultaneously maintaining healthy water status.

Potential alternative explanations

It is possible that the seasonal growth advantage was driven more by a release from intense wet season tree competition rather than a dry season growth advantage. That is, vigorous canopy tree growth during the wet season may have suppressed liana growth, and lianas may appear to have a seasonal growth advantage because they are released from competition during the dry season, when trees are largely dormant and some are deciduous. The available data, however, appear to support the seasonal growth advantage hypothesis more than the competitive release hypothesis. Lianas performed better than trees during the dry season even when individuals were grown separately and there was no possibility for competitive release. For example, lianas and trees that were grown separately in a common garden for five years performed similarly during the wet season, but lianas performed better during the dry season in terms of water status, photosynthesis, and water-use efficiency (Smith-Martin et al., *in review*). Also, trees in the common gardens grew far better when exposed to dry season irrigation (compared to non-irrigated controls), whereas lianas did not respond positively to dry season irrigation, suggesting that trees, not lianas, suffered from low soil availability during the dry season (C. M. Smith-Martin, C. L. Bastos, O. R. Lopez, J. S. Powers, and S. A. Schnitzer, *unpublished data*). In terms of aboveground competition, liana foliage is typically deployed on top of their tree hosts (e.g., Rodriguez-Ronderos et al. 2016); thus, by restricting our study to sun-exposed canopy lianas and trees, we limited the effect of competition for light from canopy trees, and thus limited the amount of competitive release that was possible. Canopy trees could possibly suppress understory lianas during the wet season by decreasing light; however, Schnitzer (2005) found that understory lianas actually grew more during the wet season than they did during the dry season, even though lianas grew proportionally more than trees

during the dry season than the wet season. Therefore, the available data support the seasonal growth advantage hypothesis. Nonetheless, little is known about the competitive effects of trees on lianas (Stewart and Schnitzer 2017), and fully factorial experimental plant removal experiments would allow us to more definitively test between these two alternative hypotheses.

Our diameter growth estimates may have been influenced by the swelling or shrinking of liana and tree stems during the seasons. The diameter of trees and presumably lianas can shrink when stem storage tissues are dehydrated due to low soil moisture availability and when bark is dehydrated due to low relative humidity (e.g., Borchert 1999, Stahl et al. 2010). For the census that began at the beginning of the dry season, soil moisture was high after the previous eight months of wet season rainfall (Reid et al. 2015), so stem storage tissues should not have been dehydrated; however, there may have been bark shrinkage due to a drop in relative humidity (Stahl et al. 2010). For the census that began at the beginning of the wet season, soil moisture may have been low after the long dry season (Reid et al. 2015), so stem storage tissues could have been dehydrated; however, stem shrinkage may have been minimized or absent because we waited until we had received at least five days of rainfall before we began the wet season census. Furthermore, there may have been bark swelling due to the increase in relative humidity after the start of the wet season. Whether seasonal stem changes not attributable to growth biased our results would depend on the relative importance of stem storage tissue and bark swelling and shrinking to stem size, which would give insight into whether we potentially underestimated or overestimated seasonal stem growth for either lianas and trees. Importantly, there is little evidence that lianas and trees differ systematically in stem storage tissues and bark characteristics, and thus there is no evidence that either growth form would shrink or swell differently during the wet and dry seasons. Therefore, based on the available evidence, a likely explanation for our findings is that lianas grew more than trees during seasonal drought.

Does seasonal water partitioning explain liana and tree coexistence?

Lianas and trees have coexisted in tropical forests for millions of years and the ability to climb was an early innovation in terrestrial plants (Burnham 2015). However, the factors that determine the relative abundance of lianas and trees, and whether liana and tree densities are inherently stable, is the subject of recent investigation (Stewart and Schnitzer 2017, Muller-Landau and Visser 2018, Visser et al. 2018*a, b*). One potential explanation is that liana and tree fitness and demographic rates are controlled by factors other than liana-tree competition, and thus a modest change in the abundance of one group does not necessarily reduce the abundance of the other. However, lianas have strong negative effects on
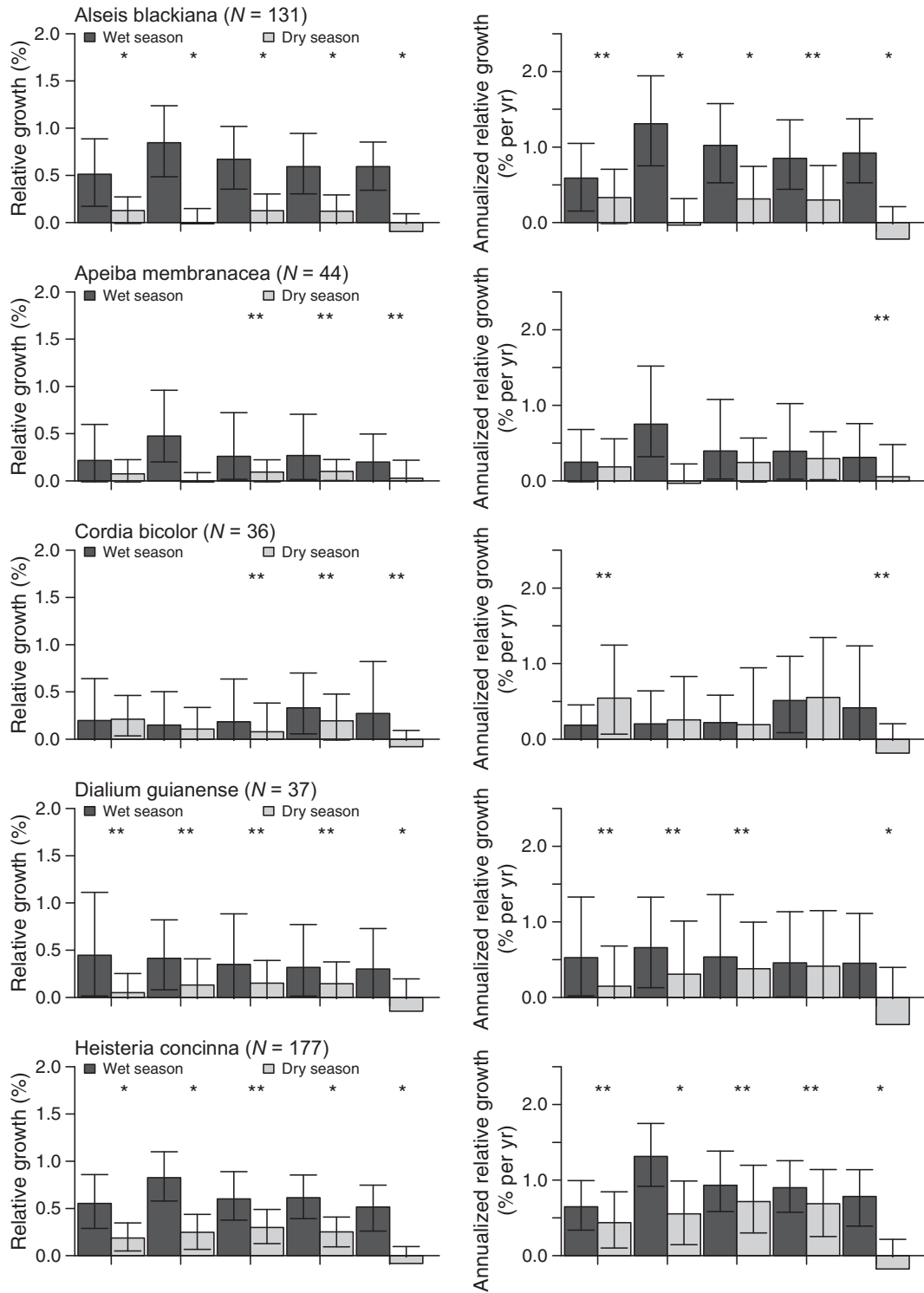
FIG. 3. Mean bootstrapped relative growth (based on initial size) and annualized relative growth for common and rare tree species over a five-year period (2011–2016) on Gigante Peninsula in central Panama. Common species were those with more than 30 replicate individuals among the eight plots. Rare species were those with fewer than five individuals, and each individual was used as a replicate to calculate a mean response. There were seven common and 96 rare tree species. Error bars indicate 95% confidence intervals based on 100,000 bootstrap iterations; * indicates $P < 0.05$, ** indicates $0.05 \geq P \leq 0.10$.
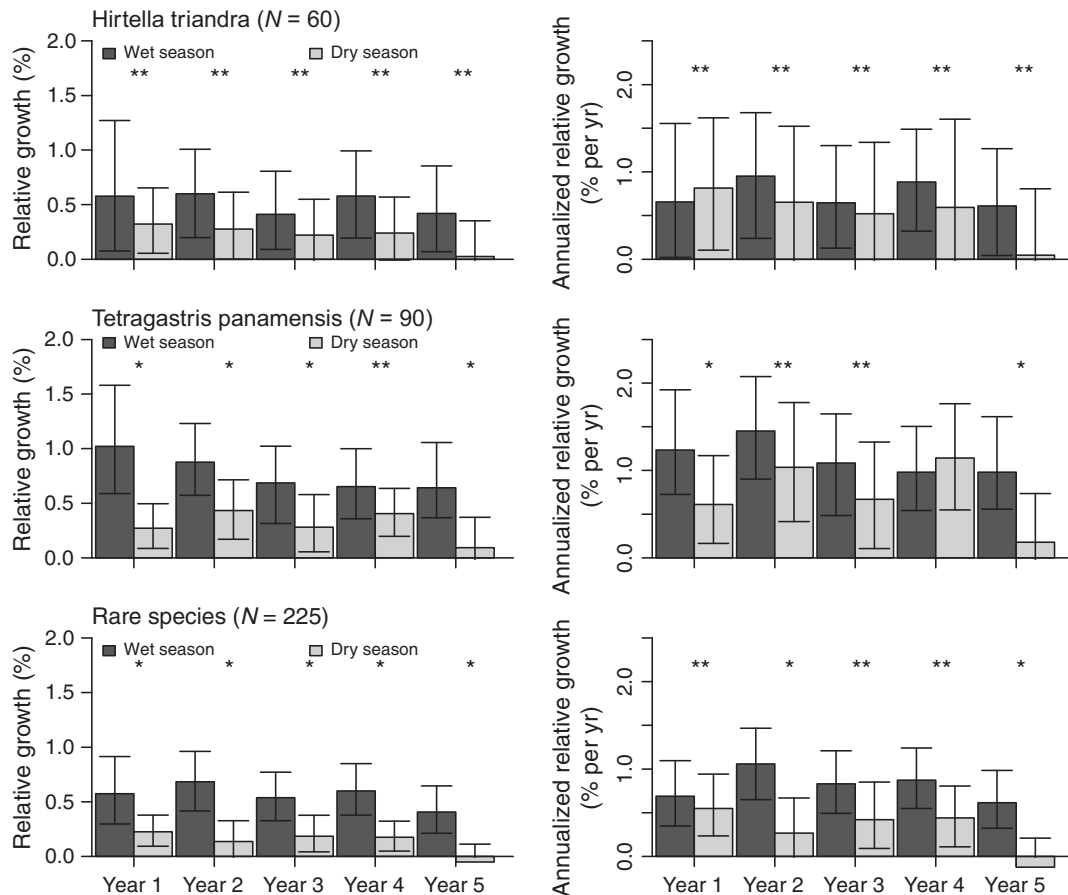
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tree growth (Schnitzer et al. 2014, van der Heijden et al. 2015, Toledo-Aceves 2015, Estrada-Villegas and Schnitzer 2018), reproduction (Kainer et al. 2014, Garcia-Leon et al. 2018), and recruitment (Grauel and Putz 2004, Schnitzer and Carson 2010), and thus it seems unlikely that lianas would have little effect on tree demography (Visser et al. 2018a).

Another explanation for liana and tree coexistence is that lianas and trees have diverged (or not fully converged) in their seasonal resource use, which theoretically could permit stable coexistence. That is, the ability of lianas to grow more during the dry season while trees grow more during the wet season may be a form of temporal resource partitioning (sensu Hutchinson 1961), which may explain long-term stable coexistence between lianas and trees. If lianas and trees had completely overlapping resource requirements, the removal of lianas should result in a strong response in trees during the dry season, the period when lianas grow most and thus presumably compete the most. However, trees in the Gigante Peninsula forest did not experience a greater competitive release after removing lianas from eight experimentally manipulated plots during the dry season compared to the wet season (van der Heijden et al.,

2019). Nor did lianas appear to have a stronger dry-season effect on trees in a forest fragment in Brazil (Venegas-Gonzalez et al., *in review*). These recent experimental findings support the possibility of ecological divergence between lianas and trees during their long history of coexistence, which may allow them to coexist rather than for either growth form to ultimately displace the other. In effect, the temporal partitioning of resources between lianas and trees during the year may represent a ghost of competition past (sensu Connell 1980).

Implications for increasing liana abundance in tropical forests

The ability of lianas to grow well in dry conditions with high evaporative demand (e.g., seasonal droughts, forest gaps, regenerating forests, and highly seasonal forests; Schnitzer 2018) may explain documented increases in lianas in neotropical forests (Phillips et al. 2002, Schnitzer and Bongers 2011, Schnitzer 2015b). Many tropical areas are now experiencing more intense droughts with increasing global climate change (Lewis et al. 2011, Fu et al. 2013). Our findings suggest that more intense

droughts would favor liana growth over that of trees, especially in seasonal tropical forests, which would presumably increase liana survival and fecundity, ultimately resulting in higher liana densities relative to trees. Furthermore, extended drought increases tree mortality, which results in greater forest disturbance and increases the availability of high light areas that favor liana proliferation (Schnitzer et al. 2000, Dalling et al. 2012, Ledo and Schnitzer 2014, Schnitzer 2018). While there may be other factors that favor lianas in a changing environment, including elevated atmospheric CO_2 (Phillips et al. 2002, but see Marvin et al. 2015) and nitrogen deposition (Schnitzer and Bongers 2011, Schnitzer 2015b; but see Pasquini et al. 2015), increasing drought and disturbance may be co-conspirators responsible for increasing liana abundance in many tropical forests.

Summary

This is the first study to demonstrate unequivocally that canopy lianas gain a large proportion of their annual growth during the dry season; whereas canopy trees grow mostly during the wet season. Vigorous dry-season growth may result in greater survival and fecundity, allowing liana stems to accumulate over time, thus explaining the relatively high abundance of lianas in seasonal tropical forests compared to aseasonal forests. This study supports the seasonal growth advantage hypothesis to explain the pan-tropical distribution of lianas, which peak in abundance in highly seasonal tropical forests. The ability of lianas to grow well even during a particularly strong el Niño dry season, when co-occurring trees essentially stopped growing, indicates that the frequency and intensity of drought, which are predicted to increase with global climate change, will favor lianas over trees and may explain observed increases in liana abundance in tropical forests.

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