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Lianas reduce biomass accumulation in early successional tropical forests

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Abstract. Early successional tropical forests could mitigate climate change via rapid accumulation of atmospheric carbon. However, liana (woody vine) abundance and biomass has been increasing in many tropical forests over the past decades, which may slow the speed at which secondary forests accumulate biomass. Lianas decrease biomass accumulation in tropical forests, and may have a particularly strong effect on young forests by stalling tree growth. As forests mature, trees may outgrow or shed lianas, thus escaping some of the negative effects of lianas. Alternatively, lianas may have the strongest effect in older successional forests if the effect of lianas is commensurate with their density, which increases dramatically in the first decades of forest succession. We tested these two hypotheses using a landscape liana-removal experiment in 30 forest stands that ranged from 10 to 35 yr old in Central Panama. We measured tree growth and biomass accumulation in the stands every year from 2014 to 2017. We found that the effect of liana removal on large trees (≥ 20 -cm diameter) decreased with forest age, supporting the hypothesis that lianas have the strongest negative effects on trees, and thus biomass uptake and carbon storage, in very young successional forests. Large trees accumulated more biomass in the absence of lianas in younger forests than in older forests (compared to controls) even after accounting for the effect of canopy completeness and crown illumination, implying that the detrimental effects of lianas go well beyond resource availability and crown health. There was no significant effect of lianas on small trees (1–20-cm diameter), likely because lianas seek light and thus do not deploy their leaves on small trees that are trapped in the forest understory. Our results show that high liana density early in forest succession reduces forest biomass accumulation by negatively impacting large trees, thus decreasing the capacity of young secondary forests to mitigate climate change. Although the negative effects of lianas on forest biomass diminish as forests age, they do not disappear, and thus lianas are an important component of tropical forest carbon budgets throughout succession.

Key words: *Agua Salud; biomass accretion; biomass relative increment; forest regeneration; leaf area index; Panama; removal experiment.*

INTRODUCTION

More than half of the world's old-growth forests have been altered or destroyed by humans (FAO 2015). Concomitantly, however, we have gained large tracts of secondary forests; between 1990 and 2007, there was an increase of 66% in forest cover in the neotropics due to the expansion of secondary forests (Aide et al. 2013), and a 50% increase in the amount of carbon stored by secondary forests (Pan et al. 2013). The rapid expansion of secondary forests is expected to compensate largely

for the loss of old-growth forests in terms of carbon sequestration and biomass storage (Baccini et al. 2012, Chazdon et al. 2016). Past and current research shows that large quantities of biomass quickly accumulate in the first four decades of forest regeneration after farmland abandonment, particularly in the tropics (Saldarriaga et al. 1988, Hughes et al. 1999, Martin et al. 2013, Poorter et al. 2016). Carbon sequestration and biomass storage are particularly rapid during the early stages of forest regeneration, when trees grow quickly in the high-light conditions. By contrast, the rate of biomass accumulation slows during the later stages of succession because tree growth slows as competition for light and space increase (Huston and Smith 1987, Pan et al. 2013, Poorter et al. 2016). Therefore, early successional forests

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are thought to be particularly important for the global carbon cycle by compensating for the loss of carbon associated with the loss of old-growth forests (Chazdon et al. 2016, Poorter et al. 2016).

The idea that secondary forests will compensate for the loss of biomass in old-growth forests may be overly optimistic. Many secondary forests may fail to regenerate as predicted because of socioeconomic issues, but most importantly because of unaccounted effects of strong plant–plant interactions. Indeed, the traditional successional model may be disrupted during early neotropical forest regeneration because of high densities of lianas (woody vines). Lianas exert strong and detrimental effects on trees, which may redirect succession in secondary forests from a high-carbon state to a low-carbon forest (Schnitzer et al. 2000, Chave et al. 2008, Tymen et al. 2016). Lianas may thus play a critical role in forest development and alter succession in tropical forests. Lianas compete intensely with trees, reducing growth and biomass accumulation (Lai et al. 2017, Estrada-Villegas and Schnitzer 2018, Visser et al. 2018). For example, in a secondary forest in Panama, Schnitzer et al. (2014) and Schnitzer and Carson (2010) demonstrated that tree biomass accumulation and growth was 180 and 55% higher, respectively, in liana-removal plots in forest gaps. In a 60-yr-old successional forest in Panama, van der Heijden et al. (2015b) found that lianas reduced biomass production by 76% per year for 3 yr. Consequently, lianas have the capacity to reduce forest regeneration and, in extreme cases, arrest succession in secondary forests, thus limiting forest biomass accumulation.

Lianas recruit rapidly and in great numbers following pasture and agricultural land abandonment (Dewalt et al. 2000, Letcher 2015, César et al. 2017). For example, liana density was 38 and 47% higher in 20-yr-old forests compared to old-growth forests in Côte d'Ivoire and Costa Rica, respectively (Kuzee and Bongers 2005, Letcher and Chazdon 2009). Even forests as young as 5 yr old can have liana densities that exceed nearby old-growth forests (Barry et al. 2015). One observational study found that the detrimental effect of lianas on tree biomass increased from 19% in 5-yr-old forests to 32% in 30-yr-old forests (Lai et al. 2017). Despite their high densities, lianas do not compensate for the amount of biomass (and thus carbon) uptake that they reduce in trees; liana displaced three times more tree biomass compared to the fraction of biomass they contributed (van der Heijden and Phillips 2009, Schnitzer et al. 2014). Thus, lianas can significantly reduce biomass and carbon accumulation in trees, while contributing little to overall forest biomass and carbon. If lianas recruit in high abundance and displace trees early in forest regeneration, then the capacity of secondary forests to accrue biomass could be greatly reduced.

The effects of lianas on tree biomass accumulation during tropical forest succession are poorly understood and may be more intense than previously thought

(Dewalt et al. 2000). The influence of lianas on forest regeneration in tropical forests may be much stronger now than in previous decades because lianas are increasing in abundance and biomass in neotropical forests (Schnitzer 2015). There are now 15 studies demonstrating that liana density, productivity, and biomass are all increasing relative to trees in tropical forests (Schnitzer 2015, Pandian and Parthasarathy 2016, Ceballos and Malizia 2017, Hogan et al. 2017). Liana density has increased in forests in Argentina, Bolivia, Brazil, Costa Rica, French Guiana, India, and Panama. In a study across multiple forest types in Amazonia, lianas increased 3.27% annually with respect to trees in a 5-yr interval (Phillips et al. 2002), a pattern that has been mirrored by more recent studies in Costa Rica, Brazil, and Panama (Ingwell et al. 2010, Enquist and Enquist 2011, Schnitzer et al. 2012, Laurance et al. 2014). These results, together with the fact that lianas recruit in high densities in early secondary forests (Barry et al. 2015, Lai et al. 2017), indicate that lianas may reduce biomass accumulation in early successional forests (Schnitzer et al. 2011).

We used a landscape-scale experimental approach in 30 secondary tropical forests to evaluate the effect of lianas on tree biomass uptake early in forest succession. The forests ranged from 10 to 35 yr in age and were located in the Agua Salud Project experimental site in central Panama (Stallard et al. 2010). We hypothesized that lianas have the strongest effect on tree biomass uptake in the youngest forests because liana proliferation has a particularly strong negative effect on young tree growth and thus on forest regeneration. As the forest matures, trees may shed lianas, thus reducing the negative effects of lianas on trees. Alternatively, lianas have the strongest effect on trees in older successional forests if the effect of lianas is commensurate with their density, which increases dramatically in the first 30 yr of forest regeneration. If the effect of lianas is negative and strong despite forest age, we would expect that tree biomass accumulation should be reduced by lianas even after accounting for differences in light availability and canopy health.

METHODS

Study site

We established a successional chronosequence of secondary forests in the Agua Salud Project experimental site in central Panama (Fig. 1). Agua Salud is a 664-ha site composed of secondary forests in different stages of succession, cattle pastures, and timber plantations. Within the secondary forests, we added on 30 liana-removal plots to the Agua Salud SFD (secondary forest network) at 30 sites. Each site is composed of two 20 × 50 m plots per forest that ranged from 10 to 35 yr old ($n = 60$, 30 removal plots, 30 control plots). We established a 5 × 5 m grid in every plot to facilitate the

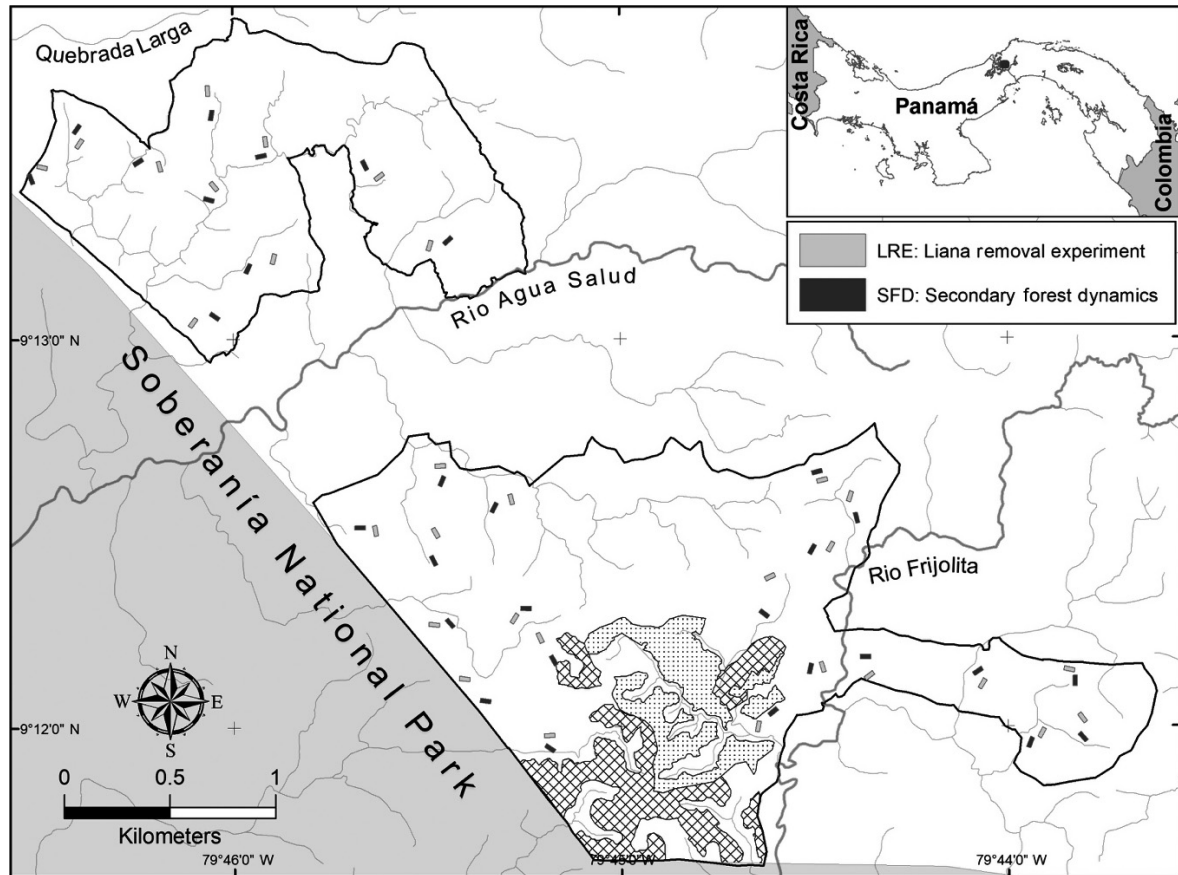


FIG. 1. Map of the Agua Salud Project in Central Panama. Rectangles represent our 30 study sites composed of a liana-removal plot (light gray), and a control plot (dark gray). Cross-hatched areas represent a mixed-species reforestation experiment; dotted areas represent teak plantations.

location of all trees, and to measure leaf area index (see below in Sampling methods). All our sites fulfill the criteria of an appropriate space-for-time substitution in chronosequence studies (Johnson and Miyanishi 2008, Walker et al. 2010) because the sites are all located on homogeneous parental material, have similar previous land-use history, have been managed similarly since they were abandoned, and only differ in forest age (Neumann-Cosel et al. 2011, van Breugel et al. 2013). The mean annual precipitation at Agua Salud is 2,700 mm, with a dry season from mid-December until mid-May (Ogden et al. 2013). Detailed information about the Agua Salud site can be found in Stallard et al. (2010) and van Breugel et al. (2013).

Sampling methods

In 2011, we tagged, measured, and identified to species all trees ≥ 5 cm in diameter at breast height (DBH) in the removal plots following the methods established for Agua Salud by van Breugel et al. (2013) for the control plots (secondary forest network). In the control

plots, where lianas were present, we also tagged, measured, and identified to species all lianas ≥ 1 cm following the standardized protocols established by Gerwing et al. (2006) and Schnitzer et al. (2008).

To determine which trees were selected for inclusion into our study, we first chose 24 species that were common across the chronosequence. We grouped them in three categories according to their wood density: light, medium, and dense (Appendix S1: Table S1). To make such groups, we used measurements of wood density from Barro Colorado Nature Monument (Wright et al. 2010) and Agua Salud (Craven et al. 2015). Agua Salud is in the same region as Barro Colorado Nature Monument, has similar soil characteristics (Neumann-Cosel et al. 2011) and receives comparable rainfall (Ogden et al. 2013). From each wood density category, we randomly selected three individuals from two different size classes; small (5–10 cm DBH) and medium (10–20 cm DBH) to include in the study. We then selected three large individuals (>20 cm DBH) from our species set regardless of their wood density, and selected the largest three individuals in each plot regardless of wood density

or species identities. According to this design, the maximum number of individuals per plot at the onset of the experiment was 24, although some individuals had more than one stem. The minimum number of trees depended on the number of trees available in every plot per wood density category and size class (see Appendix S1: Fig. S1 for sampling design scheme, and Appendix S1: Tables S2–S5 for total number of trees measured per wood density category, size class, stand age, and treatment). Selecting individuals in this manner allowed us to replicate within species across the chronosequence, enabled us to assess the effect of liana removal across species with different sizes and wood densities, and allowed us to deliberately incorporate large trees because they disproportionately accumulate more biomass than smaller trees (Stephenson et al. 2014).

In 2013, we cut all lianas in each removal plot and in 5-m buffers around each removal plot. We also cut all lianas that were rooted outside of the buffer but were growing into the plot. Lianas were cut at ground level and at shoulder level because some species (e.g., *Davilla nitida* or *Entada gigas*) are able to sprout roots from severed stems. We did not dislodge lianas from trees to avoid damaging the canopies (follows Schnitzer and Carson 2010, Schnitzer et al. 2014). As such, the structural stress imposed on trees by the weight of the dead lianas was present until natural decomposition occurred. Once each year we recut the new stem sprouts produced by cut lianas, as well as cut all new lianas growing in the plots.

Before the first liana cutting, and once every year after recutting, we calculated mean leaf area index (LAI) for each plot by measuring LAI at 1.3 m above the soil surface on 24 fixed points along the 5-m grid. We used a Li-Cor LAI-2000 (Li-Cor Biosciences, Lincoln, Nebraska, USA) to calculate LAI. Leaf area index was not measured in 2016. All measurements were taken at dawn, dusk, or during continuous overcast skies. To calculate LAI, we compared the light measurements in the plots with those taken simultaneously with a second LAI-2000 located outside of the forest. We restricted light measurements to the northern portion of the sky by capping the south-facing half of each light sensor. Methods follow Schnitzer and Carson (2010) and Rodríguez-Ronderos et al. (2016).

We measured tree growth annually using a diametric tape on all stems selected in 2012. Measurements were taken on marked locations at 1.30 m from the ground, and multiple-stemmed trees were treated independently (i.e., one stem, one measurement). If stems had irregularities at 1.30 m, we marked a location 10 cm higher or lower from the irregularity, and measured growth at this height. If trees had buttresses, we employed a ladder to mark and measure the stem. If a tree died between sampling years, we randomly selected another tree within the same wood density category and size class, if available, and measured it throughout the study period ($n = 157$). We began our study by measuring 1,443 trees

(i.e., individual stems) in 2013, and finished with 1,286 in 2017 despite the 157 trees that were replaced (Appendix S1: Table S6). Starting in 2015, we assessed light availability and crown health of each tree by assessing crown condition and illumination following standardized methods (Dawkins and Field 1978, Clark and Clark 1992). Crown condition was scored from 1 to 4, with scores determined as follows: trees with a score of 4 had 75–100% of the crown intact, trees with a score of 3 had 75–50% of their crowns intact, trees with a score of 2 had 50–25% of their crowns intact (half of the crown is gone), and trees with the lowest score had 0–25% of the crown intact (most of the crown is gone). Canopy illumination was scored from 1 to 5 with scores determined as follows: trees with score of 5 had crown completely exposed to vertical light and to lateral light, trees with a score of 4 had crowns completely exposed to vertical light but not to lateral light, trees with a score of 3 had crowns with some vertical light and some lateral light, trees with a score of 2 had crowns only exposed to some vertical light, and trees with the lowest score were not lit directly either vertically or laterally.

Data analysis

To quantify the percentage of light that was consumed by lianas in the canopy, and how trees respond to liana removal, we calculated mean LAI per plot and used the plot means to calculate mean LAI per treatment. To calculate aboveground biomass uptake at the plot level, we first transformed growth measurements per stem into aboveground biomass (AGB) uptake by using an allometric equation calculated for trees at the Agua Salud site (van Breugel et al. 2011). We then determined how much biomass each stem accumulated relative to the amount of biomass that it accumulated during the previous year. Thus, we calculated a biomass relative increment metric based on the following relative growth rate equation:

$$\text{Biomass Relative Increment} = \left(\frac{\ln \text{AGB}_{\text{year } 1} - \ln \text{AGB}_{\text{year } 0}}{\text{year } 1 - \text{year } 0} \right).$$

We calculated the mean of tree biomass relative increments per plot per year, and then tested for differences between treatments for each year of sampling. We used an ANCOVA to test whether liana removal and forest age influenced plot-level biomass relative increment for every year of sampling for all tree size classes combined, and for each tree size class separately. At the individual tree level, we tested the direction and magnitude of the effect of liana removal, forest age, crown condition, illumination, and year of sampling on the biomass relative increment data using linear mixed models (LMM; function `lme`, as implemented in the R package “nlme”; Pinheiro et al. 2018). We avoided pseudoreplication and

accounted for temporal autocorrelation by nesting trees within plots, plots within sites, and using repeated measures per tree over time. We defined treatment (liana removal vs. control), forest age, crown condition, crown illumination, and sampling year as fixed factors, and plots within sites as a random factor. To compare the effects of each fixed factor on biomass relative increment, we standardized each fixed factor by twice its standard deviation (Gelman 2008), and plotted the estimated coefficient from the LMM and their 95% confidence interval (CI). We calculated the variances explained by the LMM using marginal and conditional coefficients of determination for generalized mixed-effect models with the function `r.squaredGLMM`, using the R package “MuMIn” (Bartoń 2013). Marginal coefficient represents the variance explained by the fixed factors, whereas conditional coefficient represents the variance explained by fixed and random factors (Bartoń 2013). Finally, to rule out the effect of rainfall on biomass relative increment, we ran a separate LMM with mean annual precipitation as an extra fixed effect, and found that rainfall had a negligible effect on biomass relative increment (Appendix S1: Table S7).

RESULTS

At the canopy level, lianas contributed 18% of the canopy foliage, as measured by the loss in LAI 1 yr after cutting lianas compared to the preliana cutting differences (Fig. 2). After the first year of the experiment, control plots showed significantly more foliage and thus LAI compared to removal plots ($F_{1,56} = 20.44$, $P < 0.01$), and this difference remained significant in 2015 ($F_{1,56} = 6.356$, $P = 0.016$). By 2017, however, 4 yr following liana removal, tree canopies in the removal plots had completely filled the space vacated by lianas, and differences in LAI between the sites were nearly

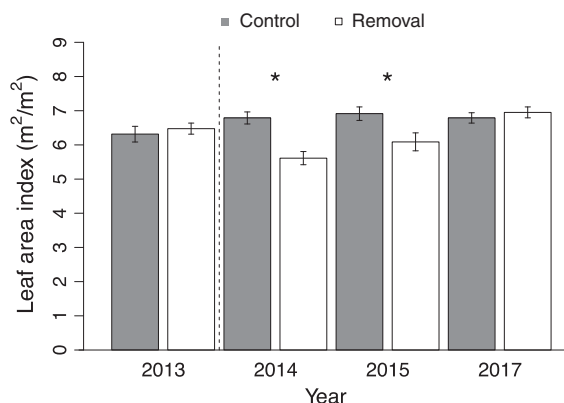


FIG. 2. Mean leaf area index for 30 control plots (gray bars) and 30 liana-removal plots (white bars) on Agua Salud Project, Central Panama. Data were collected using a LiCOR LAI-2000 optical system. Error bars represent one standard error. $*P < 0.05$. Dotted line represents liana cutting.

identical to pre-liana-cutting differences. Thus, lianas contributed a significant portion of the forest canopy and, 4 yr following liana cutting, tree foliage captured the canopy area that previously had been covered by lianas.

Tree biomass relative increment in liana-removal plots was consistently higher than in control plots throughout our experiment (Fig. 3). Biomass relative increment in removal plots was 18.5% higher in 2015, and 21.9% higher in 2017 compared to control plots (2015: $t = -2.096$, $P = 0.045$; 2017: $t = -1.863$, $P = 0.073$). We did not detect significant differences between treatments in 2016; however, the pattern was consistent with 2015 and 2017—removal plots, on average, accumulated 12.9% more biomass than control plots ($t = -1.458$, $P = 0.156$; Figs. 3 and 4). Liana removal had a significant and positive effect on biomass relative increment for large trees from 2015 to 2017 (Fig. 4, Table 1). Biomass relative increment for large trees tended to decrease with stand age for both treatments, but the difference was only significant in 2016 (Fig. 4, Table 1). For small- and medium-sized trees, and for all tree sizes combined, the removal of lianas did not have a positive effect on the biomass relative increment (Appendix S1: Fig. S2).

Liana removal had a strong positive effect on biomass relative increment at the tree level after accounting for the effect of crown condition and illumination (Fig. 5, Appendix S1: Fig. S3). Census year and forest age had negative effects on biomass relative increment, but only census year had a significant effect (Fig. 5). The linear mixed model had a low coefficient of determination; fixed factors (crown illumination, removal, crown condition, sampling year, and forest age) explained only 14% of the total variance, and fixed factors and random

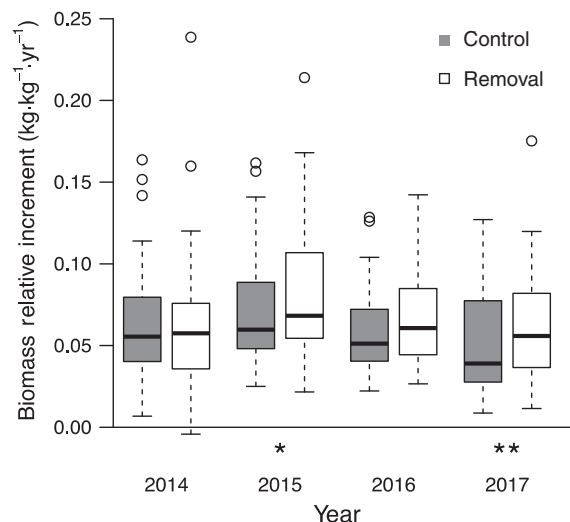


FIG. 3. Biomass relative increment for 30 control plots (gray bars) and 30 liana-removal plots (white bars) during 4 yr on Agua Salud Project, Central Panama. Error bars represent one standard error. $*P < 0.05$; $**P = 0.07$.

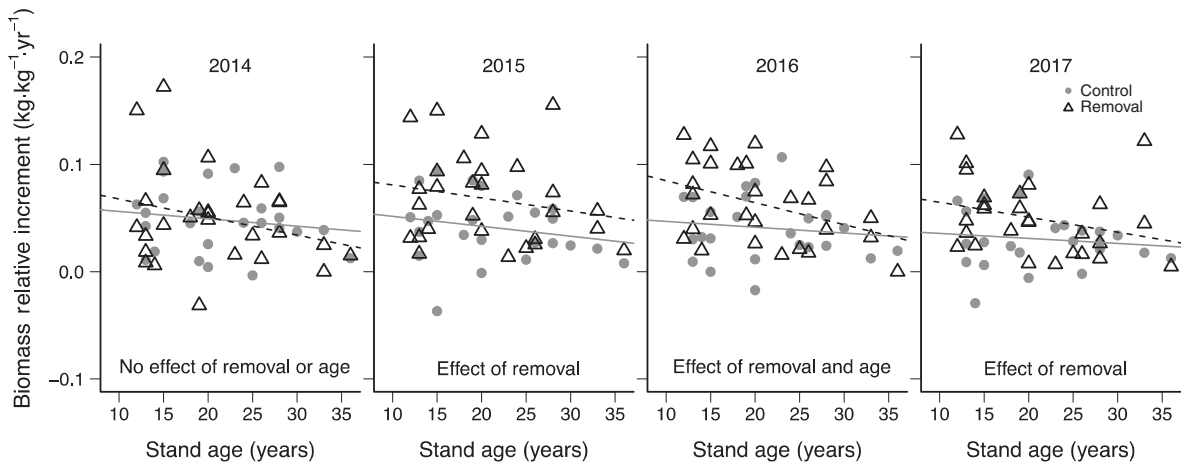


FIG. 4. Biomass relative increment for large trees (diameter at breast height >20 cm) across 30 control plots (gray circles) and 30 liana-removal plots (white triangles) during 4 yr in a secondary forest chronosequence in the Agua Salud Project, Central Panama. Gray bars represent line of best fit for control plots; dashed line represents line of best fit for liana-removal plots.

TABLE 1. Results of analyses of covariance (ANCOVA) of biomass relative increment of large trees (diameter at breast height >20 cm) across 30 control plots and 30 liana-removal plots during 4 yr in a secondary forest chronosequence in the Agua Salud Project, Central Panama.

| Year of sampling | R ² | F _{1,50} | P | Significant effect |
|------------------|----------------|-------------------|-------|-----------------------------|
| 2014 | 0.01 | 1.32 | 0.27 | |
| 2015 | 0.1 | 6.99 | 0.01 | Liana removal |
| 2016 | 0.14 | 5.38 | 0.007 | Liana removal and stand age |
| 2017 | 0.07 | 5.03 | 0.02 | Liana removal |

Note: See Fig. 4 for the distribution of the data between treatments across forest age.

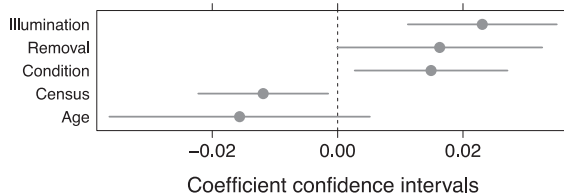


FIG. 5. Coefficient confidence intervals of biomass relative increment from linear mixed effects models for large trees across 4 yr on Agua Salud Project, Central Panama. Points are averaged coefficient estimates and bars correspond to 95% confidence intervals (CIs). Intervals that do not overlap with zero value indicate a strong and significant effect. Illumination indicates crown illumination index, removal indicates the liana-removal treatment, condition represents crown condition, census indicates year of sampling, and age indicates stand age.

factors (plots nested within sites) explained 28% of the total variance.

DISCUSSION

Our study is the first experimental quantification of the effects of lianas on early successional tropical forests.

Our results support the hypothesis that lianas dramatically reduce tree biomass accumulation in early secondary tropical forests. In fact, lianas reduced biomass accumulation on large trees regardless of forest age. Lianas strongly reduced biomass accumulation of large trees even after accounting for the health of the tree crown and canopy illumination, implying that the detrimental effects of lianas go well beyond light availability and crown health. This result is particularly relevant to carbon dynamics because large trees sequester more carbon than smaller trees (Stephenson et al. 2014), and the vast majority of the biomass in tropical forests is stored in large trees (Lutz et al. 2018).

The effect of lianas on biomass accumulation in tropical forests has gained attention recently (Paul and Yavitt 2011, Durán and Sánchez-Azofeifa 2015) because of the detrimental effects of lianas on forest carbon cycling (van der Heijden et al. 2015a). We found that lianas reduce tree biomass accumulation up to 21.9%; however, the magnitude of the effect of liana removal across studies varies greatly. For example, in a 60-yr-old successional forest in Central Panama, van der Heijden et al. (2015b) found that lianas reduced annual biomass accumulation by 76% for trees ≥10 cm diameter. Liana-removal experiments with saplings conducted in mid and older successional forests, or in forest gaps, have shown that biomass accumulation after liana removal can range from 52 up to 436% (Schnitzer et al. 2005, Schnitzer et al. 2014, César et al. 2016, Marshall et al. 2017). This variability in tree response to liana removal may be due to variation in liana density and the sizes of lianas among sites, liana species and their climbing mode, different light conditions across forest ages, or the disparity in tree size classes between studies. Nonetheless, our results and those of the other experimental studies provide compelling evidence that lianas significantly reduce tree biomass throughout forest succession.

Lianas did not have a significant negative effect on medium- and small-statured trees. Liana leaves tend to have more light-demanding physiology (Asner and Martin 2012), and liana life-history strategies are maximized to gain access to the top of the forest canopy (Avalos et al. 1999, Kurzel et al. 2006, Schnitzer 2018). By intercepting light and displacing the leaves of large canopy trees, lianas reduce tree growth and biomass accumulation (van der Heijden et al. 2015b). Once lianas are removed, large trees are able to accumulate more biomass compared to trees that still have lianas on their crowns. The benefit of liana removal to medium and small trees may be much more muted due to the lower prevalence of lianas on non-canopy trees (Muller-Landau and Visser 2018). A similar finding was reported by García León et al. (2018), where liana removal increased flower and fruit production in canopy trees, but not in understory trees.

Lianas contributed 18% of the foliage in the canopy, and trees in the removal plots took 4 yr to compensate fully for the loss of lianas in the canopy. Because we measured LAI 1 yr after the liana cutting, our 18% estimate of the amount of leaf area that lianas contribute may be an underestimation if trees had produced new leaves in response to liana cutting within that period. For example, in a large liana-cutting experiment in a nearby forest in central Panama, Rodríguez-Ronderos et al. (2016) reported that liana cutting resulted in 20% more light penetration into the forest interior 6 weeks after liana cutting, but only 17% more light 1 yr after liana cutting. Therefore, it is possible that lianas contributed 20% or more of the leaf area in our forest stands. Despite a possible underestimation, our results closely resemble the 17% more LAI in control plots with respect to removal plots after 1 yr of removal (Rodríguez-Ronderos et al. 2016), and that trees in removal plots fully compensated for the loss of lianas after 4 yr of liana removal (Schnitzer and Carson 2010, Rodríguez-Ronderos et al. 2016). Our finding that lianas contribute 18% of LAI also resembles the results of Wright et al. (2004), who found that lianas contribute up to 17% of the leaf productivity in the canopy of BCI. Although our results represent pooled data across forests of different ages and thus might obscure subtle differences between younger and older forests, the similarity with other studies suggests that lianas contribute between 18 and 20% of tropical forest LAI in central Panama. The rapid increase in tree leaves, and thus in photosynthetic capacity, which can be inferred from LAI data, is likely why large trees accumulated more biomass after liana removal.

Our experimental evidence is comparable to a recent observational study in the same field site, with both studies showing that lianas affect tree biomass accretion in young successional forests. However, both studies show important yet different nuances. Using trees of all size classes (≥ 1 cm DBH) and wood densities on plots that ranged from 3 to 35 yr at Agua Salud, Lai et al.

(2017) found that lianas significantly reduced biomass accumulation, and that the negative effect of lianas became stronger as forests aged. They also found that the detrimental effect of lianas was stronger on large trees than small trees (Lai et al. 2017). However, our experimental results indicate that lianas affect large trees regardless of forest age (Figs. 4 and 5). The seemingly contrasting results between our study and Lai et al. (2017), beyond methodological differences, might be because of the correlation between tree size and stand age; larger trees contribute an increasing proportion of total forest biomass as succession progresses (Hughes et al. 1999, van Breugel et al. 2006), and more trees move to larger size classes because of thinning throughout succession (Saldarriaga et al. 1988). As the number of larger trees increases with forest age, the detrimental effect of lianas increases (Lai et al. 2017).

In light of our results and those from Lai et al. (2017), we propose a new hypothesis with regards to the effect of lianas on tree biomass accretion during succession: the per capita effect of lianas on trees remains constant across forest age as long as the level of liana infestation per tree does not change over time. This would explain why we did not find an effect of liana removal on forest age when tree size is standardized. It would also explain why Lai et al. (2017) detected a cumulative detrimental effect of lianas over time when sampling more larger trees across forest age. In other words, the detrimental effects of lianas augment over time because larger trees become more abundant and make the greatest contribution to total forest biomass (Hughes et al. 1999, van Breugel et al. 2006), but not because the effects of lianas per capita becomes progressively stronger through time.

The reduction in biomass accumulation due to the effects of lianas on trees has important implications for the future of carbon cycling. Early successional tropical forests accumulate up to 1.6 PgC per year (Pan et al. 2011, Grace et al. 2014, FAO 2015), and if all the young and mid secondary Neotropical forests were left unperturbed for 40 yr, they could potentially accumulate up to 8.48 PgC (Chazdon et al. 2016). In fact, 4.22 PgC could be accumulated in that same time period if only 10% of current Neotropical pasture area would be allowed to return to forests and if 60% of the secondary forests are allowed to persist (Chazdon et al. 2016). Aside from socio-economic aspects, this huge potential could be thwarted for three key reasons related to lianas: (1) Lianas may be increasing in tropical forests, especially in the Neotropics (Schnitzer 2015, Pandian and Parthasarathy 2016, Ceballos and Malizia 2017, Hogan et al. 2017), (2) lianas recruit rapidly in early successional forests (Letcher and Chazdon 2009, Barry et al. 2015, Lai et al. 2017), and (3) lianas reduce biomass accumulation significantly in secondary forests (our results, van der Heijden et al. 2013, Schnitzer et al. 2014, van der Heijden et al. 2015a, Lai et al. 2017). If future forecasts of carbon accumulation and carbon sinks were to increase in accuracy, they should integrate into their calculations the strength by

which lianas reduce tree biomass across young secondary forests (di Porcia e Brugnera et al. 2019, Schnitzer et al. 2015, Verbeeck and Kearsley 2016).

In conclusion, lianas reduce a significant portion of tree biomass accumulation early in secondary forest regeneration, especially for large trees. Once the effects of lianas are removed, trees grow quickly and consume the space that was once occupied by lianas. Even when crown condition and illumination were considered, liana removal remained a significant and positive factor in biomass accumulation. Overall, the effect of lianas on biomass accumulation might remain high as young forests age, but when liana density begins to decline, the effect of lianas may also decline (Dewalt et al. 2000, Barry et al. 2015).

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