



Original article

What tree rings can tell us about the competition between trees and lianas? A case study based on growth, anatomy, density, and carbon accumulation



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ABSTRACT

In tropical forest, landscape fragmentation and the consequent degradation of disturbed forests increase the incidence of light and dry hot winds, causing a disturbance on natural regeneration. Under these conditions, lianas (woody vines) development is stimulated instead of other species, which are more suited to mature forest and under less influence of the edge effect. For this, lianas colonization is an important variable for assessing the disturbance level of a forest. In this context, it becomes important to understand the nature of the competitive relationships between hyper-abundant lianas and ring growth of the host trees. Here, we selected trees with occupation or absence of lianas from two tropical species – *Pinus caribaea* var. *hondurensis* (Caribbean pine) and *Tectona grandis* (teak) – localized in a semideciduous forest fragment in southeastern Brazil, aiming to compare growth, climatic response, anatomy (vessels and intra-annual density fluctuations), wood density and carbon, by tree-ring analysis. The results showed that the lianas caused a change in tree-ring anatomy of host trees in last 10 years, mainly. We observed that trees occupied by lianas had a decrease the radial growth and carbon in the two species, an increase of the vessels size in teak and a decrease of the IADF frequency in Caribbean pine. In teak, the climate-tree relationship indicated that trees with lianas had lower response to rainfall and higher response to temperature in the summer (rainy and hottest period); in Caribbean pine, we observed that trees with lianas had a 2-month delay in the radial growth response to rainfall in the dry season. In the teak group, we observed that host trees had higher wood density values than liana-free tree in the outer rings, and the opposite was showed for pine. These findings show that tree-ring growth of host trees are a strong bioindicator of forest disturbance caused by aggressive colonization of lianas. We believe that these methods are applicable to future studies relating to the effects of habitat fragmentation and forest degradation on biodiversity and ecosystem services, particularly in the context of global climate change.

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1. Introduction

Tropical forests play a dual role in global climate change: whereas their high potential for stocking biomass may be important for mitigating climate change, their destruction contributes to the rising concentrations of greenhouse gases in the

atmosphere (Zarin, 2012). The effects of forest degradation on global climate change are, however, less predictable. On the one hand, human-mediated disturbances may cause further losses of biomass in tropical forests; on the other hand, such disturbances may prevent the recovery of pre-disturbance biomass stocks (Ghazoul et al., 2015). Forest fragmentation in particular may contribute to both problems; although the amplification of edge effects drives declining abundances of large-sized trees and may consequently result in losses of aboveground biomass in fragmented landscapes (Chaplin-Kramer et al., 2015), the prolifer-

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ation of ruderal species in edge-dominated forest remnants may prevent the recovery of biomass stocks and maintain the forest community in an arrested successional stage (Farah et al., 2014).

Growth and expansion of ruderal lianas instead of late-successional tree species, which are better suited to mature-forest conditions, is often stimulated in edge-dominated remnants. Liana interference in tree regeneration may be observed at different life-cycle stages—establishment, growth, and reproduction—and result in a gradual and continuous reduction in the abundance of large-sized trees in forest fragments (Botosso et al., 2005; Ingwell et al., 2010; Laurance et al., 2001; Nepstad et al., 2007). Thus, a low abundance of large trees and large-scale colonization of forest canopy by lianas are often considered indicators of forest degradation (Fahrig, 2003; Laurance et al., 2002). Lianas, which are important structural parasites that can promote tree mortality (Laurance et al., 2001), may be increasing in abundance in response to global change drivers (Laurance et al., 2014). The cutting of lianas has been recommended as a strategy for encouraging tree regeneration in tropical forests, with direct implications for timber production and forest restoration (Pérez-Saliciprup et al., 2010; Schnitzer and Carson, 2010; Schnitzer et al., 2014). However, the unnecessary cutting of lianas is a waste of limited financial resources, and may compromise liana conservation. Thus, a better understanding of the competitive interactions for resources between lianas and their host trees is needed.

Dense occupation of tree crowns by lianas reduces light interception and water uptake by trees (Chen et al., 2015; Markesteijn et al., 2011; Schnitzer and Bongers, 2011), and affects cambial activity, which may be reflected as temporal signs of stress in tree rings (Botosso et al., 2005). Although tree-ring patterns have long been used as an effective tool for assessing forest population dynamics, and determining responses to changes in climate and environment (Brienen and Zuidema, 2005; Genova and Moya, 2012; Koprowski and Duncker, 2012; Liang et al., 2009), their usefulness as ecological indicators for examining competitive interactions between lianas and trees has largely been unexplored. Tree rings can be analyzed using many different approaches; for instance, vessel size in angiosperm trees (Fonti et al., 2010; Garcia-Gonzalez and Fonti, 2006; von Arx et al., 2012), frequency of intra-annual density fluctuations (false rings) in gymnosperm trees (Campelo et al., 2013; Copenheaver et al., 2010; Rozas et al., 2011), and radial variations in wood density (Jyske et al., 2008; Nock et al., 2009) may all be used for discerning cellular disorders in tree rings that result from lianas. Intra-annual wood density and volume reconstruction (Taki et al., 2014) can also be used to analyze the detrimental effects of lianas on carbon uptake by tree-ring (Babst et al., 2014a, 2014b; Pompa-García and Venegas-González, 2016).

Our goal here was to determine the usefulness of examining the rings of two tropical trees, *Tectona grandis* (teak) and *Pinus caribaea* (Caribbean pine), for use as bioindicators regarding the effects of lianas on tree development, and whether lianas contribute to the reduction of ecosystems services provided by host trees by interfering with carbon accumulation. We believe that this study has the potential to establish effective new bioindicators for liana management in ecological restoration and timber production in tropical forests.

2. Materials and methods

2.1. Study site and species

The study was conducted in a 14-ha forest fragment in Piracicaba, in the state of São Paulo in southeastern Brazil (22°42' S, 47°37' W, elevation 546 m) (Fig. S1 in the Supplementary material). This fragment consists of seasonal semi-deciduous forest, a

threatened form of Atlantic forest, and a global biodiversity hotspot (Ribeiro et al., 2009; Rodrigues et al., 2009). The climate is classified as Cfa (humid subtropical), characterized by a rainy and hot summer, with an average temperature of 24.6 °C in the warmest month (January), and a dry and cold winter, with an average temperature of 17.9 °C in the coldest month (July). Mean annual rainfall is 1200–1300 mm (Alvares et al., 2013). The forest fragment is embedded in an agricultural-urban matrix, and has been affected by cattle grazing and recurrent fires; a large fire destroyed much of this remnant in 1981 (Catharino, 1989). Early successional trees now dominate a large portion of the forest fragment, with the canopy heavily colonized by climbers consisting of both woody species (lianas) and non-woody species (vines). The dominant tree species in this forest fragment are *Acacia virgata* (Fabaceae), *Piptadenia gonoacantha* (Mimosoideae), and *Trichilia clausenii* (Meliaceae), whereas the dominant liana species are *Dolichandra unguis-cati* (Bignoniaceae), *Serjania caracasana* (Sapindaceae), *Acacia polyphylla* (Fabaceae), and *Banisteriopsis lutea* (Malpighiaceae) (Cesar, 2014).

Abandoned plantations of teak and Caribbean pine bordering the forest fragment were selected for this study. Tree and climber species that proliferated within the plantations were structurally integrated within the native forest fragment; however, although ruderal lianas heavily colonized the crowns of some individuals of both tree species, lianas were absent from other trees, thus providing a comparative sample for testing the usefulness of tree rings as bioindicators of the competitive interactions between trees and lianas. Teak and Caribbean pine were selected for this study because of their reliable formation of annual growth rings and consequent potential for dendrochronological studies (Venegas-González et al., 2016; Worbes, 1999), thus providing information that is not available from local species. Moreover, because wood anatomy and stem biomechanics differ between angiosperms and gymnosperms (Du and Yamamoto, 2007), it is thus possible to examine the difference in tree-ring response to the mechanical and physiological stresses caused by lianas between angiosperms and gymnosperms.

2.2. Sampling

We selected eight individual trees each of teak and Caribbean pine, four colonized by lianas (L: with lianas) and four without lianas (nL: no lianas), for a total of 16 trees. Core samples were extracted at diameter at breast height (DBH) with increment borers (Grissino-Mayer, 2003). Populations of both species were very small in the area, justifying the relatively small number of individuals sampled; in the case of teak, all trees were sampled, whereas about 75% of the live Caribbean pine was included. Individual trees showing signs of pathogenic infection or having compression wood were excluded from the analysis. The intensity of liana colonization was characterized by liana basal area and biomass per tree, calculated using density and stem diameter data of lianas at 130 cm above ground level, and sampled according a standard protocol for liana censuses (Gerwing et al., 2006) and measuring (Schnitzer et al., 2006). For the evaluation of the presence or absence of lianas in the canopy of pine and teak trees, we used the follow criterion (Fonseca and Rodrigues, 2000): (i) 76%–100% of pine-tree canopies were occupied by lianas, colonized mainly from the base of their trunks, with a basal area of 2.9 cm²–97.5 cm² and an aboveground biomass of 1.5 kg–137.1 kg, and (ii) 25%–50% of teak canopies were occupied by lianas, colonized principally from adjacent trees, with a basal area of 5.1 cm²–9.6 cm² and an aboveground biomass of 2.7 kg–6.3 kg (Fig. S2, Appendix A in the Supplementary material).

2.3. Development of tree-ring width chronologies and radial growth analysis

Core samples were air dried in the laboratory, mounted on wooden supports, and sanded with progressively finer sandpaper (80–800 grit) to clearly delineate annual tree-ring boundaries. Samples were then scanned at 1200 dpi for the tree-ring analysis, using an EPSON Perfection V720 PRO scanner (Epson America Inc., Long Beach, CA, USA). Tree-ring width was measured with Image Pro-Plus version 4.5.0.29 software (Media Cybernetics Inc., Rockville, MD, USA). We used the core mean of the same trees to avoid pseudoreplication. Cross-dating quality was analyzed using the program COFECHA (Holmes et al., 1986), which removes the growth trends by applying a cubic spline and allows for the determination of variations in high and low frequency trends (Grissino-Mayer, 2001). The value used to implement the cubic spline was 32 years, as this generated the highest intercorrelation values among the tree-ring series, and we used systematic correlation segments that had lower flag A values and no B values. Length and overlap values used in COFECHA are closely associated with the critical correlation values at a confidence level of $\alpha = 0.01$ (Grissino-Mayer, 2001); for teak, the segments consisted of 16 years of length and eight years of overlap ($r_{critical} = 0.574$), whereas for Caribbean pine, the segments consisted of 30 years of length and 10 years of overlap ($r_{critical} = 0.422$). We subsequently produced the chronologies for both species using ARSTAN software, which fits a regression function to construct the tree-ring measurement series. This software can be used to remove non-climatic and age-related trends, and thus ensure that the measurements of individual trees, with different annual growth rates, are calculated on a robust estimation of the mean value function (Cook, 1985).

To evaluate the effects of lianas on tree growth, we examined whether there were systematic variations in correlations between the series (L and nL groups) of COFECHA for the given timespan of each species. Pearson's correlations were performed between the standard chronological indexes (obtained by ARSTAN) of OL and AL groups in both species over the timespans analyzed with COFECHA. We included current annual increments (CAI), basal annual increments (BAI), and accumulated diametrical growths (ADG) in our analysis (López et al., 2013; Schongart et al., 2007). BAI was calculated as: $BAI = \pi(R_t^2 - R_{t-1}^2)$, where R is the radius of the tree and t is the year of tree-ring formation, with tree diameters estimated from the core lengths. An ADG-age relationship was adopted based on a sigmoidal regression model (Paredes-Villanueva et al., 2013).

2.4. Dendroclimatic analysis from tree-ring width

Tree-ring width chronologies of the two species were compared to the monthly mean temperature and total precipitation variables with bootstrap correlation coefficients using the R package BootRes (Zang and Biondi, 2013). As the trees in question tend to undergo cambial activation in months where rainfall exceeds 60 mm (Worbes, 1995), the growing season was considered to be from September–May.

2.5. Intra-annual wood anatomical features: vessels in teak and intra-annual density fluctuations in Caribbean pine

We scanned wood samples of the eight trees at 4800 dpi (EPSON Perfection V720 scanner PRO) and analyzed vessel area using the program Image Pro-Plus (Venegas-Gonzalez et al., 2015). More than 16,000 vessels were analyzed corresponding to the period 1976–2011, with an average of $20.2 \times 10^3 \mu\text{m}^2$ (Appendix B in the Supplementary material). Variables included in the analysis consisted of mean vessel area (MVA) of (i) total, (ii) earlywood, (iii) first row, (iv) latewood, (v) transition between earlywood and late-

wood, and (vi) number of vessels. Intra-annual density fluctuations (IADFs) or false rings were counted in the cross-section of the same wood of Caribbean pine trees. IADFs are the result of cambial activity changes induced by climate events over the normal course of the growing season, and are indicated by a narrow band of tracheids (Campelo et al., 2013). The frequency of IADFs over the course of a year was calculated by the equation $f = (Nn^{1/2})/n$, where f is the stabilized IADF frequency, N is the number of trees exhibiting IADFs in a given year, and n is the total number of trees sampled during that same year. We counted 565 false rings on 18 wood samples during the period 1971–2011, with an average of 0.94 IADFs occurring per year (Appendix B in the Supplementary material).

2.6. Wood density

Trees were resampled, with one wood core per tree extracted using an increment borer; the core that had the highest degree of correlation with the master series was selected for analysis. Wood samples were dried in outdoor conditions and fixed on a support structure with the fibers arranged in a horizontal direction, following which they were cut in the transverse direction (1.7 mm thick) using a double-bladed circular saw, and then stored in a conditioning chamber until 12% moisture content was attained (Tomazello et al., 2008). Wood samples were analyzed by QTRS-01X x-ray densitometry (Quintek Measurement Systems – QMS, EUA), which calculated density values every 0.04 mm. Wood density values obtained by the QMS software generated a DAT file, which is read using Microsoft Excel, allowing for the construction of tree-ring wood density radial variation graphics. In addition, the application of x-ray densitometry facilitated marking of the tree rings in the two species, which depends on the inter-annual wood density variation of the tree rings (Briffa et al., 2002). In *P. caribaea*, this differentiation occurs because latewood has high wood density as a result of greater tracheid wall thickness and smaller lumen diameter (Ferreira and Tomazello Filho, 2009), whereas in *T. grandis*, wood density was found to decrease in latewood due to the thinner wall thickness and higher lumen diameter of the axial parenchyma (Moya et al., 2009).

2.7. Carbon uptake by tree rings

Cumulative biomass (B) in the tree trunks at time t was estimated using the formula: $B = V * WD$, where V is tree volume at year t and WD is annual mean wood density at year t . To calculate V , we used the formula described for felled trees without bark, which is based on diameter at breast height (D): $\ln(V) = \beta_0 + \beta_1 * \ln D$, where β_0 and β_1 represent specific parameters for each species (Husch et al., 1993). We used the parameters calculated by Moraes Neto (2009) for *P. caribaea* ($\beta_0 = 2.90895$, $\beta_1 = 2.63808$) and Oliveira (2014) for *T. grandis* ($\beta_0 = -10.9292$, $\beta_1 = 2.9476$). Diameters were calculated from the tree-ring width series (radius). As average carbon content in tropical wood biomass is 47–51% (Martin and Thomas, 2011), we considered carbon content in woody tissues to be a constant 50%.

2.8. Statistical analyses

We performed a descriptive statistical analysis of tree-ring variables in both species and used the Mann-Whitney U non-parametric test (95% confidence level) to evaluate the influence of lianas on (i) CAI and BAI, (ii) tree-ring anatomy, and (iii) wood density. Since the Shapiro-Wilk test indicated that the values used in this analysis were non-normally distributed, subsequent analyses were conducted using non-parametric tests (Zar, 2010). Principal component analyses (PCA) were conducted between tree-ring variables and age classes (trees with and without lianas) to reduce

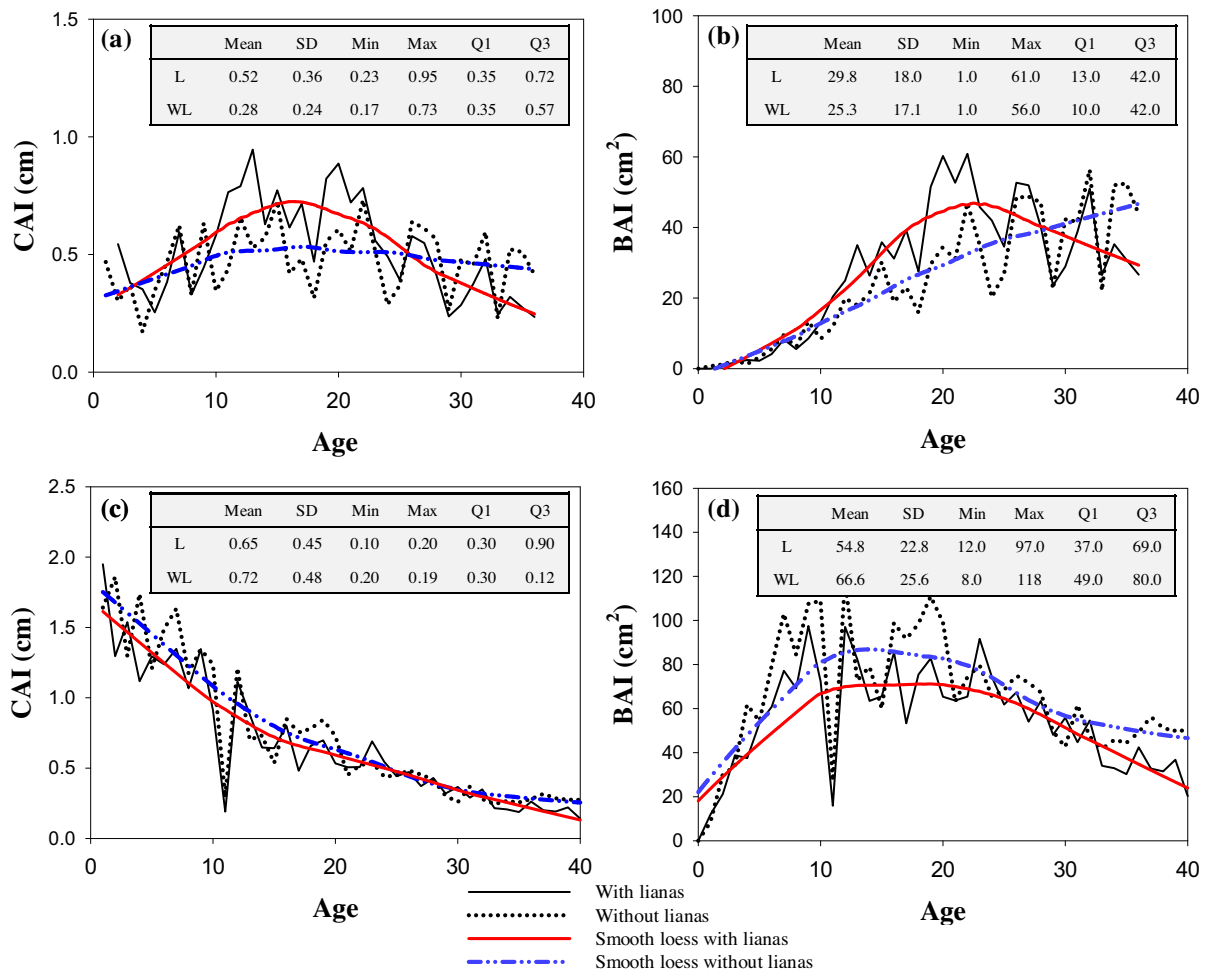


Fig. 1. Current annual increase in cm (CAI) and basal annual increase in cm² (BAI) of tree with occupation or absence of lianas. (a) and (b) teak; (c) and (d) Caribbean pine. Red line (with lianas) and blue line (without lianas) represents smoothing of curves through loess fit with span=0.5. Tables show the statistical parameters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the dimensionality of the data groups. For the accumulated diametrical growth analysis, we used a 95% confidence band for the sigmoidal regression model. To assess liana influence on tree-ring sensitivity to climate, we conducted a Pearson's correlation analysis between and amongst groups (L and nL), using a significance of $P=0.05$. To analyze the relationship among carbon mass uptake and wood density and tree growth, we performed a Pearson's correlation between annual carbon mass and annual density-growth variables. The purpose of this analysis was to determine the influence of tree growth and intra-annual wood density in the carbon accumulation by the trees. Based on the radial increment and mean annual wood density, we estimated the cumulative aboveground carbon mass over time using a sigmoidal regression model with 95% confidence bands.

3. Results

3.1. Influence of lianas on radial tree growth

Series intercorrelations (Appendix C in the Supplementary material) and standard indices (Fig. S3 in the Supplementary material) showed that tree-ring-width chronologies in the outer rings decreased in trees with lianas relative to those of trees without lianas (2000–2011 for teak, 1990–2011 for Caribbean pine). In teak, the L group exhibited lower growth than did the group without lianas in CAI and BAI from the 15th and 23rd year, respectively,

whereas CAI was stable and BAI increased continuously throughout the entire study period in the nL group (Fig. 1a,b). In this context, we observed lower CAI and BAI values in the L group than in the nL group in the last two age classes, although these differences were not significant [(25–30: CAI: $H=0.75$, $P=0.4857$; BAI: $H=0.01$, $P<0.9999$) (30–36: CAI: $H=0.08$, $P=0.8857$; BAI: $H=2.56$, $P<0.1190$)] (Appendix D in the Supplementary material). For Caribbean pine, the CAI and BAI growth trends were similar for both the L and nL groups throughout the analyzed time period, highlighting higher values for nL group (Fig. 1 c,d). There was a significant reduction in CAI and BAI over the final six years in the L group (CAI: $H=17.8$, $P<0.001$; BAI: $H=8.31$, $P=0.002$) (Appendix D in the Supplementary material). The accumulated diametrical growth also significantly decreased in the L group of both species, since 2005 for teak and 2002 for Caribbean pine, as reflected in the difference between the 95% confidence bands (Fig. 2).

3.2. Influence of lianas on sensitivity of tree rings to climate

For teak, competition with lianas appeared to be more pronounced at the end of the hot and rainy season, as the tree-ring growth of L group individuals was negatively correlated with temperature in the months from February to May ($r=-0.40$), whereas there was a positive correlation between trees in the nL group and rainfall in November (i.e., the start of the growing season; $r=0.37$) and in February/March (i.e., the end of the rainy season; $r=0.42$ and

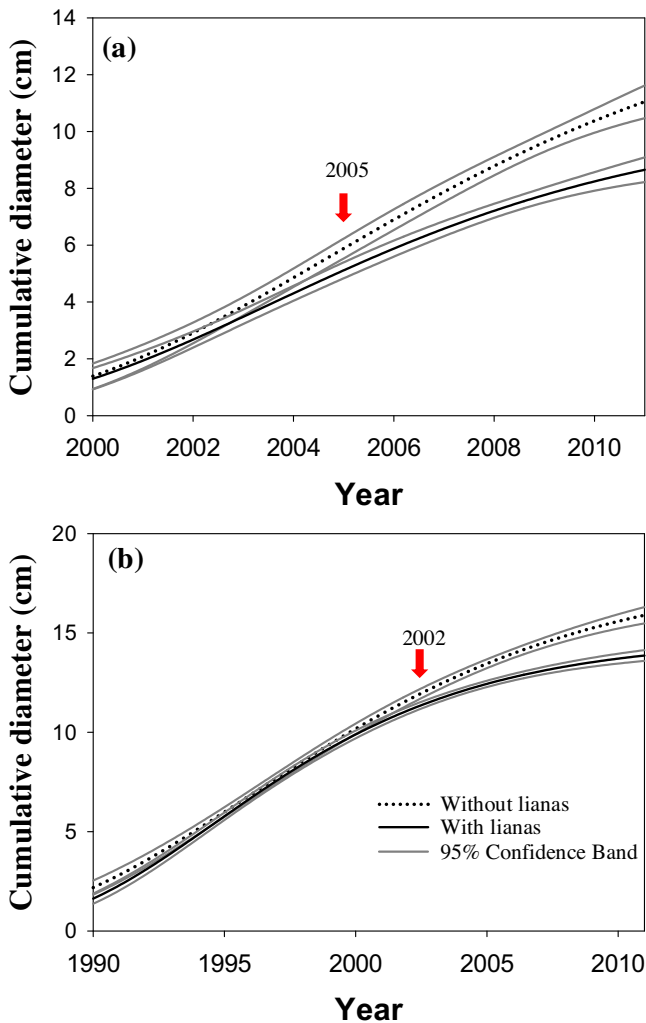


Fig. 2. Ccumulated diametrical growth of tree with and without lianas, shown by the sigmoidal regression model (95% confidence bands). (a) *Tectona grandis*, (b) *Pinus caribaea*. Red arrow indicates the year that significant differences started between tree with and without lianas, shown by the difference between confidence bands. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

0.34, respectively) (Fig. 3a). Overall, the correlations between ring width and temperature and rainfall were weaker in Caribbean pine than in teak; even so, a negative correlation between Caribbean pine L-group trees and temperature was observed for the month

of February, which may be attributed to tree-liana competition. Regarding the growth-precipitation relationship, there was a positive correlation between radial growth and rainfall in the dry season (July for the nL group, $r = 0.34$; September for the L group, $r = 0.43$) (Fig. 3b).

3.3. Influence of lianas on tree-ring anatomy

Principal components analyses of the anatomical features of the xylem (vessels for teak and IADFs for Caribbean pine) and age class (trees with and without lianas) revealed that these two principal components explained 80.7% of total variance (Fig. 4). PC1 (62.0%) was built by total MVA, transition MVA, earlywood MVA, and first row MVA; these four variables were associated with the last two age classes of the L group. Vessel number and latewood MVA were positively correlated with each other, and weakly correlated with the other variables. PC2 (18.7%) compared vessel abundance and latewood MVAs (negative weight) to IADF (positive weight). In the latter case, nL individuals in the 30–35 year age class were associated with the formation of IADFs in the tree rings. However, because the pine trees were older than the teak trees, the last age class (35–41 years old) was not included in the PCA, but we can assume that this would associate with L group.

The negative effects that lianas have on the growth of both tree species was observed in recent years (Figs. 1,2,4 and S3), in which the tree-ring anatomy (vessels and IADFs) of recent age classes was analyzed (Fig. 5, Appendix E in the Supplementary material). Lianas had an indirect effect on vessel size in teak, since that L group had higher significant values than the nL group for the variables total MVA (25–30 years: $M = 22.87, P < 0.0001$; 30–36 years: $M = 17.51, P < 0.0001$; 25–36 years: $M = 39.94, P < 0.0001$), earlywood MVA (25–36 years: $H = 5.02, P = 0.0402$), latewood MVA (25–30 years: $H = 4.10, P = 0.0428$; 30–36 years: $M = 7.97, P = 0.0048$; 25–36 years: $H = 12.16, P = 0.0005$) and transition MVA (25–30 years: $H = 21.41, P < 0.0001$; 30–36 years: $H = 18.76, P < 0.0001$; 25–36 years: $H = 39.58, P < 0.0001$) (Fig. 5a–c,e). However, vessel number appeared to be related to the absence of lianas, since this variable was higher in the nL group in recent years than in L groups (30–36 years: $H = 6.90, P = 0.0086$; 25–36 years: $H = 10.43, P = 0.0012$) (Fig. 5f), which is related directly to the radial growth in nL individuals (Fig. 1a). For pine trees, the formation of false rings seems to be affected by liana colonization, as the formation of IADFs remained constant in nL while individuals in the L group exhibited a progressive decline over the age classes (30–36 years: $H = 4.81, P = 0.0397$; 25–36 years: $H = 4.43, P = 0.0346$; 25–36: $H = 4.96, P = 0.0206$) (Fig. 5g).

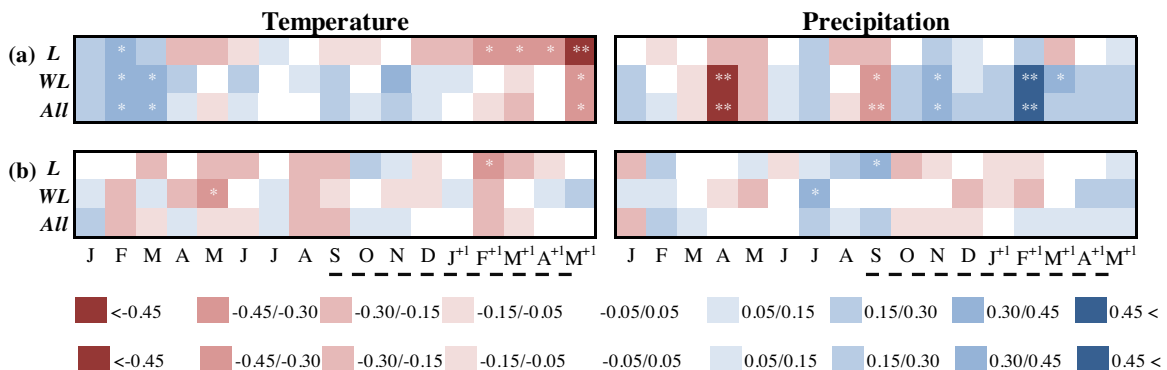


Fig. 3. Correlation between the tree-ring chronologies, average monthly temperature and total monthly rainfall from January (J) of previous year's growth to May of current year's growth (M^+1). (a) *Tectona grandis*, (b) *Pinus caribaea*. L: trees occupied by lianas, WL: trees without lianas and All: all trees. Horizontal line indicates the targeted growth session. Asterisks indicate the parameters with significant values (* $p < 0.05$ and ** $p < 0.01$).

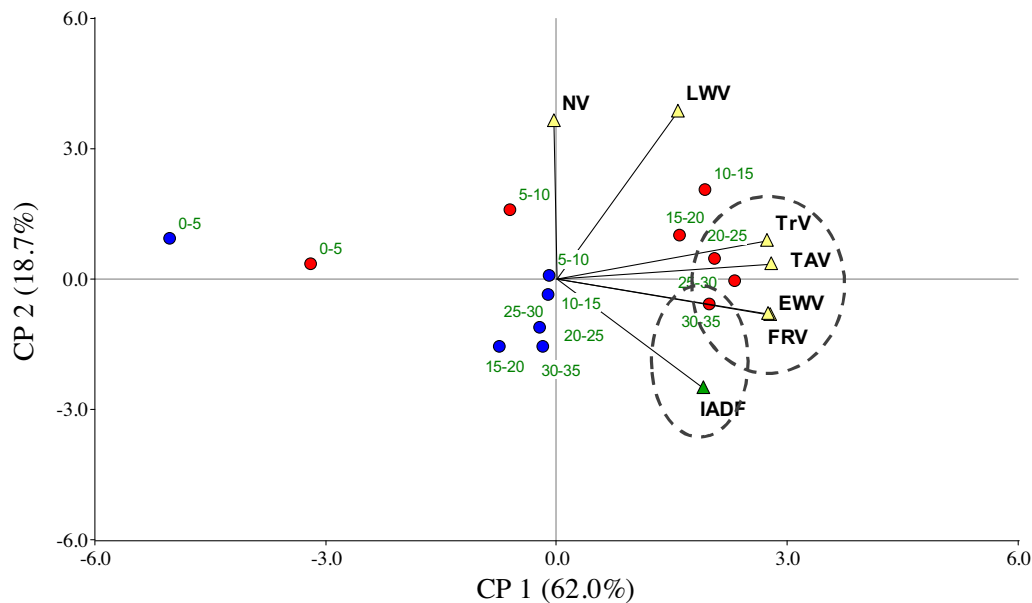


Fig. 4. Position of variables of teak trees vessels (yellow triangle) (TAV: Total MVA, EWW: Earlywood MVA, LWV: Latewood MVA, FRV: First Row MVA, TrV: Transition MVA, NV: Numbers of vessels) and false rings of Caribbean pine trees (green triangle) (IADFs: Intra-annual density fluctuations) on the first and second principal component of PCA. Red and blue points represent the trees with and without lianas, respectively. Green values indicate the same age classes of the two species on these axes. Black circles show association between anatomical variables and age class of trees with lianas. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Pearson's correlation among annual carbon mass uptake (C), tree rings width (RW), basal area increment (BAI) and wood density (WD).

	Teak			Caribbean pine		
	RW	BAI	WD	RW	BAI	WD
C	0.34*	0.99*	0.72**	0.19	0.99**	-0.36*
RW		0.41*	-0.29		0.23	-0.46*
BAI			0.65**			-0.30

Significant correlations are shown in bold *($p < 0.05$) and **($p < 0.01$).

3.4. Influence of lianas on wood density

X-ray analysis revealed significant differences in tree-ring wood density between the L and nL groups for both species (Fig. 6). For teak, nL trees had higher wood density than did L trees, with the differences being highly significant in the last three age classes (20–25 years: $H = 94.86$, $P < 0.0001$; 25–30 years: $H = 208.51$, $P < 0.0001$; 30–36 years: $H = 46.51$, $P < 0.0001$). However, pine trees exhibited the opposite trend, with L values being higher than those for nL trees over the analyzed period, highlighting a strong difference in the last ten years (30–35 years: $H = 118.1$, $P < 0.0001$; 35–41 years: $H = 348.27$, $P < 0.0001$) (Appendix D in the Supplementary material).

3.5. Influence of lianas on carbon uptake

There was a significant correlation between annual carbon uptake (C) and BAI and wood density (WD) in both species, demonstrating that variations in C depend mainly on BAI and WD (Table 1). As expected, BAI was highly correlated with C ($r = 0.99$, $P < 0.001$) in the two species. However, although WD was positively correlated with C in *T. grandis* trees ($r = 0.72$, $P < 0.01$), a negative correlation was observed between these variables for *P. caribaea* trees ($r = -0.36$, $P < 0.05$). Although wood density in both species increase in pith-bark direction, these results are associated with the unique growth patterns of each species; teak trees displayed high growth rates over the first 20 years (~ 1990) and thereafter remained con-

stant, whereas growth rates in Caribbean pine were highest early years but decreased over time, a pattern typical of gymnosperms (Fig. 1c,d). Thus, even if there are high WD values (last year) in Caribbean pine, there are also low ring width values, which influenced more in annual carbon mass uptake.

Average carbon stocks in teak and Caribbean pine were 527.2 kg and 1318.1 kg for trees with lianas, and 466.1 kg and 1423.4 kg for trees without lianas, respectively (Fig. 7). However, when assessing carbon uptake since 2001 and 2006, higher values were observed in trees without lianas for both species (Fig. 7).

4. Discussion

Although we studied tree species that differ in their response to mechanical stress, we can deduce a possible effect of lianas on growth synchronization in both species, given that the L group showed a reduced growth radial, especially over the last several decades. However, bioindicators that are commonly used to evaluate the effects of lianas on trees, such as tree survival and diametric growth (Botosso et al., 2005; Kainer et al., 2006; Malizia and Grau, 2008, 2006), only assess the direct damage of canopy infestation over short monitoring periods. As such, tree-rings could provide a means of estimating when liana colonization begins to have a detrimental effect on host trees, in both deciduous and coniferous species.

Several studies have reported that lianas benefit from forest disturbances, as they are more efficient in the utilization of water and light than are the host trees (Laurance et al., 2001; Schnitzer and Bongers, 2002; Tabarelli and Mantovani, 1999; Zhu and Cao, 2010), resulting in rapid growth and expansion of the lianas (Putz, 1984). This competitive advantage allows lianas, when colonizing forest canopies, to influence forest dynamics and interfere in secondary succession (Botosso et al., 2005; Letcher and Chazdon, 2012; Schnitzer and Carson, 2010). Nevertheless, growth reduction may depend on the type of liana, climatic conditions, and the autecology characteristics of the host trees (Schnitzer and Bongers, 2002). In degraded forests, the continued proliferation of lianas

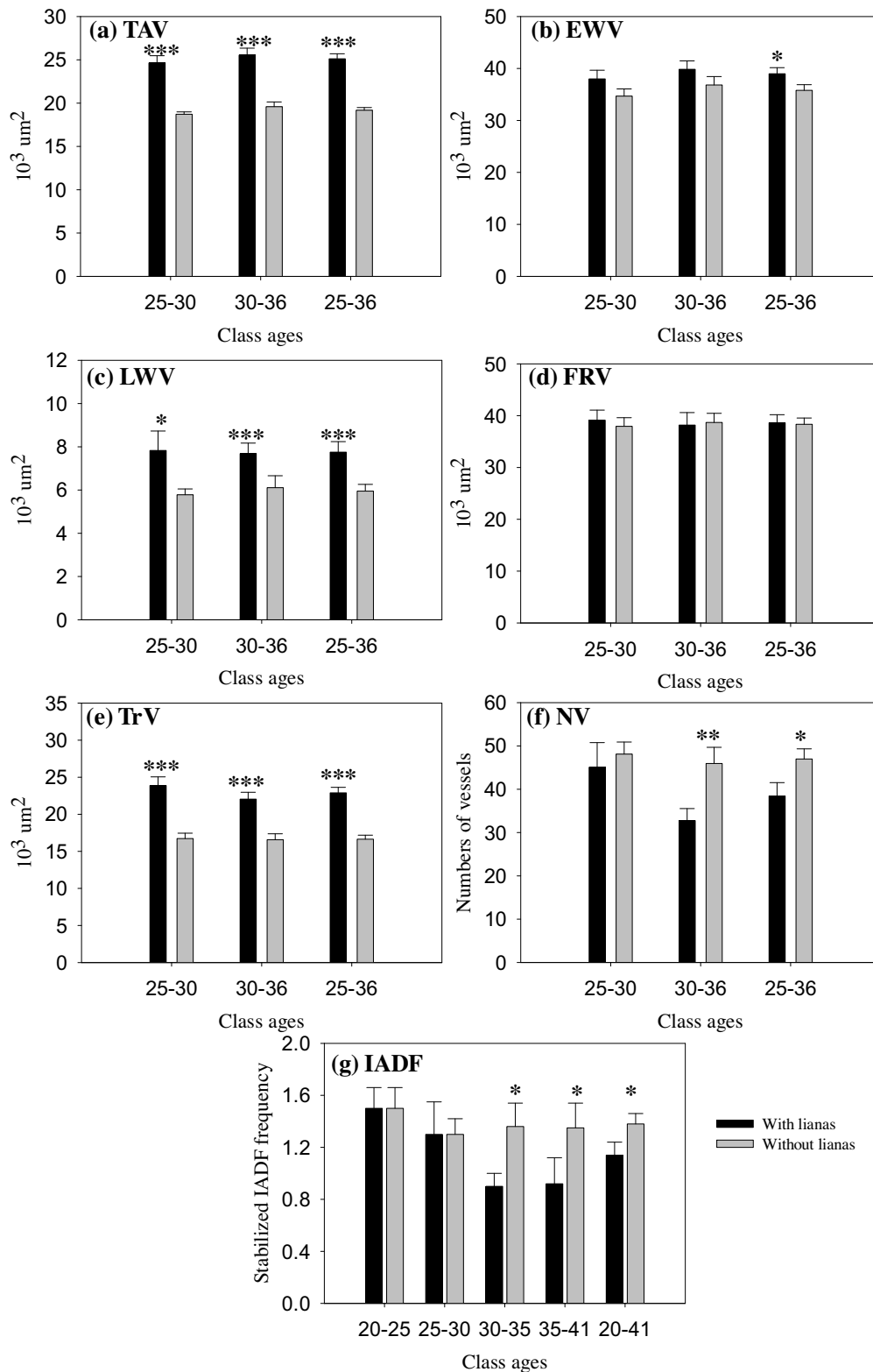


Fig. 5. Mean (+SE) of the tree-ring anatomy variables according to the lianas colonization in the last year classes. (a) TAV: Total MVA, (b) EWV: Earlywood MVA, (c) LWV: Latewood MVA, (d) FRV: First Row MVA, (e) TrV: Transition MVA, (f) NV: Numbers of vessels, (g) IADFs: Intra-annual density fluctuations. Asterisks indicate significant differences according to Mann-Whitney U nonparametric test (* p < 0.05, ** p < 0.01 and *** p < 0.001).

and increase in their mass in the canopy also causes breakage of host tree branches and/or trunks (Ingwell et al., 2010; Laurance et al., 2001; Nepstad et al., 2007), resulting in an increase in the number and size of gaps (Vidal et al., 1997), which in turn further

contributes to the dominance of lianas. Thus, examining how lianas affect the wood anatomy of host trees as a result of competition for resources represents an effective starting point for understanding the ecological role of lianas in degraded forest-fragment dynamics.

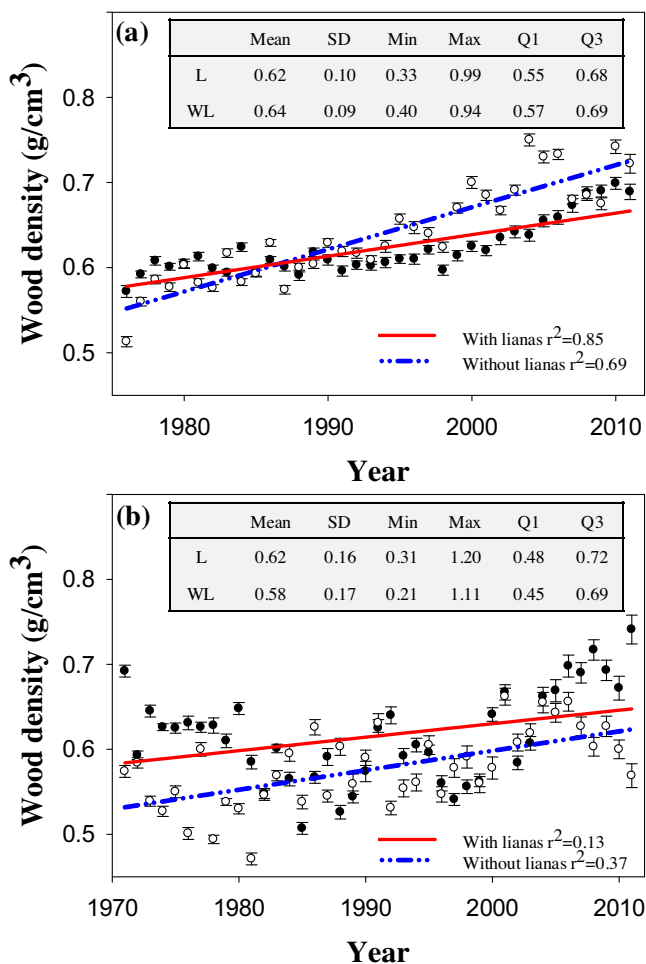


Fig. 6. Mean wood density in g/cm^3 ($\pm\text{SE}$) vs. growth ring year, as well as growth tendency according to linear regression (significant models with $P < 0.001$), red (with lianas) and blue line (without lianas). (a) *Tectona grandis*, (b) *Pinus caribaea*. Tables show the statistical parameters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The higher temperatures that occur during the hottest parts of the growing season suppress radial growth in teak trees colonized by lianas, which is most likely to be due to increased evapotranspirative demand in tropical areas during these times (Schnitzer and Bongers, 2011). Moreover, trees with lianas had no response to precipitation in the rainy season, and thus we can infer lianas consume a large proportion of the available water, as lianas have larger leaf areas and greater water and light absorption efficiency than do host trees (Gerwing and Farias, 2000; Phillips et al., 2002; Schnitzer and Bongers, 2002). Thus, the photosynthetic rate and hormone production are reduced in host trees during periods of higher water demand, affecting cambial meristem cell division and resulting in xylem tissue differentiation (Scarpella and Meijer, 2004). Therefore, higher levels of evapotranspiration demand would tend to favor the growth and development of lianas (Schnitzer and Bongers, 2011).

We observed a 2-month delay in the radial growth response of the Caribbean pines with lianas to rainfall in the dry period (September for L group, July for nL group) (Fig. 3a). This effect is presumably explained by the efficiency of water consumption by lianas in the dry season owing to their deep rooting and efficient vascular systems (Schnitzer, 2005), which give lianas a competitive advantage over pine trees for water resources; pines only grow back after the end of the dry season, when enough water is available for both lianas and trees. The increasing irregularity of future rainfall patterns as a result of global climate change is expected to benefit

lianas when competing with trees for water, especially in seasonal tropical forests (DeWalt et al., 2010; Schnitzer and Bongers, 2011). Thus, it is possible that the massive canopy colonization in tropical forest fragments by lianas will interfere with important ecosystem services, such as carbon sequestration and regulation of hydrological processes, which may have direct consequences for human welfare.

Xylem inter-annual anatomical features of the two species also exhibited signs of indirect effects of competition for water between trees and lianas, which are related to the anatomical differences in the wood of gymnosperm and angiosperm trees. For instance, larger vessels were observed in teak trees with lianas (with respect to four variables—total MVA, earlywood MVA, transition MVA, and latewood MVA), as well as a lower abundance of vessels. Such changes in the vessels of trees in the L group may represent an adaptive strategy of enhancing hydraulic conductivity efficiency to offset the negative effects on radial growth and vessel abundance (Fig. 1a,b and g), a result of the balance between efficiency and security in the upward sap flow (Carlquist, 2009), with smaller vessels maintaining reliability whereas larger vessels provide hydraulic conductivity (von Arx et al., 2013), demonstrating that trees occupied by lianas have higher water restrictions, confirming our expectations. Moreover, the mass of lianas impart additional physical strain on the trunk and canopy of trees, affecting not only tree development but also apical and cambial meristem activity (Engel et al., 1998). The additional weight of lianas subject cambial cells to higher turgor pressures, which affects their cellular plasticity and pectin composition, and results in the formation of vessels with larger diameters (Mellerowicz et al., 2001).

Given that Caribbean pine trees often respond to atypical seasonal climatic variations by producing false rings (i.e., IAFDs), we hypothesized that liana colonization would provoke a similar response. We observed that IADF formation was lower in the L group for all age classes, being significant over the last 20 years (Fig. 5g). The pattern of xylem anatomy appeared to be linked to canopy colonization by lianas, which detrimentally affected physiological processes relating to water transport, as well as the photosynthetic and respiration rates (Schnitzer and Carson, 2010), thereby decreasing the rate of cell division rate and increasing tree sensitivity to climatic seasonality. In the dry season, IADF formation in L-group trees would be reduced owing to the complete absorption of the available water by lianas (DeWalt et al., 2010).

Regarding wood density, both species had mean values similar to those found in other studies on teak and Caribbean pine plantations (Castro et al., 2014; Ferreira and Tomazello Filho, 2009; Kokutse et al., 2004; Udoakpan, 2013). In teak, we observed that nL trees were more dense than L trees in the final years, whereas this pattern was reversed for Caribbean pine, for which L trees had higher density values than nL trees (Fig. 6). The differences in wood density are likely to be due to variations in the cell structure of intra-annual wood; in teak trees, it could be explained by the smaller variations in intra-annual wood density that occurs in this species (Moya et al., 2009), and by the fact that, while under stress, teak trees produce wood with higher concentrations of parenchyma cells and lower fiber content (Bhat and Priya, 2004)—fiber cells have a thicker wall than do parenchyma cells, thus a lower fiber content decreases the density of the wood (Carlquist, 2009)—a condition that results in lower physical and mechanical resistance of the trees. In Caribbean pine trees, this difference in wood density is due to the lower tree radial growth (Fig. 1c,d), and thus a lower content of earlywood (lower density, tracheids with smaller wall thickness and larger lumen area) in relation to latewood (higher density, tracheids with greater wall thickness and smaller lumen area) in the rings (Decoux et al., 2004; Jyske et al., 2008; Mäkinen et al., 2002). In light of these conditions, it was determined that the variation in radial growth between earlywood and latewood was $0.2\text{--}0.5\text{ g}/\text{cm}^3$ and

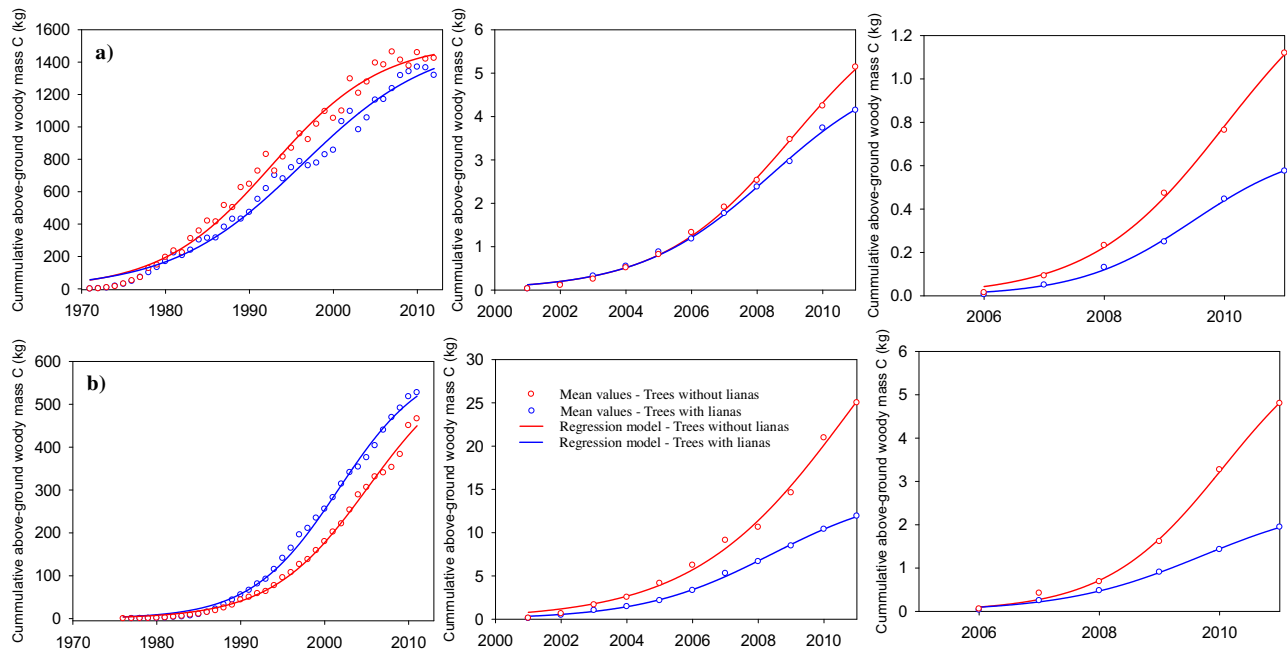


Fig. 7. Cumulative carbon in the trunk (C), in the whole period, last 10 years and last 5 years, of trees with and without lianas: (a) *Pinus caribaea* and (b) *Tectona grandis*. A sigmoidal regression model was used (95% confidence bands), $R^2 > 0.98$, $p < 0.001$.

0.8–1.2 g/cm³, respectively (Ferreira and Tomazello Filho, 2009). These results have important implications for biomass estimates, and furthermore we can infer that there was also an effect on stem carbon fixation, given that lianas reduce the total carbon stock of forests by interfering with host-tree carbon sequestration (Phillips et al., 2002; Schnitzer and Bongers, 2002).

We found that Caribbean pine trees without lianas accumulated more carbon over the study period, whereas the biomass of teak trees with lianas increased. Although it was not possible to determine whether lianas had colonized the trees since the beginning of the time periods, we were able to show that lianas began to have detrimental effects on carbon uptake by the host trees in the final growing season (last 5–10 years) (Fig. 7). The importance of large trees for carbon fixation in tropical forests has long been known, but they are mostly affected by liana colonization in disturbed habitats (Sfair et al., 2015), and liana colonization can even cause tree death (Laurance et al., 2011) (a Caribbean pine tree with lianas died two years after of the sampling this study). As such, high concentrations of lianas in fragmented environments can dramatically alter the tree community and carbon dynamics, promoting the degradation of these forests and consequently the release of large amounts of carbon into the atmosphere.

Massive colonization of lianas on trees interferes with their normal physiological processes, especially with regard to competition for water and light, thus reducing the total carbon storage of the trunk and other parts of the host trees (Schnitzer and Bongers, 2002). Carbon sequestration is an environmental service that forest ecosystems provide that contributes to the maintenance of the ozone layer and atmospheric CO₂ and O₂ balances (de Groot et al., 2002). In this context, forest ecosystems have the ability to sequester more carbon per year than do other terrestrial ecosystems, up to 50% of total terrestrial carbon stocks (Pan et al., 2011). Therefore, studies of carbon dynamics in degraded forests are critical, particularly in tropical and subtropical regions, where they remain under pressure from deforestation and fragmentation, which promotes a greater density of lianas, especially in edges and gaps. Higher densities of lianas exacerbate the loss of living biomass by contributing to the death of large trees (Laurance et al.,

2011), thereby altering carbon availability, which the accumulation of liana biomass fails to offset (Laurance et al., 1997).

5. Conclusions

Radial growth was reduced, and xylem anatomical features and wood density were modified, and hence rates of carbon sequestration were also reduced in host trees, regardless of the age of the tree, climatic conditions, or other external variables affecting forest fragments. We demonstrated here the feasibility of this method (i.e., non-destructive sampling) for use as an ecological indicator of the competitive interactions between trees and lianas, especially in cases where the latter have a detrimental effect on the former. Moreover, this approach could prove useful in assessments of ecosystem services, both commercial and ecological, provided by these tree species (e.g., carbon accumulation) in the context of future land-use change and global warming.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.dendro.2016.11.001>.

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