

This article was downloaded by: [José Rafael Lozada]

On: 24 February 2015, At: 03:59

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



[Click for updates](#)

Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tplb20>

An assessment of the floristic composition, structure and possible origin of a liana forest in the Guayana Shield

J. R. Lozada^a, C. Hernández^b, P. Soriano^c & M. Costa^c

^a Facultad de Cs. Forestales y Ambientales, Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Mérida, Venezuela

^b Departamento de Botánica, Facultad de Cs. Forestales y Ambientales, Universidad de Los Andes, Mérida, Venezuela

^c Jardín Botánico de la Universidad de Valencia, España

Accepted author version posted online: 22 Jan 2015. Published online: 19 Feb 2015.

To cite this article: J. R. Lozada, C. Hernández, P. Soriano & M. Costa (2015): An assessment of the floristic composition, structure and possible origin of a liana forest in the Guayana Shield, *Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology: Official Journal of the Societa Botanica Italiana*, DOI: [10.1080/11263504.2015.1008598](https://doi.org/10.1080/11263504.2015.1008598)

To link to this article: <http://dx.doi.org/10.1080/11263504.2015.1008598>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

ORIGINAL ARTICLE

An assessment of the floristic composition, structure and possible origin of a liana forest in the Guayana Shield

J. R. LOZADA¹, C. HERNÁNDEZ², P. SORIANO³, & M. COSTA³

¹Facultad de Cs. Forestales y Ambientales, Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Mérida, Venezuela; ²Departamento de Botánica, Facultad de Cs. Forestales y Ambientales, Universidad de Los Andes, Mérida, Venezuela and ³Jardín Botánico de la Universidad de Valencia, España

Abstract

Liana is a life form that possesses high importance in many Neotropical forests. Density of climbers apparently increases with the intervention rate (e.g. logging). The aim of this work is to characterize the structure, floristic composition and soils of a sector classified as Liana Forest (LF). We identified an LF sector in a not-logged area; three 1 ha square plots were measured (individuals ≥ 10 cm dbh, “diameter at breast height”). In each plot, we evaluate four 100 m² square understory subplots (all spermatophyta individuals < 10 cm dbh). LF has a low canopy (< 15 m) and is dominated by *Alexa imperatricis* and *Pentaclethra maculobola*. Basal area (20.4 m²ha⁻¹) and diversity ($H' = 2.6$) are lower than other surrounding plots. Understory is dominated by gnarled climbers, and the most important are *Cheilochlinium hippocrateoides* and *Bauhinia scala-simiae*. Soil is extremely acidic, with very low fertility but is similar to neighboring places. We conclude that LF was neither originated by edaphic restrictions nor logging; LF probably suffered a hurricane wind that fell down most of the canopy trees, thick individuals of climber species also disappeared, and the current successional stage favors a recovery dominated with thin individuals of this life form.

Keywords: Climber, liana tangle, forest succession, forest management, Imataca

Introduction

Lianas invasion is a serious threat in forest ecosystems (Putz & Mooney 1991). They can represent a “stalled” successional stage (Hernández 1997; Jacinto Tabanez & Viana 2000; Schnitzer et al. 2000). In various tropical forests, liana infestation fluctuates between 42% and 86% of trees ≥ 10 cm dbh (Putz 1983; Pérez-Salicrup et al. 2001). Wright et al. (2004) and Wright & Calderón (2006) have pointed out that lianas could be increasing their biomass in the tropical forests. Some of the causes can be the increment in the CO₂ concentration that has a fertilization effect (Granados & Körner 2002; Zotz et al. 2006) or the global climate change (Phillips et al. 2002; Van Der Heijden & Phillips 2008). In the Amazon forests, increments in the lianas dominance can generate changes in the floristic composition, favoring to arboreal species of quick growth and low density and reducing the carbon storage (Van Der Heijden et al.

2008). Liana Forest (LF) patches can inhabit until 20% of old-growth forests in the Eastern Amazon (Keefe et al. 2009). Lianas are responsible for 30% of the canopy species richness in an Amazonian forest (Schröder et al. 2013).

The reproduction strategies and growth of lianas allow them to be successful in many environments. Some species are epiphyte during the first stages of the life cycle, then their roots arrive to the soil and they only use the guest to climb (Hernández 1992). The stems are resistant to tension and torsion, as well as they have thorns and earrings that help them to ascend and to reach the light (Vareschi 1992). It suits to highlight that during the development of the present investigation, we opened pathways with “machete”, we observed that some hanging individuals had abundant buds of roots about 8 days after having been cut. In fact, Gerwing & Vidal (2002) reports that coppicing of cut stems is one of the principal mode of liana recruitment. Lianas have deep roots (until 10 m of depth) and efficient

vascular system that represent an advantage during the dry season (Restom & Nepstad 2004; Schnitzer 2005). According to Leicht-Young et al. (2011) increased density does not decrease lianas height growth, and they do not follow the self-thinning law at least in their early stages of growth.

Several studies reported lianas proliferation in logged forests (Neil 1984; Putz 1985). For instance, Vareschi (1992) describes the extraordinary invasion of climbers in the road sides. Laurance et al. (1997) found that, in logged sector borders, lianas biomass increases. Lianas inhibit tree regeneration and form tangles in understory, which persist for extended periods (Schnitzer et al. 2000). It is stated that tree fall gaps are the optimal regeneration site for lianas and climber cutting is a silvicultural practice in many tropical countries, focused to minimize the future effect of lianas on tree regeneration (Schnitzer et al. 2004; Schwartz et al. 2013). In logged forests, the lianas increase is particularly palpable in the skid tracks and loading areas (Guariguata & Dupuy 1997; Kouamé et al. 2004). Selective logged forest (40 years old) can exhibit almost three times more lianas stems than old-growth forests (Ding & Zang 2009).

Some ecosystems have high occurrence of lianas and are called LFs (Balée & Campbell 1990; Hernández 1997; Pérez-Salicrup et al. 2001). However, neither some of their ecological characteristics (e.g. climbers density and basal area, relationship with perturbation) nor how to make a distinction with other “standard” forests are clear. There are some evidence about lianas abundance increase in altered conditions (DeWalt et al. 2000; Laurance et al. 2001). But, Rice et al. (2004) found that very perturbed forests in Puerto Rico possess low lianas affectation in the crowns because they are dominated by pioneer trees with very quick growth, flat bark and branches with quick renovation rate. On the other hand, Van Der Heijden & Phillips (2008) and Anbarashan & Parthasarathy (2013) show that lianas basal area is higher in the old growth or relatively undisturbed forests.

Regarding the information given above, we designed a study to understand LF structure and their origin. The research was developed to evaluate how are the canopy and layers of an LF; how are the density, basal area, and importance index of all the species in an LF; which is the relationship between logging and lianas; and which another factors can influence the origin of an LF.

Materials and methods

Study site

The Guayana Shield is one of the oldest areas of the planet, is dominated by granitic, basic volcanic and

turbidic metamorphosed rocks of the Precambrian. Inside this region, the Imataca Forest Reserve (IFR) covers a surface of 3,822,000 ha, between 6°00' and 8°30'N and 59°50' and 62°10'W (MARN-UCV 2003). Our surveys were carried out in the Biological Reserve Area, Unit C4, located in the central sector of the IFR.

Annual precipitation is near to 1700 mm, and the annual average temperature is 26°C. (MARN-UCV 2003). Soils were formed in the past 200,000–100,000 years, starting from a substratum previously affected by weathering, erosion, transport and deposition processes; therefore soils are acidic, very leached, with very low cation exchange capacity, and toxic aluminum levels (Franco 1988; Lozada et al. 2014).

In the Holdridge System, the study area belongs to tropical humid forest (Ewel et al. 1976). More than 80% of the IFR possesses a forest covering that is attached to the jungles of Guyana, Suriname, French Guiana and the Amazon rainforest, forming one of the largest regions of the planet with continuous forest cover (Huber & Foster 2003; MARN-UCV 2003).

Research design

We used three 1 ha square plots (lf1, lf2, and lf3). In each plot, all the trees, palms and lianas were measured (dbh \geq 10 cm). Furthermore, a census of all the spermatophyta species was carried out (dbh < 10 cm) in four understory subplots (100 m²) inside each plot. Voucher specimens are located at Herbarium MER (Universidad de Los Andes, Mérida, Venezuela) and species list was verified at The Plant List website.

Data analysis

The Importance Value Index (IVI) was calculated for each species (Curtis & McIntosh 1951), according to the following equation:

$$IVI = \text{Abundance\%} + \text{Dominance\%} + \text{Frequency\%}.$$

In addition, an Enlarged Importance Index (EII) was used, according to Lozada et al. (2011):

$$EII = IVI + UA\% + UF\%$$

UA%: understory relative abundance. UF%: understory relative frequency.

We estimate the biomass, using the equation from Brown et al. (1989) corresponding to tropical humid

forest:

$$Y = 38.49 - 11.788(d) + 1.193(d^2);$$

Y = weight of the individual (kg); d = dbh (cm).

Diversity was evaluated through the Index of Shannon-Wiener (H') and the Fisher's Alpha (α), according to the following equations:

$$H' = -[\pi \times \text{Ln}(\pi)],$$

where π = number of individuals of a species/total of individuals of the plot (Magurran 1988).

$$S = \alpha \text{Ln}[1 + N\alpha^{-1}]$$

(Fisher et al. 1943, mentioned by ter Steege et al. 2003; to make these calculations it was used a subroutine available in www.bio.uu.nl/~herba/Guyana/ATDN/pagina5.html).

We did an analysis of abundance in each diametric category, and the Index Uhl-Murphy (IUM) was calculated to illustrate the dominance of thick or thin individuals (Uhl & Murphy 1981):

$$\text{IUM} = \frac{\text{Number of Individuals} \geq 10 \text{ cm dbh}}{\text{Number of Individuals} \geq 20 \text{ cm dbh.}}$$

Soil evaluation

To evaluate the soil, we opened a trial pit, the horizons were identified, and in each one, we took samples that were dried to the air, crushed, and a 2 mm sieve was used to separate the thick skeleton. Then, samples were subjected to the following analyses (Klute 1986; Sparks et al. 1996): texture determination (method of Bouyoucos); pH (determination in water, relationship 1:1 and using the

potentiometric method); organic matter (Walkley & Black method); total nitrogen (Micro-Kjeldahl method); organic carbon (Walkley & Black method); phosphorus (P; colorimetric method with Vanadate-Molybdate); sodium-Na, potassium-K, calcium-Ca, magnesium-Mg, and iron-Fe (spectrophotometer of atomic absorption, with North Carolina extractor solution); exchangeable aluminum (potassium chloride method).

Results

Floristic composition and structure

When considering the structure of the forest and the physiographic position, this LF corresponds to a hillside low forest. It possesses a canopy less than 15 m height, with some emergent individuals that arrive to 23 m. The highest trees belong to species *Carapa guianensis* Aubl., *Cordia exaltata* Lam., *Inga alba* (Sw.) Willd., *I. ingoides* (Rich.) Willd., *Jacaranda copaia* (Aubl.) D. Don, *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin, *Tachigali* sp., *Simarouba amara* Aubl., and *Sterculia pruriens* (Aubl.) K. Schum.; these trees are isolated and make a cover lower than 10%.

There is a layer between 5 and 15 m, with 70–80% covering, and the most important species are *Alexa imperatricis* (R. H. Schomb.) Baill. and *Pentaclethra macroloba* (Willd.) Kuntze.; another relevant species are *Mabea piriri* Aubl., *Inga punctata* Willd., *Protium decandrum* (Aubl.) Marchand, *Duguetia pycnastera* Sandwith, and *Carapa guianensis* Aubl. (Table I).

We call understory to the inferior layer (< 5 m), has a 60–70% cover, and is dominated by herbs, shrubs, little palms, and climbers. The main species are *Faramea torquata* Müll. Arg., *Bactris maraja* Mart.,

Table I. Enlarged Importance Index (EII%) for the main species in all the plots (lf1, lf2, lf3).

LP	Species	lf1	lf2	lf3	Average
Sup	<i>Alexa imperatricis</i> (R. H. Schomb.) Baill.	16.96	16.28	17.00	16.75
Sup	<i>Pentaclethra macroloba</i> (Willd.) Kuntze.	15.46	12.72	13.12	13.77
Sup	<i>Mabea piriri</i> Aubl.	2.36	2.91	4.46	3.24
Sup	<i>Inga punctata</i> Willd.	4.14	2.62	1.97	2.91
Sup	<i>Protium decandrum</i> (Aubl.) Marchand	1.68	2.64	3.54	2.62
Sup	<i>Duguetia pycnastera</i> Sandwith	1.97	1.90	3.08	2.32
Sup	<i>Carapa guianensis</i> Aubl.	1.42	2.18	2.95	2.18
Und	<i>Faramea torquata</i> Müll. Arg.	0.68	1.33	1.22	1.08
Und	<i>Bactris maraja</i> Mart.	0.85	1.03	1.00	0.96
Und	<i>Rinorea</i> cfr. <i>riana</i> Kuntze	1.47	0.37	0.00	0.61
Und	<i>Ischmosiphon arouma</i> (Aubl.) Körn.	0.32	0.57	0.51	0.47
Cli	<i>Cheiloclinium hippocrateoides</i> (Peyr.) A.C. Sm.	1.89	1.60	1.12	1.54
Cli	<i>Bauhinia scala-simiae</i> Sandw.	1.18	1.02	0.94	1.04
Cli	<i>Bignonia sordida</i> (Bureau & K. Schum.) L.G. Lohmann	0.97	0.66	0.47	0.70
Cli	<i>Stizophyllum riparium</i> (Kunth) Sandw.	0.74	0.63	0.45	0.61

Abbreviations: LP, layer position (Sup: superior layer, big trees and palms; Und: exclusive for understory; Cli: climbers).



Figure 1. Liana forest appearance.

Rinorea cfr. *riana* Kuntze, *Ischmosiphon arouma* (Aubl.) Körn., *Geonoma deversa* (Poit.) Kunth, *Calathea* sp., *Dimerocostus strobilaceus* Kuntze, *Miconia* sp., and *Adiantum petiolatum* Desv.

There are 32 climber species, and the most notable are *Cheilochlinium hippocrateoides* (Peyr.) A.C. Sm., *Bauhinia scala-simiae* Sandw., *Bignonia sordida* (Bureau & K. Schum.) L.G. Lohmann, *Stizophyllum riparium* (Kunth) Sandw., *Machaerium quinatum* (Aubl.) Sandw., *Bignonia corymbosa* (Vent.) L.G. Lohmann, *Rourea frutescens* Aubl., *Forsteronia* cfr. *gracilis* Müll. Arg., *Mucuna urens* (L.) Medik., and *Uncaria guianensis* (Aubl.) J. F. Gmel. All climbers are very gnarled, and they constitute good part of the understory covering. For this reason, these communities have been denominated as LF (Figure 1).

Structural and floristic results for all the plots and all the species are showed in *electronic supplementary material*. We found a total of 161 species, but in 1 ha plots, the species-area curves do not become asymptote with the x -axis (Figure 2). However, 1 ha plots was estimated right for the purpose of this research.

Density oscillates between 524 and 579 ind ha⁻¹, the basal area oscillates between 19.6 and 21.8 m² ha⁻¹, and the biomass oscillates between 191 and 217 ton ha⁻¹ (Table II). The diametric structure for all the species (Figure 3(a)) shows a truncated pyramid-shaped distribution, typical of tropical

Table II. Summary of structural characteristics.

Plots	Abundance (trees ha ⁻¹)	Dominance (m ² ha ⁻¹)	Biomass (ton ha ⁻¹)
lf1	579	21.77	216.86
lf2	524	19.87	198.25
lf3	570	19.66	190.79
Average	558	20.43	201.97
Hillside forests ^a	503	24.9	269.8

^a Data from Lozada et al. (2007) in other plots of the IFR.

forest ecosystems. But, practically there are not individuals bigger to 50 cm dbh, which is also observed in the structure (Figure 3(b)) of the most important species (*A. imperatricis*). Obviously, they are vigorous populations, with a wide base and dynamic development without difficulties for the regeneration.

Soil characteristics

In general, the soil texture is dominated by clays, but due to the high rain and the physiography, there is an intense vertical washing that increase clay particles toward the deepest horizons (Table III). The same washing process, acting during millions of years (typical of the Guayana Shield), has originated diminishing of exchangeable bases (K, Na, Ca, and Mg), increase of exchangeable acid cations (Al, H), and iron (Fe); therefore, the pH is extremely acidic (<4.5). The contents of phosphorus (P), nitrogen (N), and organic matter (OM) in general are low. All these characteristics give this soil a very low quality, and it can be identified as oligotrophic ecosystem.

Lianas significance

An analysis about the lianas importance was carried out, and these data were contrasted with 30 surrounding plots in logged and old-growth forests at the central area of the IFR (Figure 4(a), (b)). Logged forests were selectively harvested, and post-disturbance time varies between 3 and 18 years. Total

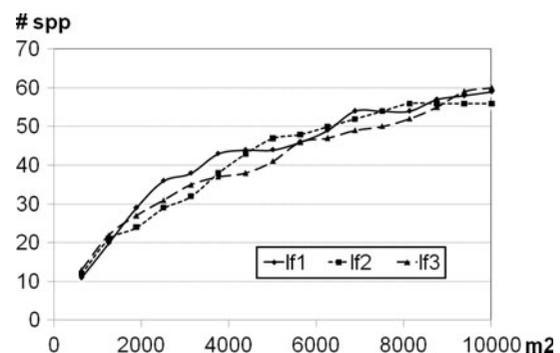


Figure 2. Species-area curves.

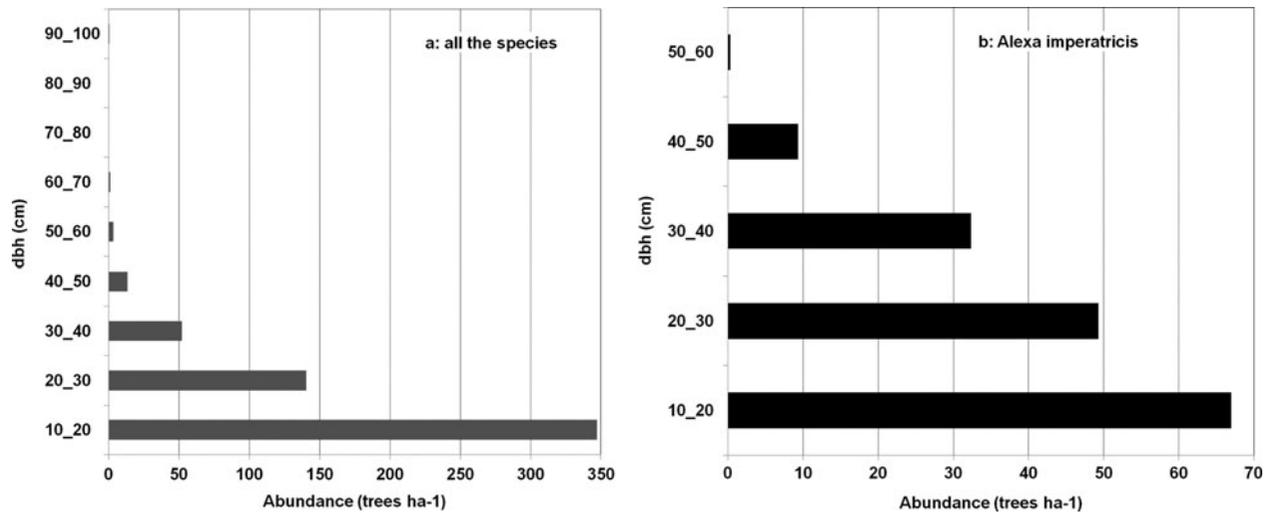


Figure 3. Diametric structure for all the liana forest plots.

importance (EII%) of all the liana species does not have a defined correlation neither with the age after logging nor with logging intensity (measured as the number of found cut stumps). In this analysis, not-logged forests appear with zero years or zero cut stumps and includes LF because they are located in a biological reserve.

The relationship between the lianas basal area (individuals ≥ 10 cm dbh) and the logging level was analyzed (Figure 4(c)). LFs are those that have smaller lianas dominance and, again, there is no connection between lianas presence and logging intensity. Some not-logged forests exhibit higher lianas basal area than plots in high logging intensity (six to nine cut stumps).

Another analysis in all the understory subplots was carried out using the lianas abundance and a posteriori analysis by means of the Scheffé test (Table IV). Although a high variability exists, the LF has the highest averages, and it is significantly different to all the other plots. Ecologically, 20% seems to be an appropriate level (in the abundance% of all the climbers, among all the individuals < 10 cm dbh) to differ the LF. It is observed that this value overcomes thoroughly to the value of 14%, and all the other plots are below this value. The sector

lgf18 has the second higher average of climbers, bigger to 20%, and indeed has the typical physiognomy of a LF (although with many tall trees). But it should be remembered again that this it is not the most impacted place and another sector (lgf6) has more cut stumps and fewer lianas presence.

Discussion

Liana forest description

The size of the plot (1 ha) is considered guessed right because in that surface there is not a significant amplification of the floristic richness because an increase in 10% of the study area generates an increment lower to 10% in the species number (approach of Cain 1938, mentioned by Müller-Dombois & Ellenberg 1974).

In the LF, the dominance and biomass are lower than the surrounding plots measured by Lozada et al. (2007), which indicate that LFs have smaller development than other communities located in the same physiographic position.

The data confirm that, from the floristic point of view, these plots belong to the *Alexa imperatricis* Facies inside the *Carapo guianensis-Pentaclethrum*

Table III. Soil characteristics.

Plot	sld	C	Sl	Sn	pH	P	TN	OC	OM	K	Na	Ca	Mg	Al	H	Ca/Al	Fe
smf ^a	—	35.1	11.9	53.1	3.6	7	0.1	1.3	2.2	0.05	0.10	0.22	0.19	0.68	0.73	0.3	498
hmf ^a	—	40.9	22.3	36.8	4.1	6	0.1	1.2	2.1	0.08	0.32	0.29	0.17	0.93	0.25	0.3	125
lf _a	0_10	26.4	7.2	66.4	3.5	11	0.2	2.1	3.7	0.12	0.09	0.52	0.45	0.66	0.40	0.8	370
lf _b	10_80	46.4	11.2	42.4	3.9	8	0.1	1.3	2.2	0.04	0.10	0.20	0.13	0.60	0.40	0.3	130
lf _c	80_180	56.4	9.2	34.4	4.4	0	0.0	0.4	0.6	0.03	0.07	1.01	0.14	0.48	0.40	2.1	45

^a Data from Lozada et al. (2014) in other hillside plots of the IFR. lf_a, lf_b, lf_c: soil layers in the liana forest trial pit. *Abbreviations and units*: sld (soil layer deep, cm); C (clay,%); Sl (silt,%); Sn (sand,%); P (phosphorus, ppm); TN (total nitrogen,%); OC (organic carbon,%); OM (organic matter,%); K (potassium); Na (sodium); Ca (calcium); Mg (magnesium); Al (exchangeable aluminum); H (exchangeable hydrogen); K, Na, Ca, Mg, Al, and H (Cmol kg⁻¹); Ca/Al (calcium/aluminum ratio); Fe (iron, ppm).

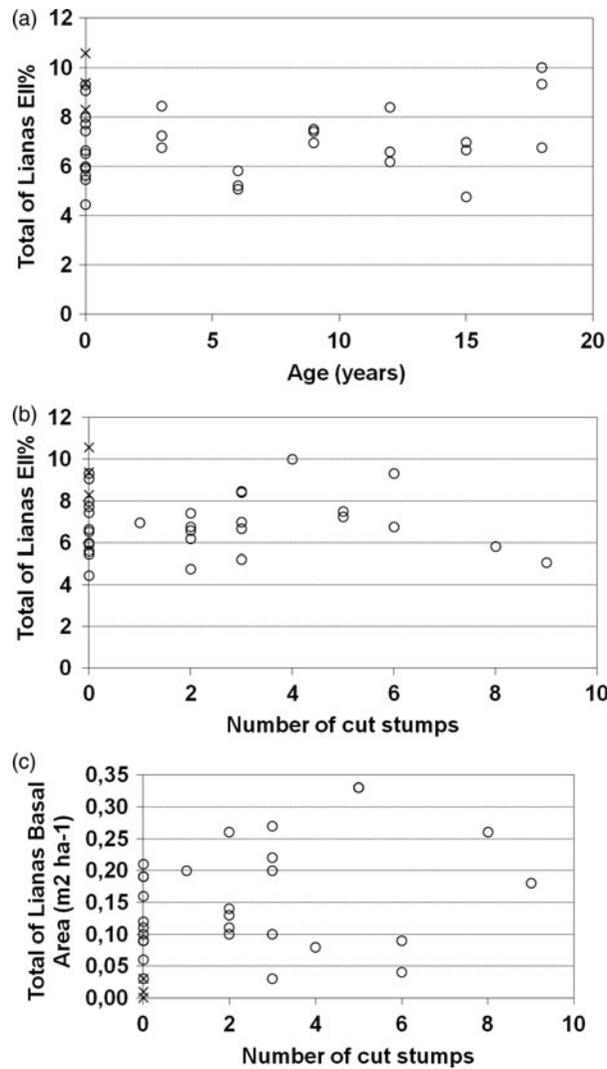


Figure 4. Lianas presence in liana forests (“X” points) and other old-growth and logged forests evaluated by Lozada (2008) (“O” points). A. Lianas importance vs age after logging. B. Lianas importance vs logging level. C. Lianas basal area vs logging level.

macroblobae Association that typify the central region of the IFR (Lozada et al. 2011).

The Uhl-Murphy Index is 2.65, confirming that these communities are very dominated by thin individuals (Uhl & Murphy 1981). The percentage of individuals bigger than 70 cm dbh is 0.06%, which is noticeably lower than the value of 1–2%, usually found in “terra firme” forests (Zent & Zent 2004). The main species *A. imperatricis* is a medium tree, can reach about 70 cm dbh, but others species of the same physiographic position grow over 100 cm dbh (Lozada et al. 2007).

These ecosystems are located in the tops and sides of the small topographical elevations of the study area. The climbers are very common, and they can have big woody individuals (> 10 cm dbh), associated with the highest and stout trees in the canopy. In some cases, lianas regeneration is

abundant and many of them have remarkable importance index values (Lozada et al. 2007).

Concerning LF definition, it is considered that Hernández (1997) makes a trustworthy description of this ecosystem:

... a forest community with small basal area, with a low canopy, very irregular and densely covered by an almost continuous mantel of climbers, most of them woody: lianas. The still standing trees are distanced of others in such a way that they don't make a closed canopy. A great quantity of the bigger trees has broken crowns ... the inferior stratum blends with the understory ... the liana forest ... offers a chaotic aspect ...

To these concepts, we have to add that lianas abundance (individuals < 10 cm dbh) should be higher than 20% to designate an ecosystem as LF. Therefore, the definition of an LF is not linked to climbers dominance (basal area). In a “standard” forest, lianas can exist as some few thick individuals, perhaps long-lived and contemporary with the trees where they lean on. Under this point of view, a very strong intervention harms the lianas dominance because it eliminates their thicker individuals. Later paragraphs expose some examples about these arguments.

“Liana tangles” have been reported in many ecosystems (Balée & Campbell 1990; Oliveira-Filho et al. 1997; Kennard 1998; Gerwing 2001; Vieira & Scariot 2006; Garrido-Pérez & Gerold 2009). Liana tangles start in a treefall that pulls down adult lianas. These individuals sprout new stems which compete with another derived from seed regeneration. If a liana do not find a trellis it shows rapid lateral growth rather than vertical growth, contributing to the liana tangle (Putz 1984b; Schnitzer et al. 2000).

Environmental and successional features

Soil does not have outstanding differences with the soils of other hill plots. Our results are similar to those obtained by Franco (1988), Lugo (2006), Schargel and Marvaez (2009) in another lowland sites of the Guayana Shield. These oligotrophic ecosystems have some constrains to plant development, but they have adaptations that allow their existence and majority of these forests are high, dense, and diverse. So, there are not particular edaphic restrictions that impede the development of the vegetation in LF; in any case, lianas density is unrelated to soil fertility or to other soil gradients (Van Der Heijden & Phillips 2008). As it has been established by Lozada et al. (2014), it should not have environmental limitations for the development of trees to great height. In fact, LF has emergent

Table IV. "A posteriori" analysis (Scheffé test; $P < 0.1$), for the lianas abundance% in logged and old-growth understory plots.

	vf2	smf	lf	hmf	lgf12	lgf15	lgf18	lgf3	lgf6	lgf9	vf1
vf2	–	0.95	0.00	1.00	0.98	1.00	0.00	0.99	1.00	0.99	0.94
smf	–	–	0.15	0.97	1.00	0.93	0.33	1.00	0.80	1.00	0.11
lf	–	–	–	0.00	0.08	0.00	1.00	0.07	0.00	0.07	0.00
hmf	–	–	–	–	0.99	1.00	0.00	1.00	1.00	1.00	0.89
lgf12	–	–	–	–	–	0.98	0.20	1.00	0.90	1.00	0.19
lgf15	–	–	–	–	–	–	0.00	0.98	1.00	0.98	0.95
lgf18	–	–	–	–	–	–	–	0.17	0.00	0.18	0.00
lgf3	–	–	–	–	–	–	–	–	0.93	1.00	0.22
lgf6	–	–	–	–	–	–	–	–	–	0.92	0.99
lgf9	–	–	–	–	–	–	–	–	–	–	0.21
vf1	–	–	–	–	–	–	–	–	–	–	–

Homogeneous groups. Average of lianas abundance%.

vf1	4.74		
lgf6	8.12		
lgf15	8.96		
vf2	9.20		
hmf	9.58		
lgf3	12.68	12.68	
lgf9	12.73	12.73	
lgf12	12.86	12.86	
smf	13.53	13.53	13.53
lgf18		20.92	20.92
lf			21.89

vf1 and vf2: valley forests; smf: summit medium forest; lf: liana forest; hmf: hillside medium forest; lgf3, lgf6, lgf9, lgf12, lgf15, and lgf18: respectively 3, 6, 9, 12, 15, and 18 years old logged forests. Bold values indicate significant differences.

individuals, and we understand them as relict from the old-growth forest. So, the current low canopy (15 m) should be the expression from a successional stage later to any interference. Next evaluations will indicate the rate of growth of the biomass of this community and will allow obtain conclusions more guessed right on its successional stage.

With regard to diversity, we got average values of 2.6 in H' , 58 spp ha⁻¹ and 16.4 in α (Table V). It is considered that these values are low, when comparing them with other plots in the same sector and physiographic position (Lozada et al. 2007). These results confirm the theories that point out the existence of low diversity in the early stages of a forest succession, originated by a strong disturbance (Odum 1972; Lamprecht 1990; Finegan 1997; Guariguata & Ostertag 2001; Terradas 2001).

Table V. Summary of diversity results.

Plots	H'	α	Richness
lf1	2.4	16.4	59
lf2	2.7	15.9	56
lf3	2.7	16.9	60
Average	2.6	16.4	58
Hillside forests ^a	3.1	22.8	71

H' : Index of Shannon-Wiener; α : Fisher's Alpha. ^aData from Lozada et al. (2007) in other plots of the Imataca Forest Reserve.

Another aspect to stand out is the dominance of *Alexa imperatricis*. In these plots, this species has an average of 16.8 in EII% (Table I). But in other hill forests, where it is also the most important species, it reaches an average of 9.1 in EII% (Lozada et al. 2007). It is interpreted that this is a late secondary species, is able to take advantage of the small gaps, frequent in the forest due to windthrows and also other possible strong disturbances.

Liana forest origin

One of the main results of this research is that it can have as many lianas in not-logged forests as in those logged. This is opposite to findings of Schnitzer et al. (2000), Schnitzer et al. (2004), Kouamé et al. (2004), and Ding and Zang (2009). But, Hernández (1992) found similar results to ours in the Caparo Forest Reserve (Venezuela). In fact, our LFs are in a biological reserve without logging use. Mascaró et al. (2004) ascertain that light logging can be the cause of the lack of differences in liana presence between old growth and selectively logged forests. Van Der Heijden & Phillips (2008) established that when lianas reach the canopy they expand in diameter and invest in leaves and reproductive organs; to do that they need suitable hosts, but, many secondary species have structural characteristics that avoid

liana infestation; so, lianas basal area is highest in undisturbed forests.

Another element to stand out is that, the communities with less lianas presence (vf1 and lgf6; Table IV) are dominated by *Mora excelsa* (Lozada et al. 2011), a species that seems to gather the set of characteristics that keep away from the attack of climbers (Putz 1984a; Balfour & Bond 1993; Van Der Heijden et al. 2008): high rate of diametrical growth, flexible young shafts, big leaves, trunks free of big branches, flat bark, and great height mature individuals.

In summary, we can neither qualify the logging nor edaphic restrictions as causes of LF origin. Therefore, why does the LF exist? There are no current evidence, but it is believed that our LF is linked to some type of a hard perturbation that destroyed most of the original canopy. Then, there is a possibility that LF happens after an alteration by hurricane winds.

Some natives, workers, and helicopter pilots have mentioned the occurrence of strong winds that result in desolated areas in the IFR. Fortunately some credited references support these popular beliefs. Webb (1958) indicates that high velocity wind produces "... cyclone scrubs. Because of extensive windthrows, these have a low uneven canopy with scattered emergents densely draped by vines ...". This description seems to be analogous to that observed in the present investigation. The work of Rollet (1971), in the IFR, designates the hurricanes as the cause of the LF and suggests that this appearance "can be perpetuated during several years"; this author mentions numerous studies that have reported this phenomenon in Suriname, Guyana, Brazil, Nigeria, Congo, and Malaysia. Likewise, Allen et al. (2005) found that lianas density increased more than 50% in the forests affected by the Hurricane Hugo in 1989, in the south-east of United States. The LFs in the basin of the Caura River, seen during an overflight by plane, have an oval shape, similar to the forest areas affected by strong windthrows (personal communication Lionel Hernández). However, it is appreciated that hurricanes are more frequent in the Caribbean and other coastal areas. There are not many references of the effects of strong winds in "inland" places as the IFR. Therefore, it is considered that this aspect justifies detailed investigations in the future, mainly in the meteorological characterization of the phenomenon, their localization, and frequency.

Concluding remarks

We can conclude that, in our study site, logging is not the cause of lianas increase. The current area occupied by LF very probably suffered a hurricane

wind that knocked down most of the canopy trees (but some of them are still standing and they are considered emergent), the thick individuals of climbers also disappeared (which generates a minimum basal area for this species), and the current successional stage favors a recovery dominated with thin individuals belonging to this way of life.

Acknowledgments

Special thanks to the management personnel, technician, and workers of Aserradero Hermanos Hernández for their valuable assistance during the development of the fieldwork.

Funding

This work was supported by the International Tropical Timber Organization-ITTO under [grant number 094/04S].

Supplemental data

Supplemental data for this article can be accessed at doi: [10.1080/11263504.2015.1008598](https://doi.org/10.1080/11263504.2015.1008598).

References

- Allen B, Sharitz R, Goebel P. 2005. Twelve years post-hurricane liana dynamics in an old-growth southeastern floodplain forest. *Forest Ecol Manage* 218(1–3): 259–269. doi: [10.1016/j.foreco.2005.08.021](https://doi.org/10.1016/j.foreco.2005.08.021).
- Anbarashan M, Parthasarathy N. 2013. Diversity and ecology of lianas in tropical dry evergreen forests on the Coromandel Coast of India under various disturbance regimes. *Flora Morphol Distrib Funct Ecol Plants* 208(1): 22–32. doi: [10.1016/j.flora.2012.12.004](https://doi.org/10.1016/j.flora.2012.12.004).
- Balée W, Campbell G. 1990. Evidence for the successional status of liana forest (Xingu River basin, Amazonian Brazil). *Biotropica* 22: 36–47.
- Balfour D, Bond W. 1993. Factors limiting climber distribution and abundance in a southern African Forest. *J Ecol* 81(1): 93–99. doi: [10.2307/2261227](https://doi.org/10.2307/2261227).
- Brown S, Gillespie A, Lugo A. 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Sci* 35: 881–902.
- Curtis J, McIntosh R. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32(3): 476–496. doi: [10.2307/1931725](https://doi.org/10.2307/1931725).
- DeWalt S, Schnitzer S, Denslow J. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *J Trop Ecol* 16(1): 1–19. doi: [10.1017/S0266467400001231](https://doi.org/10.1017/S0266467400001231).
- Ding Y, Zang R. 2009. Effects of logging on the diversity of lianas in a lowland tropical rain forest in Hainan Island, South China. *Biotropica* 41(5): 618–624. doi: [10.1111/j.1744-7429.2009.00515.x](https://doi.org/10.1111/j.1744-7429.2009.00515.x).
- Ewel J, Madriz A, Tosi J. 1976. Zonas de Vida de Venezuela. Caracas: Ministerio de Agricultura y Cría, Fondo Nacional de Investigaciones Agropecuarias.
- Finegan B. 1997. Bases ecológicas para el manejo de bosques secundarios de las zonas húmedas del trópico americano,

- recuperación de la biodiversidad y producción sostenible de la madera. Taller Internacional sobre el Manejo y Desarrollo del Bosque Secundario Tropical en América Latina, 2–6 Junio 1997, Pucallpa, Perú.
- Franco W. 1988. Los suelos del Lote Boscoso San Pedro y Reservas Forestales Imataca, Guarapiche y Ticoporo. Facultad de Cs. Forestales. Mérida: Universidad de Los Andes.
- Garrido-Pérez EI, Gerold G. 2009. Land-use history and the origins and effects of lianas on tree-communities. The case of secondary forests in Northeastern Yucatan Peninsula, Mexico. *Erdkunde* 63(3): 211–227. doi: [10.3112/erdkunde.2009.03.01](https://doi.org/10.3112/erdkunde.2009.03.01).
- Gerwing J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. *J Appl Ecol* 38(6): 1264–1276. doi: [10.1046/j.0021-8901.2001.00677.x](https://doi.org/10.1046/j.0021-8901.2001.00677.x).
- Gerwing J, Vidal E. 2002. Changes in liana abundance and species diversity eight years after liana cutting and logging in an eastern Amazonian forest. *Conserv Biol* 16(2): 544–548. doi: [10.1046/j.1523-1739.2002.00521.x](https://doi.org/10.1046/j.1523-1739.2002.00521.x).
- Granados J, Korner C. 2002. In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biol* 8(11): 1109–1117. doi: [10.1046/j.1365-2486.2002.00533.x](https://doi.org/10.1046/j.1365-2486.2002.00533.x).
- Guariguata M, Dupuy M. 1997. Forest regeneration in abandoned logging roads in lowland Costa Rica. *Biotropica* 29(1): 15–28. doi: [10.1111/j.1744-7429.1997.tb00002.x](https://doi.org/10.1111/j.1744-7429.1997.tb00002.x).
- Guariguata M, Ostertag R. 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecol Manage* 148(1–3): 185–206. doi: [10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1).
- Hernández C. 1992. Incidencia de lianas en parcelas con diferentes límites diamétricos de explotación en un sector de la Unidad I de la Reserva Forestal Caparo. MSc thesis. Universidad de Los Andes, Mérida.
- Hernández L. 1997. La selva de bejucos, ejemplo de bosque natural inestable de la Guayana Venezolana: Avance de investigación. *Revista Científica Unet* 9(2): 16–20.
- Huber O, Foster M. 2003. Prioridades de conservación para el Escudo de Guayana. Consenso 2002. Washington, DC: Conservation International, Center for Applied Biodiversity Science.
- Jacinto Tabanez A, Viana V. 2000. Patch structure within Brazilian Atlantic forest fragments and implications for conservation I. *Biotropica* 32(4): 925–933 Sp Iss SI 2000. doi: [10.1646/0006-3606\(2000\)032\[0925:PSWBAF\]2.0.CO;2](https://doi.org/10.1646/0006-3606(2000)032[0925:PSWBAF]2.0.CO;2).
- Keefe K, Schulze M, Pinheiro C, Zweede J, Zarin D. 2009. Enrichment planting as a silvicultural option in the eastern Amazon: Case study of Fazenda Cauaxi. *Forest Ecol Manage* 258(9): 1950–1959. doi: [10.1016/j.foreco.2009.07.037](https://doi.org/10.1016/j.foreco.2009.07.037).
- Kennard D. 1998. Biomechanical properties of tree saplings and free-standing lianas as indicators of susceptibility to logging damage. *Forest Ecol Manage* 102(2-3): 179–191. doi: [10.1016/S0378-1127\(97\)00159-X](https://doi.org/10.1016/S0378-1127(97)00159-X).
- Klute A, editor. 1986. Methods of soil analysis. Part 1. Physical and mineralogical methods Madison, WI: American Society of Agronomy and Soil Science Society of America.
- Kouamé F, Bongers F, Poorter L, Traoré D. 2004. Climbers and logging in the Forêt Classée du Haut-Sassandra, Côte-d'Ivoire. *Forest Ecol Manage* 194: 259–268.
- Lamprecht H. 1990. Silvicultura en los trópicos. Eschborn: Agencia de Cooperación Técnica Alemana (GTZ).
- Laurance W, Laurance S, Ferreira L, Rankin-de Merona J, Gascon C, Lovejoy T. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278(5340): 1117–1118. doi: [10.1126/science.278.5340.1117](https://doi.org/10.1126/science.278.5340.1117).
- Laurance W, Pérez-salicrup D, Delamo'nica P, Fearnside P, D'Angelo S, Jerozolinski A, et al. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82(1): 105–116. doi: [10.1890/0012-9658\(2001\)082\[0105:RFFATS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0105:RFFATS]2.0.CO;2).
- Leicht-Young S, Latimer A, Silander J. 2011. Lianas escape self-thinning: experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. *Perspect Plant Ecol Evol Syst* 13(3): 163–172. doi: [10.1016/j.ppees.2011.04.002](https://doi.org/10.1016/j.ppees.2011.04.002).
- Lozada J. 2008. Sucesión vegetal en bosques aprovechados de la Reserva Forestal Caparo y Reserva Forestal Imataca, Venezuela. PhD thesis. Universidad de Valencia, Valencia.
- Lozada J, Guevara J, Soriano P, Costa M. 2007. Bosques de colinas y lomas, en la zona central de la Reserva Forestal Imataca, Venezuela. *Rev Forest Latinoam* 22(2): 105–131.
- Lozada J, Guevara J, Soriano P, Costa M. 2011. The organismic and the continuous approaches applied to phytosociological relationships in a lowland neotropical forest, Venezuela. *Plant Biosyst* 145(Suppl 1): 65–73. doi: [10.1080/11263504.2011.602735](https://doi.org/10.1080/11263504.2011.602735).
- Lozada J, Soriano P, Costa M. 2014. Relaciones suelo-vegetación en una toposecuencia del Escudo Guayanés, Venezuela. *Rev Biol Trop (Int J Trop Biol)* 62(1): 385–401.
- Lugo L. 2006. La fisiografía, los suelos, la vegetación y su relación con el sistema de agricultura migratoria, en el Sector Norte de la Reserva Forestal Sipapo, Estado Amazonas, Venezuela. PhD thesis. Universidad de Valencia, Valencia.
- Magurran A. 1988. Ecological diversity and its measurement. London: Croom and Helm.
- MARN-UCV. 2003. Bases Técnicas para el Ordenamiento Territorial de la Reserva Forestal Imataca. Caracas: Ministerio del Ambiente y de los Recursos Naturales, Universidad Central de Venezuela.
- Mascaro J, Schnitzer S, Carson W. 2004. Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica. *Forest Ecol Manage* 190(1): 3–14. doi: [10.1016/j.foreco.2003.10.002](https://doi.org/10.1016/j.foreco.2003.10.002).
- Muller-Dombois D, Ellenberg H. 1974. Aims and methods of vegetation ecology. New York, NY: John Wiley & Sons, Inc.
- Neil P. 1984. Climber problems in Solomon Islands forestry. *Commonwealth Forest Rev* 63(1): 27–34.
- Odum E. 1972. Ecología. México: Interamericana.
- Oliveira-Filho A, Márcio de Mello J, Scolforo J. 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). *Vegetatio* 131(1): 45–66. doi: [10.1023/A:1009744207641](https://doi.org/10.1023/A:1009744207641).
- Pérez-Salicrup D, Sork V, Putz F. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33(1): 34–47.
- Phillips OL, Vásquez Martínez R, Arroyo L, Baker TR, Killeen T, Lewis SL, et al. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418(6899): 770–774. doi: [10.1038/nature00926](https://doi.org/10.1038/nature00926).
- Putz F. 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro basin, Venezuela. *Biotropica* 15(3): 185–189. doi: [10.2307/2387827](https://doi.org/10.2307/2387827).
- Putz F. 1984a. How trees avoid and shed lianas. *Biotropica* 16(1): 19–23. doi: [10.2307/2387889](https://doi.org/10.2307/2387889).
- Putz F. 1984b. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6): 1713–1724. doi: [10.2307/1937767](https://doi.org/10.2307/1937767).
- Putz F. 1985. Woody vines and forest management in Malaysia. *Commonwealth Forest Rev* 64: 359–365.
- Putz F, Mooney H. 1991. The biology of vines. Cambridge, UK: Cambridge University Press.
- Restom T, Nepstad D. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecol Manage* 190(1): 109–118. doi: [10.1016/j.foreco.2003.10.010](https://doi.org/10.1016/j.foreco.2003.10.010).

- Rice K, Brokaw N, Thompson J. 2004. Liana abundance in a Puerto Rican forest. *Forest Ecol Manage* 190(1): 33–41. doi: [10.1016/j.foreco.2003.10.004](https://doi.org/10.1016/j.foreco.2003.10.004).
- Rollet B. 1971. La regeneración natural en un bosque denso siempreverde de llanura de la Guayana Venezolana. *Boletín del Instituto Forestal Latinoamericano* 35: 39–73.
- Schargel R, Marvaez P. 2009. Estudio de los suelos y la vegetación (estructura, composición florística y diversidad) en bosques macrotérmicos no-inundables, Estado Amazonas, Venezuela. *Biollania* 9: 99–109.
- Schnitzer S. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *Am Nat* 166(2): 262–276. doi: [10.1086/431250](https://doi.org/10.1086/431250).
- Schnitzer S, Dalling J, Carson W. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *J Ecol* 88(4): 655–666. doi: [10.1046/j.1365-2745.2000.00489.x](https://doi.org/10.1046/j.1365-2745.2000.00489.x).
- Schnitzer S, Parren M, Bongers F. 2004. Recruitment of lianas into logging gaps and the effects of pre-harvest climber cutting in a lowland forest in Cameroon. *Forest Ecol Manage* 190(1): 87–98. doi: [10.1016/j.foreco.2003.10.008](https://doi.org/10.1016/j.foreco.2003.10.008).
- Schröder T, Fleig F, Spadetto V. 2013. Liana community ecology and interaction with *Parapiptadenia rigida* (Benth) Brenan in a fragment of secondary forest. *Forest Ecol Manage* 307: 84–89.
- Schwartz G, Lopes J, Mohren G, Peña-Claros M. 2013. Post-harvesting silvicultural treatments in logging gaps: A comparison between enrichment planting and tending of natural regeneration. *Forest Ecol Manage* 293: 57–64. doi: [10.1016/j.foreco.2012.12.040](https://doi.org/10.1016/j.foreco.2012.12.040).
- Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, et al., editors. 1996. *Methods of soil analysis. Part 3. Chemical methods*. Madison, WI: Soil Science Society of America & American Society of Agronomy.
- Ter Steege H, Pitman N, Sabatier D, Castellanos H, Van Der Hout P, Daly DC, et al. 2003. A spatial model of tree α -diversity and tree density for the Amazon. *Biodivers Conserv* 12(11): 2255–2277. doi: [10.1023/A:1024593414624](https://doi.org/10.1023/A:1024593414624).
- Terradas J. 2001. *Ecología de la Vegetación. De la ecofisiología de las plantas a la dinámica de comunidades y paisajes*. Barcelona: Omega.
- Uhl C, Murphy P. 1981. Composition, structure and regeneration of a Tierra Firme forest in the Amazon Basin of Venezuela. *Trop Ecol* 22: 219–237.
- Van Der Heijden G, Healey J, Phillips O. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. *J Veg Sci* 19(6): 747–756. doi: [10.3170/2008-8-18459](https://doi.org/10.3170/2008-8-18459).
- Van Der Heijden G, Phillips O. 2008. What controls liana success in Neotropical forests? *Global Ecol Biogeogr* 17(3): 372–383. doi: [10.1111/j.1466-8238.2007.00376.x](https://doi.org/10.1111/j.1466-8238.2007.00376.x).
- Vareschi V. 1992. *Ecología de la Vegetación Tropical*. Caracas: Sociedad Venezolana de Ciencias Naturales.
- Vieira D, Scariot A. 2006. Effects of logging, liana tangles and pasture on seed fate of dry forest tree species in Central Brazil. *Forest Ecol Manage* 230(1–3): 197–205. doi: [10.1016/j.foreco.2006.05.002](https://doi.org/10.1016/j.foreco.2006.05.002).
- Webb L. 1958. Cyclones as an ecological factor in tropical lowland rain-forest, North Queensland. *Aust J Bot* 6(3): 220–228. doi: [10.1071/BT9580220](https://doi.org/10.1071/BT9580220).
- Wright JP, Calderón O. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett* 9(2): 35–44.
- Wright S, Calderón O, Hernández A, Paton S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85(2): 484–489. doi: [10.1890/02-0757](https://doi.org/10.1890/02-0757).
- Zent E, Zent S. 2004. Floristic composition, structure, and diversity of four forest plots in the Sierra Maigualida, Venezuelan Guayana. *Biodivers Conserv* 13: 2453–2483. doi: [10.1023/B:BIOC.0000048447.40238.f2](https://doi.org/10.1023/B:BIOC.0000048447.40238.f2).
- Zotz G, Cueni N, Körner C. 2006. *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO₂. *Funct Ecol* 20(5): 763–769. doi: [10.1111/j.1365-2435.2006.01156.x](https://doi.org/10.1111/j.1365-2435.2006.01156.x).