Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: results from a liana removal experiment in Panama

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Abstract

1. Lianas are prevalent in Neotropical forests, where liana-tree competition can be intense, resulting in reduced tree growth and survival. The ability of lianas to grow relative to trees during the dry season suggests that liana-tree competition is also strongest in the dry season. If correct, the predicted intensification of the drying trend over large areas of the tropics in the future may therefore intensify liana-tree competition, resulting in a reduced carbon sink function of tropical forests. However, no study has established whether the liana effect on tree carbon accumulation is indeed stronger in the dry than in the wet season.
2. Using six years of data from a large-scale liana removal experiment in Panama, we provide the first experimental test of whether liana effects on tree carbon accumulation differ between seasons. We monitored tree and liana diameter increments at the beginning of the dry and wet season each year to assess seasonal differences in forest-level carbon accumulation between removal and control plots.
3. We found that median liana carbon accumulation was consistently higher in the dry (0.52 Mg C ha^{-1} yr^{-1}) than the wet season (0.36 Mg C ha^{-1} yr^{-1}), and significantly so in three of the years. Lianas reduced forest-level median tree carbon accumulation more severely in the wet (1.45 Mg C ha^{-1} yr^{-1}) than the dry (1.05 Mg C ha^{-1} yr^{-1}) season in all years. However, the relative effect of lianas was similar between the seasons, with lianas reducing forest-level tree carbon accumulation by 46.9% in the dry and 48.5% in the wet season.
4. *Synthesis*: Our results provide the first experimental demonstration that lianas do not have a stronger competitive effect on tree carbon accumulation during the dry season. Instead, lianas compete significantly with trees during both seasons, indicating a large negative effect of lianas on forest-level tree biomass increment regardless of seasonal water stress. Longer dry seasons are unlikely to impact liana-tree competition directly; however, the greater liana biomass increment during dry seasons may lead to further proliferation of liana biomass in tropical forests, with consequences for their ability to store and sequester carbon.

Key words: liana-tree competition, dry season advantage, carbon balance, dry season length, liana biomass increase

Introduction

Many Neotropical forests experience seasonality in rainfall with periods of abundance in precipitation being followed by pronounced periods of seasonal drought (Allen et al., 2017; Feng, Porporato, & Rodriguez-Iturbe, 2013). Consequently, canopy phenology, such as photosynthetic activity, in these forests differs markedly between seasons (Guan et al., 2015). Due to anthropogenic climate change, the length of the dry season has been increasing in many Neotropical forests (Fu et al., 2013), and tropical forests have been subjected to additional severe drought events, e.g. in 2005 and 2010 in the Amazon (Marengo, Tomasella, Alves, Soares, & Rodriguez, 2011; Zeng et al., 2008). Furthermore, these drying trends are projected to continue into the future (Boisier, Ciais, Ducharne, & Guimberteau, 2015; Duffy, Brando, Asner, & Field, 2015; Feng et al., 2013; Marengo et al., 2012). A decrease in rainfall or an increase in the length and severity of seasonal drought is also thought to be one of the putative mechanisms behind the proliferation of lianas (woody vines) in the Neotropics (Phillips et al., 2002; Schnitzer & Bongers, 2011; Wright, Calderón, Hernandéz, & Paton, 2004).

Lianas are a characteristic component of tropical forests, where they generally peak in abundance, biomass and species richness (Gentry, 1991; Schnitzer & Bongers, 2002). Lianas rely on the structural investment of trees to deploy leaves in the forest canopy. Consequently, lianas potentially invest less resources than trees into the formation of carbon-dense stems and more into generating a widespread leaf canopy (van der Heijden, Schnitzer, Powers, & Phillips, 2013). Lianas compete strongly with trees for above and belowground resources, such as light, essential nutrients and water (Pérez-Salicrup & Barker, 2000; Schnitzer, Kuzee, & Bongers, 2005; van der Heijden & Phillips, 2009a). Liana-tree competition is generally much more intense than tree-tree competition (Tobin, Wright, Mangan, & Schnitzer, 2012), resulting in reduced growth (Ingwell, Wright, Becklund, Hubbell, & Schnitzer, 2010; Schnitzer, van der Heijden, Mascaro, & Carson, 2014; van der Heijden & Phillips, 2009b), fecundity (García León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2018; Kainer, Wadt, Gomes-Silva, &

Capanu, 2006; Nabe-Nielsen, Kollmann, & Peña-Claros, 2009) and survival (Ingwell et al., 2010; Phillips, Vásquez Martínez, Monteagudo Mendoza, Baker, & Núñez Vargas, 2005) of liana-infested trees. Accordingly, lianas affect many important ecosystem processes (Reid, Schnitzer, & Powers, 2015; Schnitzer & Carson, 2010; Schnitzer, Dalling, & Carson, 2000; van der Heijden, Powers, & Schnitzer, 2015). Most notably, they reduce forest biomass (Durán & Gianoli, 2013) and the carbon sink potential of tropical forests (van der Heijden et al., 2015).

Lianas may have a competitive advantage over trees by maintaining their ability to grow during the dry season (Cai, Schnitzer, & Bongers, 2009; Sánchez-Azofeifa et al., 2009; Schnitzer, 2005, Schnitzer & van der Heijden, in press). Lianas differ from trees in foliar nutrients, hydraulic traits, and allocation to defence, especially in tropical dry forests (Asner & Martin, 2012; Collins, Wright, & Wurzburger, 2015; Werden, Waring, Smith-Martin, & Powers, 2017), which may augment carbon fixation during seasonal drought (Collins et al., 2015; Wyka, Oleksyn, Karolewski, & Schnitzer, 2013; Zhu & Cao, 2010). In addition, lianas are able to uptake water from deeper soil layers (Andrade, Meinzer, Goldstein, & Schnitzer, 2005; Chen et al., 2015) and/or different water sources during the dry season (De Deurwaerder et al., 2018). Many liana species therefore remain photosynthetically active during the dry season, whilst many trees are dormant, potentially allowing lianas to expand their dominance relative to trees (Schnitzer, 2005; Zotz & Winter, 1996). Their capacity for growth during the dry season suggests that the strength of liana-tree competition may also peak in the dry season, particularly in forests where trees are evergreen or brevi-deciduous. Lianas have been shown to compete intensely with trees for water in the dry season, when soil moisture content is low (Álvarez-Cansino, Schnitzer, Reid, & Powers, 2015; Chen et al., 2015; Tobin et al., 2012). However, whether this potential competitive advantage of lianas over trees results in a stronger reduction in the rate of forest carbon accumulation in the dry season has not yet been tested.

Tropical forests are critical ecosystems in terms of global carbon storage, and they have a substantial effect on the global carbon balance, storing approximately 285 Pg C in aboveground biomass (Feldpausch et al., 2012) and contributing 1.0 Pg C yr^{-1} to the global carbon sink (Pan et al., 2011). Therefore, liana-induced effects on tropical forest carbon sequestration may have global consequences for the rate and magnitude of climate change. If the impact of lianas on tree carbon accumulation is indeed stronger in the dry season, the predicted intensification of the drying trend in the future (Marengo et al., 2012) may lead to further proliferation of lianas (Schnitzer & Bongers, 2011) and liana-induced reduction in the carbon sink function particularly of seasonal forests (van der Heijden et al., 2015). Determining the seasonal effects of lianas on tree growth rates will therefore provide insights into the potential impacts of lianas on forest biomass dynamics with changing climatic conditions, and how these changes may affect carbon sequestration of tropical forests now and in the future. Here, we used a large-scale liana removal experiment to provide the first experimental test of whether: i) forest-level liana biomass increment is elevated in the dry season, ii) lianas affect seasonal tree biomass increment, and, if so, iii) the absolute and relative strength of the liana effect on tree biomass increment is stronger in the dry than the wet season.

Material and methods

Site description and treatment design

The liana removal experiment was carried out at the Gigante Peninsula in Panama, which is located on the mainland within the Barro Colorado Nature Monument (BCNM; 9.15˚N, 79.85˚W) and adjacent to Barro Colorado Island (Fig. 1). Gigante Peninsula is covered by a mix of early and late secondary seasonally moist lowland forest (Álvarez-Cansino et al., 2015; García León et al., 2018; Schnitzer & Carson, 2010). In 2008, we located sixteen 80 x 80 m (0.64 ha) plots situated 116-1690 m apart in floristically and structurally similar areas within the ~60-year old forest area of Gigante Peninsula (Fig. 1). Plots similar in liana biomass and tree structure were paired to randomly assign treatments (either liana removal or unmanipulated control). Before liana removal, the control and removal plots were statistically indistinguishable in terms of liana biomass and liana infestation rate (van der Heijden et al., 2015). In March 2011, all lianas were removed from eight of the plots, leaving eight unmanipulated control plots. Lianas were cut near the forest floor using machetes and were not removed from the trees to avoid damaging tree crowns (Schnitzer & Carson, 2010; van der Heijden et al., 2015). Liana debris was left in the plots to decompose. The removal plots were kept liana-free by cutting all resprouting lianas monthly for the first 2 months and bimonthly for the next 6 months, after which lianas were not resprouting vigorously, and plots were subsequently monitored and resprouting liana stems cut every 3–4 months. Control plots were visited at the same frequency and intensity as the liana removal plots, to avoid a visitation effect (Cahill, Castelli, & Casper, 2001; Schnitzer, Reich, Bergner, & Carson, 2002), and the liana removal plots have been kept liana-free until present. The liana removal experiment follows the fate of more than 30,000 lianas and trees > 1 cm diameter to assess the forest-level impacts of lianas on forest community and ecosystem level dynamics (Adams, Schnitzer, & Yanoviak, 2018; Álvarez-Cansino et al., 2015; García León et al., 2018; Martínez-Izquierdo, García, Powers, & Schnitzer, 2016; Rodriguez-Ronderos, Bohrer, Sanchez-Azofeifa, Powers, & Schnitzer, 2016; van der Heijden et al., 2015). This paper presents results of the first six years (2011-2017) of the experiment and focuses on 841 lianas ≥5 cm and 2717 trees ≥10 cm, which comprise the vast majority of the woody plant biomass in this forest.

The BCNM has average daily temperatures of 27.5 °C and receives a mean annual precipitation of approximately 2,600 mm per year. There is a distinct 4-month dry season from mid-December to the end of April, during which rainfall rarely exceeds 100 mm per month and temperatures are slightly higher than during the rainy season (Leigh, 1999; Fig. 2). During the six years of the experiment, annual rainfall ranged from 1,807-3,262 mm yr^{-1} with average daily temperatures ranging from 27.2-27.8 °C Due to an El Niño event in 2016, year 5 of the experiment was an unusually dry year in general. In particular, the wet season (end of 2015) was shorter and one of the driest since 1971 with ~1480 mm of rain. The onset of the following dry season was earlier and, consequently, lasted longer than usual.

Biomass increment measurements

In November 2010, four months before liana removal manipulation, we installed dendrometer bands 10 cm above the point where tree diameter measurement were taken (i.e. diameter at breast height (DBH), which is ~1.3 m above the forest floor). These were used to monitor the growth of all dicotyledonous trees ≥10 cm DBH in the central 60 x 60 m (0.36 ha) area of both the removal and the control plots, leaving a 10 m buffer zone at the plot edge to prevent lianas growing outside the plot from infesting the core plot area. Tree diameter increment was monitored using dendrometer bands and electronic callipers twice yearly, at the beginning of the wet and dry seasons with censuses generally starting at the end of April and beginning of January, respectively (Fig. 2). Tree stem diameter in subsequent censuses was calculated based on these dendrometer measurements, while correcting for stem curvature (van der Heijden et al., 2015). We calculated biomass of each tree stem by applying the following equation (Chave et al. 2014):

$$AGB_{tree} = 0.0673 * (WD * D^2 * H)^{0.976} \quad (1)$$

where AGB is above-ground biomass, *WD* is wood density, *D* is diameter at breast-height and *H* is height. *H* was calculated for each stem for each census using a local height-to-diameter allometric model based on 6,256 trees (van der Heijden et al., 2015). *WD* information for each tree was taken from Wright et al. (2010) or, when not available, from the Global Wood Density Database (Zanne et al., 2009). If species-level wood density data was not available, we used genus or family-level wood density averages and a site-based average wood density of 0.62 g m^{-3} for stems which were not represented in either database (0.3 %; *cf.* Lewis et al. 2009). In the control plots, the diameters of all lianas ≥5 cm were measured at the same location along the stem at the beginning of the wet and dry seasons (mid-dry season in year 1) using diameter tapes and appropriate liana census techniques (Gerwing et al., 2006; Schnitzer, Rutishauser, & Aguilar, 2007). We excluded diameter measurements for lianas that decreased in size over the course of more than two years and subsequently died within the study period. We calculated liana stem biomass for each liana stem using the allometric equation from Schnitzer, DeWalt, & Chave (2006):

$$AGB_{liana} = \exp[-0.968 * 2.657 * \ln(D)] \tag{2}$$

where D is diameter at 1.3 m from last rooting point. Plot-level tree or liana biomass was calculated by summing the individual biomass of all tree and liana stems within a plot, respectively. To convert biomass estimates from Mg dry mass to Mg C, we used available species-specific wood carbon-fraction values for each tree stem. For tree stems for which species-specific information was unavailable and for all lianas, we used an average wood carbon-fraction of 47.35 % (Martin & Thomas, 2011). We excluded palms from our analyses, because mature palms tend to grow apically rather than radially (Rich et al. 1986) and height measurements were not available. As palms tend to have less liana infestation than trees (van der Heijden, Healey, & Phillips, 2008), and thus are expected to show less response to liana removal, it is unlikely that the exclusion of palms affected our overall results. Biomass values for each tree and liana stem are available from van der Heijden et al. in press.

Seasonal biomass increments were calculated as the difference between two censuses spanning either the dry or the wet season. We only considered biomass increment as a result of tree diameter growth during the census period; hence biomass gain by recruits that reached 10 cm DBH or biomass loss due to trees that died within the census period were not taken into account. Seasonal biomass increments were annualized and converted into Mg C ha^{-1} y^{-1} to facilitate seasonal comparisons. The effect of lianas on biomass increment was calculated both as the difference in biomass increment between the removal and control plots in Mg C ha^{-1} y^{-1} and as the percentage reduction in biomass increment (% yr^{-1}), i.e. the difference in biomass increment between the removal and control plots divided by the biomass increment in the removal plots.

Error correction

Seasonal drought can cause desiccation of the bark and changes in water storage in the wood of tropical trees. Seasonal water loss from tree stems can therefore lead to stem shrinkage that is unconnected to changes in dry biomass (Baker, Affum-Baffoe, Burslem, & Swaine, 2002; Baker, Burslem, & Swaine, 2003; Stahl et al., 2010). Effects of stem shrinkage may therefore underestimate biomass accumulation in the dry season and overestimate biomass accumulation in the wet season. To account for changes in incremental biomass accumulation associated with changes in how much water is being retained by the stem, we estimated stem shrinkage for each season from the median negative growth pattern in trees which exhibited no growth over the six years since the start of the experiment (diameter growth <0mm; N=124). The shrinkage term for each season was estimated separately for the control and removal plots and applied to all trees in each treatment to account for shrinkage on our biomass accumulation estimates (cf. Rowland et al. 2014). We did not include a shrinkage correction for liana stems for two reasons: i) liana stems were measured with diameter tapes which have an accuracy of 1 mm and shrinkage terms were therefore considerably inflated compared to shrinkage calculated from the tree dendrometer measurements, and ii) liana stems generally grew faster in the dry than in the wet season (Schnitzer & van der Heijden, in press) and adding any shrinkage correction would amplify any differences in liana growth between the dry and the wet season. By not correcting liana diameter measurements for shrinkage effects, we therefore present a more conservative pattern in seasonal differences in liana biomass increment.

Prior to analysing the data, we tested whether spatial dependency was present in our data using the Moran's *I*. We did not find evidence of spatial autocorrelation in total biomass values within the 16 plots (Moran's *I* = -0.124, P = 0.291) nor within individual treatments prior to cutting (control: Moran's *I* = -0.213, P=0.211; removal: Moran's *I* = -0.118, P = 0.669), or within tree and liana biomass growth within the treatments in any of the census periods (all Moran's *I* ranging between -0.240 and -0.112, all P-values > 0.05). Thus, there was no need to adjust for spatial dependency in our analyses.

We tested for differences in mean plot-level biomass growth between the treatments and seasons in each year using a Monte Carlo bootstrap approach (Harmon, Fasth, Halpern, & Lutz, 2015; Holdaway, McNeill, Mason, & Carswell, 2014; van der Heijden et al., 2015). This approach has the advantage that it allows direct comparison of biomass increment between treatments and between seasons in each year using a single analysis and without the need for post-hoc testing. The Monte Carlo bootstrapping approach also allowed us to integrate error inherently caused by measuring tree and liana stems into calculating the confidence intervals of seasonal biomass increment (cf. van der Heijden et al, 2015). We accounted for the uncertainty in the diameter measurements by varying the initial diameter of each tree and the diameter of each lianas in each census in each plot by randomly selecting a value from a normal distribution with a SE of 5% around the observed diameter measurement (cf. Holdaway et al. 2014). Subsequently, tree diameters for subsequent censuses were calculated by adding a randomly selected value from a normal distribution with an SE of 3% around the observed dendrometer reading to the initial tree diameter. The errors in diameter tape measurement (5%) and dendrometer readings (3%) were based on error measurements for each method by Holdaway et al. (2014) and Butt, Slade, Thompson, Malhi, & Riutta (2013), respectively. The resulting tree and liana diameters for each census were then used to calculate biomass and subsequently biomass increment for each tree or liana and each plot.

We used this approach to calculate 1,000 realizations of biomass increment for all trees and lianas in all 16 plots, and then used an additional bootstrap approach using 1,000 iterations to calculate the mean biomass increment per treatment and per census and the absolute and relative differences in mean biomass increment between the treatments for each of those realizations. This resulted in 1,000,000 iterations, which were used to calculate the median, upper and lower boundaries of the 95% and 90% confidence interval (CI) as the 50th, 97.5th, 95th, 5th and 2.5th percentiles, respectively, of the mean biomass increment for each treatment and the relative and absolute difference in biomass increment between treatments for each of the seasons. Differences in liana and tree biomass increment estimates between the removal and control treatments and between seasons were considered significant when the CI of the difference did not include zero. Accounting for the uncertainty in the diameter measurements increased the variation in biomass increment, but it did not alter the median as median biomass increment calculations per treatment and differences between treatments and seasons were similar to not taking the measurement uncertainty into account. We therefore present conservative estimates of differences in tree and liana biomass growth between treatments and seasons.

All analyses were carried out in R 3.1.2 (R Core Team 2016).

Results

Median forest-level liana biomass increment in the control plots was 0.64 (95%-bootstrap CI: 0.31 - 1.02) Mg C ha^{-1} yr^{-1} in the dry and 0.39 (95% bootstrap CI: 0.18 - 0.58) Mg C ha^{-1} yr^{-1} in the wet season from year two to six of the experiment. Median forest-level liana biomass increment was higher in the dry than in the wet season in those five years, but the difference was only significant at the 0.05 level in three of the five years (Fig. 3). Liana biomass increment was higher, though not significantly so, during the longer dry season due to the 2016 El Niño in year 5. Median liana biomass increment was 0.81 [95% bootstrap CI: 0.34 - 1.07] Mg C ha^{-1} yr^{-1} and 0.64 [95% bootstrap CI: 0.31 - 0.96] Mg C ha^{-1} yr^{-1} during the dry season in the El Niño and non-El Niño years, respectively.

Forest-level median tree biomass increment was generally higher in the wet than in the dry season for both the control and removal plots. However, tree biomass increment in the removal plots was significantly higher than in control plots both in the wet (Fig. 4a) and the dry (Fig. 4b) season for all six years of the experiment, consistent with a strong competitive effect of lianas on trees. Tree biomass increment in year 5 was severely reduced due to the El Niño in both liana-free and liana-infested plots (Fig. 4a). However, the relative effect of the El Niño was similar for both treatments. Compared to non-El Niño years, the El Niño reduced median plot-level tree biomass increment in the dry season by 31.0% (95% bootstrap CI: 13.0 - 51.0) in the control plots and by 37.2% (95% bootstrap CI: 23.2 - 48.4) in the removal plots.

The presence of lianas reduced median tree biomass increment more severely in the wet than in the dry season in all six years, with a median reduction of 1.05 (95% bootstrap CI: 0.34 - 1.89) Mg C ha^{-1} yr^{-1} in the dry and 1.45 (95% bootstrap CI: 0.53 - 2.38) Mg C ha^{-1} yr^{-1} in the wet season (Fig. 5a). The absolute effect of lianas on tree biomass increment was lowest during the El Niño dry season (0.70 [95% bootstrap CI: 0.45 – 1.01] Mg C ha^{-1} yr^{-1}) due to the low tree growth during this season in both the removal and control plots (Fig. 4a). However, the proportional effect of lianas was similar during both seasons as well as during the El Niño (Fig. 5b). Competition by lianas reduced tree biomass increment by 46.9% (95% bootstrap CI: 24.6 – 66.2) and 48.5% (95% bootstrap CI: 21.8 – 73.8) in the dry and wet season on average, respectively. Contrary to expectations, our results do not indicate that the strength of liana-tree competition is stronger in the dry compared with the wet season.

Biomass increment of lianas themselves did not compensate for the liana-induced reduction in tree biomass increment during the wet season, with lianas offsetting only 26.0% of the biomass increment that they displaced in trees (95% bootstrap CI: 10.9 – 44.5). During the dry season, lianas offset the liana-induced reduction in tree biomass increment by 56.1% (95% bootstrap CI: 18.4 – 164.6). However, as the upper boundary of the CI exceeds 100%, this indicates that it is possible for liana biomass increment to completely offset the liana-induced reduction in tree biomass increment during periods of seasonal drought. The compensatory effect of lianas was strongest in the El Niño dry season, when median liana biomass increments counter balanced the reduction in tree biomass increment completely (110.1% [95% bootstrap CI: 46.7 - 194.1]). However, on a yearly basis, taking both the wet and the dry seasons into account, liana biomass increment did not counter balance the liana-induced reduction in tree biomass increment, with lianas only offsetting 35.4% [95% bootstrap CI: 28.1 – 46.2] in non-El Niño years and 59.8% [95% bootstrap CI: 34.4 – 90.4] in the El Niño year.

Discussion

This is the first study that has experimentally tested whether liana-induced effects on forest-level tree biomass increment are stronger during periods of seasonal drought compared to seasonally wet periods. Our results indicate that, even though liana biomass increment was higher in all five years during the dry season (significantly so in three of the years; Fig. 3), there is no evidence for a stronger competitive liana effect on tree biomass increment during the dry season, even in exceptionally dry years, like during the 2016 El Niño (Fig. 5b). Instead, lianas competed significantly with trees both in the dry and the wet season (Fig. 4 & 5), indicating a large negative effect of lianas on forest-level tree biomass increment, regardless of seasonal water stress. Our results are consistent with Tobin et al. (2012), who also found that the competitive effect of lianas was similar in both the wet and the dry season based on tree sap flow measurements after liana cutting.

Compared to trees, lianas have different leaf, root and hydraulic characteristics that may increase their ability to fix carbon during periods of seasonal drought (Asner & Martin, 2012; Collins et al., 2015; Maréchaux, Bartlett, Iribar, Sack, & Chave, 2017, Wyka et al., 2013; Zhu & Cao, 2010). For example, lianas have the potential for stronger osmotic adjustment compared to trees (Maréchaux et al., 2017), which contributes to turgor maintenance and is therefore critical for growth (Boyer & Slik, 2004). Lianas may also sustain their water potential by either accessing deeper water (Andrade et al. 2005, Chen et al. 2015) or different water sources (De Deurwaerder et al. 2018) than trees, or by exercising strong stomatal control under drought conditions. Lianas may therefore have the ability to remain photosynthetically active during periods of seasonal drought (Cai et al., 2009; Sánchez-Azofeifa et al., 2009; Schnitzer, 2005), thereby taking advantage of the increase in irradiance as a result of reduced cloud cover during the dry season (Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; Schnitzer 2018) to vigorously grow (Schnitzer & van der Heijden, in press). However, even though liana biomass increment during the dry season was greater than during the wet season in all five years (Fig. 3), the relative impact of lianas on tree biomass increment did not differ between the seasons (Fig. 5). A potential explanation for this result may be that during the dry season the negative effects of abiotic stressors, such as reduced water availability, limits tree biomass increment and outweighs the competitive effects of lianas (Lewis, Brando, Phillips, van der Heijden, & Nepstad, 2010; Phillips et al., 2009). Even during a particularly severe dry season due to the 2016 El Niño event, when biomass increment of lianas was slightly higher than in the years with a normal length dry season, the relative effect of lianas was similar to non-drought years (Fig. 5b). The increased length of the seasonal drought during the El Nino dry season rather than liana competition may therefore have affected the reduction in tree biomass increment more strongly (Fig. 4a). In seasonal forests where trees are evergreen or brevi-deciduous, both life forms may compete more intensely with each other for light in the canopy during the wet season, when water is in ample supply, reducing both tree and liana biomass increment (Fig. 3 & 4). If the wet season response is analogous for wet forests and that of the dry season is analogous for forests with more pronounced dry seasons, these results may indicate that the relative liana-induced effect on forest carbon sequestration may be fairly constant in forests along a rainfall gradient. However, additional experimentation is necessary to test this hypothesis.

Our study is the first to show that lianas offset almost twice as much of the liana-induced reduction in tree biomass increment in the dry season (56%) than in the wet season (26.0%). Furthermore, lianas have the ability to completely offset (110.1%) the liana-induced reduction in biomass growth during an exceptionally strong dry season, e.g. as experienced during the 2016 El Niño year. An explanation for the greater compensatory effect of lianas during periods of seasonal water stress is the combination of: i) more vigorous growth of lianas; and ii) a reduction in the absolute liana effect as a consequence of the diminished tree biomass increment due to seasonal water stress (Fig. 4). However, on a yearly basis (i.e. combining the wet and dry season), even in exceptionally dry years, liana biomass increment was unable to compensate the liana-induced reduction in tree biomass increment, with lianas offsetting 35.4% in non-drought years and 59.8% in the El Niño year. This yearly compensatory effect of lianas is similar to previous work in Peru and Panama, where lianas compensated for 30 and 24% of tree biomass increment, respectively (van der Heijden et al., 2009, Schnitzer et al., 2014). The small compensatory effect of lianas is probably due to their small investment in woody tissue compared to that in leaves (van der Heijden et al. 2013, 2015) and their high stem turnover (Phillips et al., 2005), which leads to short woody biomass residence times.

The higher liana biomass increment in the dry season observed in all years may, at least partly, explain the observed variation in liana biomass over space and time (DeWalt et al., 2010; Ingwell et al., 2010; Phillips et al., 2002; Schnitzer, 2005). As lianas take advantage of the dry season to advance their growth, their biomass increment, and therefore ultimately their biomass, may therefore be higher in forests naturally experiencing longer periods of seasonal droughts. This trend has indeed been observed pantropically, where liana abundance and biomass tend to increase with longer seasonal drought (DeWalt et al., 2010; Schnitzer, 2005). Similarly, augmentation and intensification of the dry season in combination with recurrent El Niño and other severe drought events, as experienced by Neotropical forests in the last decades (Fu et al., 2013; Marengo et al., 2011; Zeng et al., 2008), may have amplified liana biomass increment and therefore may have contributed to the continent-wide increase in liana biomass (Phillips et al., 2002; Schnitzer & Bongers, 2011). We used a simple back-of-the-envelope calculation to estimate the relative increase in liana biomass increment due to increasing dry season length. Based on median liana biomass increment per day in the wet (1.09 kg C ha^{-1} day^{-1}) and dry (1.79 kg C ha^{-1} day^{-1}) season, we calculated yearly liana biomass increment for a year with an average Panamanian dry season length (135 days) and for a year with a 33% longer dry season (180 days), equivalent to the dry season during the 2016 El Niño. This simple analysis indicates that a 33% increase in dry season length may lead to a 5.3% yr^{-1} increase in liana biomass increment in these forests. The projected decreases in precipitation and increases in seasonal drought patterns during this century (Boisier et al., 2015; Duffy et al., 2015; Marengo et al., 2012) may therefore further amplify liana proliferation.

There are a number of limitations to the current study. First, although the liana removal experiment in Panama has elucidated several key effects of lianas on tropical forests, it is currently unclear whether the implications from the experiment can be extended to other tropical forests. Furthermore, the density of lianas in this 60-year-old forest is relatively high, and thus the impact of lianas may be notably different in areas with lower liana densities. Liana removal experiments in sites ranging in stand age, precipitation patterns and liana densities are therefore necessary to corroborate whether the patterns found in this study in Panama can be generalized across tropical forests. Second, although our study indicates more vigorous liana growth during periods of exceptional seasonal water stress, the current study spans a six-year period and a longer dataset would be useful to conclusively elucidate patterns between liana biomass increment and seasonal precipitation patterns. Third, the allometric equation used to convert liana diameter measurements into biomass is based on a limited number of individuals and contains data from tropical sites across the globe. As allometric relationships between liana stem diameter and biomass may vary across specific forest types (Schnitzer et al., 2006), we may therefore have over- or underestimated liana biomass increment in this study. However, this bias will have been similar in the dry and the wet season and a more accurate allometric biomass equation would not negate the observed pattern of increased liana biomass increment in the dry season. Finally, carbon accumulation during the dry season may be stored as non-structural carbohydrates (NSC) rather than used for growth (Würth et al., 2005, Martínez-Vilalta et al., 2016). However, there is no evidence that lianas and trees differ in the amount of NSC. Additionally, NSC stores appear to remain constant during periods of drought stress, and they do not appear to influence growth (Rowland et al., 2015); rather, NSC may be more important for plant survival and water management than for growth (Poorter & Kitajima, 2007; Sala et al., 2012). Even if NSC were used for growth during periods of drought stress, NSC concentrations are relatively low (<10%, Würth et al., 2005) and would therefore unlikely have changed the resulting pattern in tree or liana biomass increment.

In conclusion, using an experimental approach, we have shown for the first time that there are no seasonal differences in the relative impact of lianas on stand-level tree carbon sequestration, even though biomass increment of lianas themselves was higher in the dry season. Based on these data, changing climatic conditions are unlikely to directly alter the negative effects of lianas on tree carbon sequestration. However, as growth of lianas themselves is amplified during the dry season, the predicted additional severe drought events and extended periods of seasonal drought in parts of the tropics (Boisier et al., 2015; Duffy et al., 2015; Marengo et al., 2012) may lead to a further proliferation of liana biomass in these areas. Tropical forests are vulnerable to increasing moisture stress, which can result in large carbon losses (Lewis et al., 2011; Phillips et al., 2009). Biomass increment of lianas themselves does not compensate for the liana-induced reduction in tree biomass increment even in exceptionally dry years, although their compensatory effect may increase. Potential increases in liana biomass due to enhanced drought may therefore exacerbate the effects of droughts on tropical forests to store and sequester carbon (van der Heijden & Phillips, 2009a; van der Heijden et al., 2015), with the potential to exert feedback on climate change.

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Data accessibility statement: The data supporting the results is archived in the Dryad repository: van der Heijden et al. (in press). Data from: Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: results from a liana removal experiment in Panama. Journal of Ecology doi:10.5061/dryad.n7r0qk8.

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Figure legends

Figure 1. Map of the liana removal experiment located on Gigante, Panama, showing the eight control (white squares) and eight removal plots (dark grey squares). The insert shows the location of the liana removal experiment in the context of the Barro Colorado Nature Monument (BCNM) and nearby Barro Colorado Island (BCI).

Figure 2. Average monthly temperature and total monthly precipitation from January 2011 until end of May 2017. Dashed line indicates the start of the liana removal experiment. The grey and white areas indicate dry and wet season census periods, respectively. The El Niño influenced the wet season in 2015 and the dry season in 2016 (year 5 of the experiment). (Meteorological data provided by the Physical Monitoring Program of the Smithsonian Tropical Research Institute)

Figure 3. Median and 95% bootstrap confidence intervals in annualized plot-level liana biomass increment (Mg C ha^{-1} yr^{-1}) during the dry (white bars) and wet (dark grey bars) season in the control plots (N=8) for years 2 to 6 of the experiment. Differences in liana biomass increment in the dry and wet season are indicated by ** for $P \leq 0.05$ and * for $0.05 < P \leq 0.10$. Year 5 had an extended dry season compared to previous years due to the 2016 El Niño event. Measurements in year 1 were taken mid-dry season and were therefore excluded.

Figure 4. Median and 95% bootstrap confidence interval of annualized plot-level tree biomass increment (Mg C ha^{-1} yr^{-1}) in the control (N=8, light grey bars) and the removal (N=8, dark grey bars) during the A) wet and B) dry season. All differences in plot-level tree biomass increment between the

removal and control plots are significant ($P \leq 0.05$). Year 5 had an extended dry season compared to previous years due to the 2016 El Niño event.

Figure 5. Median and 95% bootstrap confidence intervals of the effect of lianas on annualized plot-level tree biomass increment during the wet (dark grey bars) and dry season (light green bars. A) Absolute liana effect, calculated as the difference between tree biomass increment in the removal (n=8) and the control plots (n=8, Mg C ha^{-1} yr^{-1}), and B) liana effect (%), calculated as the difference in plot-level tree biomass increment between treatments divided by plot-level tree biomass increment in the removal plots for each season for each of the six years of the experiment. **$P \leq 0.05$. Year 5 had an extended dry season compared to previous years due to the 2016 El Niño event.