2012-11-21

Freestanding and Support-seeker Liana Seedlings: Spatial Distribution, Life History and Physiological Traits in Tropical Forests of Central Panama.

Eric J. Manzané Pinzón
University of Miami, bioerman@gmail.com

Recommended Citation

Manzané Pinzón, Eric J., "Freestanding and Support-seeker Liana Seedlings: Spatial Distribution, Life History and Physiological Traits in Tropical Forests of Central Panama." (2012). *Open Access Dissertations*. 878.
https://scholarlyrepository.miami.edu/oa_dissertations/878

UNIVERSITY OF MIAMI

FREESTANDING AND SUPPORT-SEEKER LIANA SEEDLINGS: SPATIAL DISTRIBUTION, LIFE HISTORY AND PHYSIOLOGICAL TRAITS IN TROPICAL FORESTS OF CENTRAL PANAMA.

By

Eric J. Manzané Pinzón

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

December 2012

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

FREESTANDING AND SUPPORT-SEEKER LIANA SEEDLINGS: SPATIAL DISTRIBUTION, LIFE HISTORY AND PHYSIOLOGICAL TRAITS IN TROPICAL FORESTS OF CENTRAL PANAMA

Eric J. Manzané Pinzón

Approved:

Guillermo Goldstein, Ph.D. Professor of Biology	M. Brian Blake, Ph.D. Dean of the Graduate School
Carol Horvitz, Ph.D. Professor of Biology	David P. Janos, Ph.D. Professor of Biology
Stefan Schnitzer, Ph.D. Professor of Biology University of Wisconsin-Milwaukee	

MANZANE PINZON, ERIC (Ph.D., Biology)

Freestanding and Support-seeker Liana Seedlings: Spatial Distribution, Life History and Physiological Traits in Tropical Forests of Central Panama. (December 2012)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Guillermo Goldstein.
No. of pages in text. (108)

Lianas is a term that identifies vines that produce secondary wood tissue and whose distribution is mostly restricted to the tropics. They usually start their lifecycle as seedlings in the forest understory an after a period of time they climb to the canopy forest supported by the surrounding vegetation. The seedling itself is an important stage on the plant's life cycle; in this stage plants are susceptible to high mortality rates due to biotic or abiotic factors, such as predation, diseases, drought or flooding. Depending on the survival at this stage, they can extend their habitat range and colonize new environments, but failure to do so can decrease their natural habitat range. Liana seedlings can be classified in two separated functional groups: freestanding seedlings: the ones that can grow without a mechanical support and can remain as small woody plants for a relatively long period of time and support-seekers seedlings: the seedlings that reach for a host to climb on earlier in their life cycle. Until now little is known about the ecological or the physiological differences or similitudes between this two different functional groups. My main objective in this work was to evaluate the distribution and density of liana seedlings in general and of this two functional groups, first at regional scale using a series of plots across a rainfall gradients and different types of soil, then evaluate the population trends of liana seedlings at local scale using a series of datasets from the 50 hectare plot located

in Barro Colorado Island in the Gatun Lake of the Panama Canal. The data sets consist on a series of seedling censuses from 2001 to 2004, soil data for all the 50 hectare and canopy forest census for the same period of time. Finally I have studied the physiology and life history traits of each group, comparing traits such as relative growth rates, stem diameter, leaf area and leaf mass per area, hydraulic architecture, and photosynthetic rates in plants with similar age.

At regional scale liana seedlings were more abundant in sites that have limestone soil, independently of the rainfall pattern. But laterite soil sites in contrast had higher diversity of liana seedlings. Freestanding liana seedlings were more abundant in wet sites than in dry sites, while the support-seekers liana seedlings were more abundant in drier sites than in wet areas. On a smaller scale at the 50 hectare plot I observed that liana seedlings were increasing in population size together with shrub seedlings, meanwhile tree seedlings were decreasing in number. Out of the two liana seedling functional groups, freestanding and support-seekers, the support-seekers contribute more to this trend in liana population changes because they had a higher rate of yearly increase. Neither soil nutrients nor gap opening showed a strong effect over changes in population trends.

Experiments determining the differences in life history and physiological traits between the two functional groups, freestanding versus support-seekers liana seedlings using eight different species of liana, showed that although the groups do differ in traits such as leaf area, leaf mas per area, stem diameter, relative growth rate, specific and leaf specific hydraulic conductance, and electron transport rate, the freestanding seedlings seems to be en general more closely related in those characteristics, while the support-seekers, seems to have some characteristics in common between them and also some in common with freestanding seedlings

Overall these two groups of seedlings seems to have different distributions patterns at regional scale, different population patterns at local scale, but the physiological and life traits characteristics seems to overlap in some species. Perhaps we can view these groups as either two complete separate functional groups with some species more closely related to each other in terms of life history and physiological traits or as a gradient of characteristics in which each species is located in a different position along a continuum of life history and physiological characteristics.

Dedication

I would like to dedicate this dissertation to my family, who gave me unconditional support through all these years, and to my wife, daughter, and friends;

To my parents, Heliodoro and Denys, who taught me how hard work can overcome any obstacle in life;

To my sister, Thadany, who always told me that I can do it no matter what;

To my wife Lizenia, who believes and loves me and who unconditionally supported the jump into the void when I began work on this Ph.D.;

To my daughter, Valeria, who had to bear my absences but always waited for me with a smile and huge hug asking, “How are you, daddy?”

I would also like to dedicate this dissertation to the memory of my uncles, Pompilio and Misael.

Acknowledgements

First, I am grateful to my advisor Guillermo Goldstein for all his support, guidance, words of wisdom, and readiness to always signal the good results of my work which made this dissertation possible. Dave Janos was more a friend than just a committee member. Without him and the Mycorrhiza discussions I would never have learned so many valuable lessons about scientific writing and thinking. Carol Horvitz, a great teacher, made suggestions and comments that were key to improving this dissertation. Stefan Schnitzer helped me with a lot of questions regarding lianas biology in the field and also while writing the dissertation.

Without my wife Lizenia, I would never have made it here. She was always there to support me and to tell me not to quit, even though we had to endure long separations. I say the same of my daughter Valeria. When I started on this path you were my little one and now you are such a big girl. I thank my parents who were there to listen to me and help me when I needed it. My dad helped me set up greenhouses, get soil, and even collect data in the field. My sister Thadany was my first greenhouse assistant and endured all the heat and humidity while gathering data inside the small shade houses. I am grateful to all the Manzane and Pinzon families and of course my grandparents, Reyes, Irene and Juana, my mother-in-law Ana Vanegas, and all the Moreno family.

I thank my fellow biograd friends at UM: Ana Salazar, Floria Mora, Randol Villalobos, Hao, John C, John Z, Nathan Muchhala, Adrienne Dubois, David Matlaga, Tanya Matlaga, Robert McElderry, Andrea Westerband, Naveen Wijesena, Baghya

Janananda, and Joanna Weremijewicz, I especially thank Robert and Orou Gauoe for their invaluable help with the data analysis.

TABLE OF CONTENTS

Page

Chapter

LIST OF TABLES

LIST OF FIGURES

Chapter 1

Introduction

Background

Ecology and physiology of lianas

Lianas are defined as woody climbers that begin their life cycle as seedlings on the forest floor, but instead of developing their own support structures, they rely on external mechanical sources for support to grow and reach the forest canopy (Gentry, 1991; Gerwing, 2004; Putz, 1984; Schnitzer & Bongers, 2002). Lianas are a polyphyletic growth form present in nearly 60% of plant taxa (Alcantara & Lohmann, 2011; Gentry, 1991; Gianoli, 2004; Lohmann, 2006). The liana strategy arose independently in several different groups of plants and exhibits different characteristics depending upon the taxa and the habitat where they have evolved (Gentry, 1991; Putz, 1984; Schnitzer & Bongers, 2002).

Because lianas are so diverse and abundant in the tropical forest, they have been called the single most relevant feature of tropical forests (Clark & Clark, 1992; Gentry, 1991; Schnitzer & Bongers, 2002). Liana seedlings are very common in tropical forests, comprising as much as the 22% of vascular plants in the forest understory (Putz, 1984). Among the different tropical forests, lianas are more abundant in seasonally dry tropical forests than in wet forests (Schnitzer, 2005; Swaine & Grace, 2007). This pattern is related to resource allocation in lianas. Because lianas do not have to invest in support tissue, they can invest in long roots that can tap water from deep sources, thus they can maintain growth activities during the dry season (Andrade, Meinzer, Goldstein, & Schnitzer, 2004; Schnitzer, 2005; Schnitzer, Kuzee, & Bongers, 2005)

Lianas also are important players in forest gap regeneration and usually are abundant in forest gaps and edges (Putz, 1984; Schnitzer & Carson, 2000; DeWalt et al., 2000; Schnitzer & Carson, 2001). Liana seedlings growing in gaps usually have higher growth rates than tree seedlings, and in some cases liana seedlings can dominate forest gaps, thereby delaying the succession process (Dewalt, Schnitzer, & Denslow, 2000; Schnitzer & Carson, 2001). This pattern of distribution has led many biologists to the conclusion that lianas can be considered light-demanding plants, but some studies have shown that lianas also can grow well in shaded environments (Gilbert et al. 2006).

Liana stem xylem is characterized by having wide and long vessels, which may result in more efficient water transport over long distances than in any other vascular plant group (Ewers, 1985; Ewers & Fisher, 1989; Ewers, Fisher, & Chiu, 1989). Wide and long xylem conduits provide an advantage in water transport to from soil to leaves when compared to other growth forms (Ewers, 1985; Ewers et al., 1989; Gartner et al., 1990). Additionally, lianas have higher specific hydraulic conductivity than trees; and although they have thinner stems than trees, they can transport larger volumes of water (Chiu & Ewers, 1992; Gartner, 1991a) at similar stem cross sectional areas.

Freestanding and support-seeker liana seedlings

With the exceptions of vascular parasites, epiphytes and hemi-epiphytes, tropical plants usually start their life cycle as seedlings on the forest floor. The seedling stage is a critical part of the life cycle, because seedlings can be exposed to ecological constraints such as predation, density dependent mortality and pathogens (Augspurger, 1984; Harms, Wright, Calderón, Hernandéz, & Herre, 2000). But this also is the stage where successful establishment will lead to colonization of new areas (Garwood, 2009).

Most lianas start as freestanding seedlings until they reach a certain critical stage in their life cycle when they start to climb to the canopy by using trees or other lianas as hosts (Campanello, Garibaldi, Gatti, & Goldstein, 2007; Gerwing, 2004; Putz, 1984). In this study, I tested if freestanding liana seedlings maintain themselves upright without support for a relatively long period of time (Gallenmuller, Rowe, & Speck, 2005; Kennard, 1998) before they start searching for a mechanical support to climb into the canopy. In contrast, support-seeker liana seedlings require a suitable host soon after germination. This latter group of seedlings is defined as those plants that are entangled with the surrounding vegetation and are mechanically unstable without a support when they are very small (Gallenmuller et al., 2005).

Many physiological studies of seedlings have classified plants and seedlings as being light-demanding or shade-tolerant (Coley & Kursar, 1999; Swaine & Whitmore, 1988). Support-seeker liana seedlings usually are associated with forest gaps, where light is abundant. Freestanding liana seedlings instead are associated with the dark forest understory where light is a limited resource (Denslow, Ellison, & Sanford, 1998; Hubbell, 1999; Swaine & Whitmore, 1988; Whitmore, 1989). Although lianas have been traditionally described as light demanding plants that thrive in gaps (Dewalt et al., 2000; Schnitzer & Carson, 2001) some species can thrive in the understory (Granados & Körner, 2002, Gilbert et al. 2006).

In this study, I predicted that freestanding liana seedlings with low grow rates will be more common in the forest understory and will invest relatively more biomass in leaves and stems than support-seeker liana seedlings. Most of the trees in the understory habitat are adults with relatively large stem diameters that may inhibit the rate of colonization and growth of liana seedlings. But the freestanding seedlings and saplings overcome this limitation by growing slowly as a small shrub until they encounter a suitable host.

The support-seeker seedlings, on the other hand, are expected to be common in forest gaps, where they can outgrow the surrounding trees and climb onto them. Instead of investing many resources in support tissue, they grow quickly, similar to light demanding plants. In the gaps, high growth rates coupled with the abundance of slender seedlings and saplings of trees used by the support-seeker liana seedlings as hosts may lead to a high density of this functional group.

Although several studies have concluded that the freestanding seedling stage is a common feature of lianas (Gerwing, 2004; Mascaro, 2002; Putz, 1990; Rowe, Isnard, & Speck, 2004), very few have distinguished between freestanding and support-seeker seedlings and have instead focused on liana climbing strategies. For example, while Mascaro et al. (2004) gave a general number of freestanding and provided support-seeker liana seedlings in a Costa Rican tropical forest, Dewalt et al. (2000) reported that support-seekers are most common when there are many suitable supports, such as in gaps, and then they play an important role in forest regeneration. Other studies have focused on the general ecology of liana seedlings for one or a few species (Nabe-Nielsen, 2004; Restom

& Nepstad, 2004), but until now few studies have evaluated liana seedlings as freestanding and support-seekers at an ecosystem and regional level (Putz, 1984).

I investigated differences between lianas as freestanding and support-seeker seedlings and determined, at the ecological level, patterns of distribution, diversity and abundance of these two liana seedling groups. Additionally, I determined species-specific physiological and/or morphological traits of the two groups of liana seedlings.

Study Site

My study took place in the forests that surround the Panama Canal, Panama. In this geographical area a rainfall gradient from the wet Caribbean to the drier Pacific has been documented (Condit, 1998; Condit et al., 2004), and the Center for Tropical Forest Science (CTFS), associated with the Smithsonian Tropical Research Institute (STRI), has established a series of one hectare plots across this gradient. I used information on those plots, to test for differences in density and diversity of liana seedling across the rainfall gradient. I also analyzed a large data set comprising seedling censuses that took place from 2001 to 2004 in the Forest Dynamic Plot of 50 hectares located on Barro Colorado Island, a facility managed by STRI. Additionally, I carried out common garden experiments in the town of Gamboa, located halfway across the isthmus alongside the Panama Canal.

Theoretical framework, objectives and hypotheses

My main objective was to assess if freestanding and support-seeker liana seedlings correspond to two different functional groups. I expect the freestanding seedlings to be best adapted to the low light, low number of available supports that prevail in the understory, and the support-seekers to be best adapted to high light and abundance of tree saplings that serve as trellises which are abundant in forest gaps. Therefore, I expect a tradeoff in liana seedlings between growing fast and thereby developing a long stem to find a suitable host for support versus developing a wide stem that improves self-support and provides, as well, an efficient water transport system to the transpiring leaves. This tradeoff also may reflect maximizing growth rate at the expense of support and maximizing water transport efficiency by investing much in stems but losing a potential growth advantage.

For my dissertation, I focused on the patterns of species distribution of freestanding and support-seeker liana seedlings and on physiological tradeoffs between maximizing growth rates and improving resource efficiency in terms of leaf production, growth rates and stem elongation. Specifically, I determined: 1) the abundance and diversity of liana seedling across a rainfall gradient on two different soil types; 2) population patterns of the liana seedling bank in the 50 ha plot; and 3) morphological and physiological differences between freestanding and support-seeker liana seedlings.

In my second chapter, I focus on the effects of a well-established rainfall gradient coupled with two soil types on the overall density and abundance of liana seedlings. I selected six field sites across the rainfall gradient, two on the dry end, two on the wet end, and two in the middle of the gradient. For the sites in the middle and on the wet end, one site has lateritic soil and the other has limestone soil. Unfortunately, I was unable to find a suitable limestone soil on the dry end of the gradient. I also tested the hypothesis that freestanding seedlings will be most common on the wet-end of the gradient while support-seekers will show the opposite pattern of distribution by being more common in the dry sites than in the wet area. This distribution will be the result of these two groups of liana seedlings having different adaptations to the different environments, i.e., while the freestanding seedlings are better adapted to the dark understory of the forest on the wet end, the support-seekers will thrive in dry forests where more light will be available to them.

For my third chapter, I used a large data set of liana seedlings from the 50 ha plot at Barro Colorado Island collected by Lisa Comita. A seedling census was initiated in 2001, and then the plot was re-censed in 2002, 2003 and 2004. More than 15,000 liana seedlings have been mapped and identified to species with their growth rate, height and diameter of stems as well as number of leaves recorded annually. I coupled these data with two other data sets. The first data set includes soil variables, nutrients and pH across the 50 ha plot. The second data set contains a canopy census that was performed in the same years as the seedling censuses. The analyses of these three data sets were related to the distribution of liana seedlings in general which should provide insights on liana seedling population dynamics and how liana seedlings are associated with either soil or canopy characteristics. I predict that freestanding seedlings are most common in the understory and support-seekers are most common in gaps.

In chapter four, I analyzed the morphological and physiological differences between the two groups of seedling growth forms. I used eight species of liana seedlings, four freestanding and four support-seekers. My general hypothesis was that the two groups will show contrasting patterns in their morphology and physiology as a result of trade-offs in which the freestanding seedlings will exhibit adaptations to tolerate shade and the support-seeker seedlings will exhibit adaptations as light-demanding plants. I compared the growth rates and photosynthetic light responses of freestanding and support-seeker seedlings growing under high and low light conditions. I took measurements of stems, leaves and water transport of those lianas growing in a common garden experiment. Finally, I used all those variables to evaluate relationships to test my original hypothesis that liana seedlings can be characterized as two different functional groups.

My dissertation provides novel information on differences between freestanding and support-seeker liana seedlings. 1) Freestanding seedlings were most abundant in forests with low availability of light at the understory level, while support-seeker liana seedlings were most abundant in forests with relatively high light availability at the understory level. 2) In the 50 ha plot, liana seedlings seem to be increasing in total population size with higher recruitment rates than trees and shrubs. At the same time, tree seedling populations are decreasing and shrub seedlings are somewhat in equilibrium. Among the liana seedlings, the support-seekers seem to be increasing at higher rates than the freestanding. It seems that liana seedling distribution is not affected by differences in soil nutrients. 3) Freestanding and support-seeker seedlings showed different patterns in morphology, hydraulic conductivity, and photosynthetic response. I not only demonstrate that these two groups do exist in nature, but also report their differences in ecology and physiology, showing how their patterns of distribution are the result of their differences in physiological characteristics. I did also showed that life history traits and physiology can be analyze in terms of functional relationships instead of distinct group of species

Chapter 2

Distribution of freestanding and support-seeker liana seedlings across a tropical rainfall gradient

Rainfall and seasonality are some of the most important factors influencing the diversity and abundance of tropical plant species (Clinebell, Phillips, Gentry, Stark, & Zuuring, 1995; Gentry, 1988). Most plant species are restricted to a specific range of rainfall and seasonality (Pyke et al. 2001).Together with rainfall and seasonality, soil characteristics also play a major role in the composition of tropical forests (Gentry 1988).

Lianas, woody vines, are one of the most common features of tropical forests (DeWalt, Ickes, Nilus, Harms, & Burslem, 2006; Putz, 1984; Schnitzer & Bongers, 2002). Liana seedlings are common in tropical forests, accounting for as much as 22% of the plants found in the understory (Putz, 1984). Liana seedlings can be assigned to either of two functional groups according to their growth strategy. One of the growth strategies is represented by liana seedlings that need to find a suitable host to reach the canopy soon after germination; otherwise they lie on the forest floor for a relatively long period of time. In my study I will call this seedling category the support-seeker (SS) seedlings (Rowe, N. Speck 1996; Gallenmuller, Rowe, and Speck 2005). The second group of liana seedlings do not need a support host immediately after germination and can remain freestanding and grow like a small shrub for a period that can last from a few weeks to a few years, eventually establishing contact with a tree host. This type of seedling will be called a freestanding (F) liana seedling (Campanello et al., 2007; Putz, 1984, 1990).

I propose that these two functional groups of liana seedlings represent a tradeoff in biomass allocation in which freestanding seedlings invest greatly in support tissue which allows them to grow as small shrubs in the dark conditions of the wet tropical forest understory until they can find a suitable host. Meanwhile, support-seeker seedlings invest more resources in growth and less in self-support than the freestanding seedlings, thereby being better adapted to the open canopy or gaps with high light conditions.

Lianas in general are more abundant in tropical seasonal dry forests than in tropical wet forests without seasonality (Schnitzer, 2005; Schnitzer & Bongers, 2002). Schnitzer (2005) hypothesized that the main factor determining this abundance pattern related to rainfall is the ability of lianas to outgrow trees during the dry season because the lianas tend to have deep root systems that allow them to tap water from deeper soil sources than neighboring trees. But there is a discrepancy with some studies showing the opposite pattern: lianas increasing in density with increasing rainfall (Molina-Freaner et al., 2004). Van der Heijden & Phillips (2008) have suggested that there is not a clear relationship with precipitation, and they suggest that maybe any pattern depends on the geographic region that is under study. For example, this last study takes into account a broad set of Neotropical forests, but the Molina-Freaner et al.'s (2004) study was done across a local rainfall gradient on the Pacific coast of Mexico.

Lianas are most diverse and dense in gaps (Schnitzer and Carson 2001; Schnitzer et al 2000). This trend in liana populations is maintained at a large scale with lianas being most abundant in young disturbed forest (Dewalt et al 2000; Schnitzer and Bongers 2002).

Some previous studies have suggested that the availability of suitable host trees is more important in determining liana abundance than the physical environment, such as precipitation and soil characteristics (van der Heijden & Phillips, 2008). There are no studies, however, that include different growth strategies of liana seedlings simultaneously with a gradient analysis that investigates rainfall and soil characteristics.

In the central part of Panama a clear gradient of rainfall exists from the wet Caribbean to the drier Pacific coast which has been used in several plant studies (Condit, 1998; Pyke et al., 2001; Sautu, Baskin, Baskin, & Condit, 2006). This gradient ranges from the wet Atlantic coast through the mid part of the Panama Isthmus to the drier Pacific coast (Condit et al., 2004; Pyke et al., 2001). Because soil water availability affects the mortality of seedlings and consequently species distributions (Engelbrecht et al 2005; Engelbrecht et al. 2007), I hypothesized that this rainfall gradient would have an effect on the distribution of liana seedlings.

Across the whole isthmus, rainfall is strongly seasonal with a marked dry season from mid-December until mid-April (Condit et al., 2000). The length of the dry season, however, increases by 23 days from the wet Atlantic to the dry sites on the Pacific end of the gradient (Condit, 1998; Condit et al., 2000). Together with the availability of different soil substrates, limestone and laterite, this gradient provides a suitable system to test how rainfall and soil influence the abundance and diversity of liana seedlings and also to assess if these two factors influence the distribution of freestanding versus support-seeker liana seedlings (Gentry, 1988; Pérez-Salicrup, Sork, & Putz, 2001).

This study will be the first testing the influence of a gradient in rainfall and seasonality, as well as two soil substrates on the diversity and abundance of liana seedlings. Also, I will show how two functional groups of liana seedlings are distributed across the rainfall gradient and the two soil substrates. I hypothesize that liana seedlings will be more abundant and diverse in the seasonal dry forest than at the wet forest end of the gradient, and this pattern will not be influenced by the type of soil. In other words, the sites in the wet part of the gradient will have fewer liana seedlings than those in the dry part regardless of whether they are located on limestone or laterite soils. I also expect that freestanding liana seedlings will be relatively more abundant on the wet side of the gradient than on the dry side of the gradient. Freestanding seedlings will grow better in the wet forest understory than will support-seeker seedlings.

Methods

Study Sites

This study took place in six sites that are within the network of plots established by the Center for Tropical Forestry Science (CTFS) across the Panama Canal Watershed. Two plots were located on the Caribbean side of the isthmus, two plots were halfway across the gradient in the center of the Panama isthmus, and two more plots were located on the Pacific coast (Figure .2.1). Environmental variables (rainfall, dry season length, soil substrate, elevation, topography, canopy height, density of trees ≥ 50 cm DBH) for each of the six study sites are shown in Table 2.1.

The rainfall across the gradient ranges from the wet Atlantic coast (≈ 3000 mm mean annual rainfall) through the mid part of the Panama Isthmus (2400 mm mean annual rainfall) to the drier Pacific coast (≈ 1500 mm mean annual rainfall)(Condit et al., 2004;

Pyke et al., 2001). The length of the dry season is 106 days on the Atlantic side, 118 days in the middle of the gradient and 129 days on the Pacific side (Condit, 1998; Condit et al., 2000).

Although I found a limestone site on the wet Caribbean side and in the middle of the Isthmus, there were no limestone sites available in the dry Pacific area of the Isthmus. Each site was named as follows: sites on the wet side LA-W1, LS-W2, sites in the middle of the rainfall gradient LA-M1, LS-M2 and finally the sites on the dry side LA-D1, LA-D2. In these acronyms the two initial letters indicate the soil, LA for laterite or LS for limestone, and the second letter stands for the position along the rainfall gradient, W for wet, M for middle, and D for dry.

Field Methodology

The study took place from November 2008 to March 2009. Each plot of the CTFS network is a 1 hectare (ha) square, and is divided into 20 m x20 m sub-plots which, in turn, are divided into 5 m by 5 m quadrats. Within each plot, I placed three 1 m wide x 100 m long transects, totaling 300 m^2 sampled at each site. The first transect was located in the middle of the plot, and then the two others were located 40 meters to either side of the first. For each transect, the sampling methodology was as follows: using a one m^2 PVC frame with marks at 0.5 meter on all sides, I placed it over a rope that indicated the center of the transect in such a way that the 0.5 mark was directly over the rope. I started (at one origin) at 0 meters distance along the transect line and censed all liana seedlings at that position, and then I moved the PVC frame to the second meter and so on until the end of that transect. This procedure was repeated along each of the three transects.

In every square meter, I tagged individually every liana seedling over ten centimeters in length. The length or height of the liana was measured because some of the support-seeker lianas lie on the forest floor. I used the length or the height as an absolute measure of the liana size. Transect number and the distance from the origin of the transect where the liana was located were recorded. For each liana, I recorded the species name, length, seedling functional group (freestanding or support-seeker), number of leaves, stem diameter at 5 cm from the soil (to be used as basal diameter) and stem diameter at 5 centimeters before the apical bud (to be used as the apical diameter). If the plant was longer than 1.3 meters, then I recorded stem diameter at 1.3 meters distance along the stem from the ground. Independently of whether the plant was freestanding or lying on the forest floor, I used the diameter at 1.3 m as a measure of the diameter at breast height (DBH). But if the plant was attached to a tree and was longer than 3 meters, then it was considered out of the seedling/sapling category and was not included in the census.

Together with the seedling census, I measured the canopy height and the leaf area index (LAI) of the forest. The canopy height was measured using a Nikon Pro Staff Laser 440 Rangefinder (Nikon Corporation, Japan) every five meters along each transect. At each five meter point along every transect, three measurements were recorded, one directly above the transect and two more five meters to one side and five meters to the other side of that point. The LAI was measured using a PAR/LAI ceptometer LP-80 (Decagon Devices Inc. Pullman, Washington, USA).

Statistical Analysis

I calculated diversity indexes using PAST (Paleontological Statistics) software ver. 2.06 (Hammer et al 2001), available on line at http://folk.uio.no/ohammer/past/. Shannon's diversity index, H', was transformed to an equivalent number of species using the transformation:

$$N = exp^{(H')}$$

In this transformation *N* is a true diversity number that represents the number of equally common species that will produce the same Shannon diversity index (Krebbs 1999; Jost, 2006) as the censused plants .

I performed a bootstrapping analysis also using PAST to compare the Shannon diversity index between sites. I used the results of the bootstrapping of the Shannon diversity index to build a matrix of pairwise comparisons between sites. I also used the same program to compare similarities in the species composition of the sites across the gradient. After that, I built similarity trees using the Bray-Curtis similarity index. For the first tree, I used a data matrix that just included the presence or absence of species, and for the second, I used a data matrix that comprised the abundances of species. This reveals how the plots are related when using just species presence versus how the abundance of species influences the relationship among the plots. I analyzed the canopy height with a one-way ANOVA followed by a Tukey HSD post-hoc test in PAST. The LAI was graphed against the mean canopy height for each of the sites.

I used R ver. 2.9.2 software (R Development Core Team, 2010,Oksanen et al 2011) to run a log-linear analysis of the distributions of the freestanding and support-seeker species across the study sites. First, I compared the distribution of the freestanding and support-seeker seedlings across the rainfall gradient. Second, I tested the effect of the interaction between rainfall and soil on the distributions of the two liana seedling categories. Finally, I compared the mid and wet sites that have both limestone and laterite soil to assess the effect of soil substrate independently of the rainfall pattern.

Results

Across the six sites a total of 1455 seedlings were sampled comprising a total of 74 species. Eleven species were identified only to the level of family and consequently were removed from the final species count, reducing the total number of species to 63, corresponding to 43 genera in 19 families. The final number of identified liana seedlings was 1397. The most diverse families with respect to the numbers of genera were the Bignoniaceae with 9 genera and Fabaceae with 4 genera. The most species-diverse family, the Sapindaceae, had 11 species in 3 genera while the Bignoniaceae and the Fabaceae both have 9 species (Tables 2.2 and 2.3).

The site with the highest number of seedlings was LS-W2 (Limestone soil) with 479 individuals and a seedling density of 1.6 seedlings/m^2, followed by LS-M2 (388, 1.29), LA-M1 (190, 0.63), LA-D1 (147, 0.49), LA-W2 (141, 0.47) and LA-D2 (131, 0.44), (Table 2.2, Figure 2.2).

The site with the highest species richness was LA-M1 with 31 species, followed by LS-M2 with 30, LA-W2 (29), LA-D2 (27), LS-W2 (26) and LA-D1 (26). On the other hand, LS-M2 and LA-W2 had the largest number of families: 14, while LS-W2 had 13; LA-M1: 12 and LA-D1 and LA-D2: 11 (Table 2.2, Figure 2.2).

Although the LA-M1 site had the highest species richness, two sites shared the highest H’: LA-M1 and LA-D2 with an H′ index of 2.88. Both were followed by LA-W1 (2.82), LA-D1 (2.71), LS-W2 (2.07) and LS-M2 (1.85) (Table 2.2).

The transformation to species number of the Shannon diversity index resulted in a clear contrast between the laterite and limestone sites (Figure 2.2, C). LA-D2 was the site with the highest number of species (17.89) and LA-M1 had a similar species number (17.76). Both were followed by LA-W1 (16.73), LA-D1 (15), LS-W2 (7.96) and LS-M2 (6.33) (Table 2.2, Figure 2.2).

When I did the bootstrapping analysis comparing Shannon diversity indices among the different sites, it showed that there was a significant difference in species diversity between the lateritic and the limestone soil (p=0.001), with the laterite soil showing higher diversity than the limestone soil (Figure 2.2).

The evenness index (e^H/S) depicted an interesting pattern with LA-D2 showing the highest evenness (0.66), and three sites showing similar values: (LA-W1, LA-D1 and LA-M1 with 0.58, 0.58 and 0.57, respectively). The two limestone sites LS-W2 and LS-M2 had the lowest evenness with 0.31 and 0.21, respectively (Table 2.2, Figure 2.3). In these latter two sites, only a few species are dominant and thus the species dominance curves show a rapid decrease (Figure 2.3). In LS-W2, I found 26 species, but the two most abundant species, *Connarus turckzaninowi* and *Hippocratea volubilis*, accounted for 58 % of the total number of seedlings. In LS-M2, I found 30 species, but one species, *Anthodon panamense,* accounted for 50 % of all the individuals.

Liana species in my study seem to be generalists, 45 out of 63 species were present in all sites across the gradient; only 9 species were restricted to the wet side and 7 species to the dry side of the gradient (Table 2.4). Similarly for the soil substrates, 26 out of 56 species were present on both soil substrates (Table 2.5), while 13 and 17 were restricted to limestone and laterite, respectively (Table 2.5).

Cluster analyses were used to understand how the plots cluster according to their species composition and abundance. The analysis yielded two distinct patterns, when I used the presence/absence data to calculate the Bray-Curtis similarity index, it grouped the two wet sites (LA-W1, LS-W2) in the same branch, but the site LA-D1 was on its own branch while LA-D2 clustered together with the Middle sites (LA-M1, LS-M1). Consequently, there was no clear pattern in this similarity analysis. In contrast, when I used the abundance data to calculate the Bray-Curtis index, this analysis grouped the two limestone sites, (LS-W2, LS-M2) together and then their laterite counterparts in the rainfall gradient (LA-W2, LA-M1) leaving the two Dry sites (LA-D1, LA-D2) in their own group (Figure 2.4).

The ANOVA analysis and the Tukey´s HSD post hoc test performed on the mean maximum canopy height resulted in a statistical difference among sites with the canopy being significantly lower for the limestone soil sites than for the other sites. There were no differences among the lateritic soil sites across the rainfall gradient according to the Tukey´s HSD pairwise comparisons between means (Table 2.1). The LAI for the limestone sites was lower than for the laterite sites, but did not differ significantly among sites. The relationship between LAI and canopy height is depicted in Figure 6 which shows that the limestone sites, LS-W1 and LS-M2, tended to have a lower canopy and also a lower LAI than the laterite sites.

I built a series of log-linear models; for the first model I tested the influence of rainfall and therefore I used all the sites across the rainfall gradient. That model showed significant differences in the relative proportion of freestanding and support-seeker seedlings across the rainfall gradient: the proportion of support-seekers was higher on the dry side of the gradient than for sites in the middle or wet sites ($df=2$, $G^2=99.486$, $p<0.001$).

The second model tested the interaction of soil and rainfall for the distributions of the two groups of lianas. For this model, I used only the sites in the middle and the wet side of the gradient, because the dry sites lack limestone soil. This model showed no significant effect of the interaction of these two variables, soil and rainfall, on the relative abundance of freestanding and support-seeker seedlings ($df=1$, $G^2=0.041757$, $p=0.838$).

For the third model, testing the interaction between soil and rainfall across the entire gradient, I decided to use all the sites across the rainfall gradient and all the soil substrates, but it too failed to show a significant effect over the distributions of the support-seekers and freestanding seedlings ($df=1$, $G^2 =0.4797$, $p= 0.4886$).

For the fourth model testing the effect of soil substrate, I used only the sites in the wet and in the middle of the gradient because those sites were the ones that have limestone and laterite soil within the same rainfall regimes. This model provided support for the hypothesis that there is a difference in the distribution of support-seekers and freestanding seedlings with a higher proportion of support-seeker seedlings at the limestone sites and a lower proportion of support-seekers at the laterite sites ($df=1$, $G^2 =5.3103$, $p=0.0212$) (Figure 2.5).

Discussion

This is the first study of which I am aware; that analyzes liana seedling populations along a rainfall gradient with different soil substrates. I analyzed not only the distribution and diversity of liana seedlings in general, but I also provide insight into effects of the two environmental factors (rainfall and soil characteristics) on the distributions of freestanding and support-seeker liana seedlings.

Density and Diversity

The influence of rainfall and seasonality on liana density and diversity has been a subject of frequent discussion. Several authors found lianas to be more abundant in tropical dry forest than in tropical wet forest (Gentry 1991; Gentry 1992; Schnitzer 2005). This has led to the hypothesis that the general pattern of liana abundance is affected by the seasonality and amount of rainfall, with highest liana abundance in seasonally dry tropical forests (Schnitzer 2005). Other studies, however, have found the opposite result with lianas being less abundant with decreasing rainfall (Molina-Freaner et al., 2004). Other studies have found no relationship whatsoever between liana abundance and precipitation (van der Heijden & Phillips, 2008). In my study, neither the density nor the diversity of liana seedlings seems to be influenced by the rainfall pattern.

This discrepancy among studies probably results from the different scales of the studies, either geographical or with respect to rainfall patterns. While my study uses a rainfall gradient of approximately a 1300 mm difference in annual rainfall from the dry seasonal side to the wet end, Molina-Freaner et al. (2004) used a rainfall gradient of about 400 mm difference in annual rainfall, from 122 mm to 524 mm. Their study involved sampling lianas in a substantially drier environment than my study, from desert vegetation to deciduous forest vegetation.

Other studies used a large rainfall gradient and different regional scales, for example, using Neotropical data (van der Heijden & Phillips, 2008) or a Pantropical approach (Schnitzer, 2005). From the results of my study about the density of lianas across the rainfall gradient, I conclude that liana density is influenced by rainfall only at regional geographic and broad rainfall scales.

A previous study using the same rainfall gradient that I used did find differences in the abundance of lianas, with lianas being more abundant in the dry forest than in the wet forest (Schnitzer, 2005). Perhaps this discrepancy is the result of the two studies having used different sites. Schnitzer's (2005) study used a better preserved forest in the drier Pacific side of the gradient that was at least 120 years old and almost free of human disturbance over the last 70 years (Schnitzer, 2005) while my sites on the dry Pacific side are located in young, highly disturbed forests.

Overall the density of lianas seems to be more influenced by soil than by rainfall. My two limestone sites had much higher numbers of seedlings than the laterite sites. If I disregard the two limestone sites (LS-W2, LS-M2), the numbers of seedlings in the other sites are similar despite differences in annual rainfall and length of the dry season. The difference in seedling density between the limestone and laterite soil sites on the wet side of the gradient (LA-W1 and LS-W2) was especially dramatic when I consider that these two sites are less than three kilometers apart, both receiving a similar amount of mean annual precipitation.

In spite of having higher numbers of liana seedlings, the limestone sites have lower liana seedling diversity than the laterite sites. Bootstrap analyses of the number of equivalent species demonstrated that the two limestone sites are not only significantly different from each other but that they are different from all other sites. Interestingly, the bootstrap analysis showed no statistical difference among the other sites. Combining this result with the results of the cluster analysis, it is clear that the soil is the main factor influencing liana seedling diversity. Soil type, but not fertility, previously has been reported to influence the density, diversity and the species composition of liana communities located in different types of soils (Ibarra-Manriquez and Martinez-Ramos 2002; DeWalt et al. 2006), my results reinforce this idea.

I compared the species composition among sites by using Bray-Curtis similarity indices and two different data matrices: presence/absence and abundance data. When I used the presence/absence data, the sites clustered without any apparent pattern, but when I used abundance data, the limestone sites (LS-W2, LS-M2) not only were in the same cluster but also were separated from the laterite sites. The limestone sites seem to be more closely related to the dry sites than to their adjacent sites along the rainfall gradient. Taking into account that both limestone soil sites also have low evenness indices, it is clear that there are few species that can thrive in limestone soil, and those species that do thrive have great dominance. This result also indicates the importance of using a data matrix that includes the relative abundance of each species in the studied forest stands.

Because limestone soils have higher density but not higher diversity of liana seedlings, it is clear that my results reinforce previous research showing that liana diversity patterns are independent of their abundance (Reddy & Parthasarathy, 2003; Schnitzer, Kuzee, & Bongers, 2005).

The limestone site on the Caribbean, LS-W2, has been found to differ also in its tree species composition, being more similar to the drier sites of the Pacific side. It has been hypothesized as being either a refugee of older forest from when a drier climate allowed the dry forest to be more spread-out than nowadays, or to be a subsample of the drier forest in which species from the dry side have reached that specific area by random dispersal (Pyke et al., 2001). Because both limestone sites, on the wet side (LS-W2) and in the mid site (LS-M2) have more species in common than with any of the other sites, I can extend these hypotheses to the LS-M2 site.

It is interesting to note that although lianas appear to be most abundant and diverse in disturbed forest (Putz, 1984; Schnitzer and Bongers, 2002; Gerwing and Vidal, 2002), in my research the dry sites (LA-D1, LA-D2) are the most disturbed of the six study sites, but they do not show a higher density of liana seedlings than the other sites. The bootstrap analysis did not show a statistical difference between the two dry sites and the rest of the laterite soil sites across the gradient.

Lianas in my study sites are habitat generalists with very few restricted to either dry or wet areas or to limestone or laterite areas. There have been disagreements on whether lianas are habitat specialists, with previous studies giving different results (DeWalt et al., 2006). Lianas can be habitat specialists at a regional scale, but it seems that the pattern of distribution will depend on the characteristics of the sites were a study is conducted.

Freestanding and Support-seeker seedlings

My results show that the relative abundance of freestanding and support-seeker seedlings differs statistically among sites. In the wet and mid sites, the distribution of freestanding and support-seeker seedlings was significantly different from the dry sites, with the dry sites showing a higher proportion of support-seeker seedlings. If I segregate sites by substrate, wet and mid sites with limestone versus laterite, then the influence of the interaction between rainfall pattern and soil becomes null and the major factor influencing the distribution of these two functional groups of seedlings appears to be soil type.

Previous work has failed to show a relationship between soil fertility and liana density. For example, De Walt and Chave (2004) did not find differences in abundance of lianas across a soil fertility gradient, which included four biological stations: La Selva, Costa Rica; Barro Colorado Island, Panama; Cosha Cashu, Peru; and a field station north of Manaus, Brazil. Phillip el al. (2005) working in a series of sites in the Peruvian Amazon also found no evidence for an effect of soil fertility on the abundance of lianas. Furthermore, De Walt (2006) found the same lack of relationship between liana density and soil fertility in the forest of Borneo, but that pattern holds just for smaller lianas with lianas of a large size being especially abundant in fertile, alluvial soil.

Notwithstanding the previous studies, in my study limestone soil appears to be the main driver not only for the abundance of liana seedlings in general, but also for the distribution of freestanding and support-seeker seedlings, surpassing the effect of the rainfall pattern and disturbance. Because limestone generally has better drainage than laterites, perhaps this effect is not a direct effect of fertility of the limestone soil itself, but it is an effect of forest structure common to limestone soils. Analysis of the maximum canopy height data support this idea with statistical differences in canopy height between the limestone and laterite soil sites. The two dry sites, both lateritic, do not differ in mean maximum canopy height from the other lateritic soil sites.

The analysis of the leaf area index fails to support a significant difference among sites. But when LAI is plotted against mean canopy height, it is evident that both limestone sites not only have a lower canopy but also have a lower LAI, reflecting the effect of the limestone soil in the structure of both sites. The LAI is commonly defined as one half the total green leaf area per unit ground surface area (Chen, Rich, Gower, Norman, & Plummer, 1997) and can be used to predict how much light is transmitted to the understory (Kull, 1995). I infer that it also can be used as a predictor of how much light is available for seedlings living in the understory

Perhaps because a low canopy height coupled with low LAI allows more light to reach the understory in dry sites, this could be the factor leading to a high density of liana seedlings in the limestone sites. It probably favors the growth of support-seeker seedlings. Sites with high canopy and high LAI probably have dark understories where freestanding liana seedlings prolong their survival by growing as a shrub until they find a suitable host at a greater height than do support-seeker seedlings. Support-seeker lianas that have high growth rates and thus are light demanding will thrive in areas with low canopy.

I hypothesize that the distributions of freestanding and support-seeker liana seedlings is not only the result of the forest structure but also a result of their pattern of biomass allocation. Freestanding seedlings may invest more in self-support and less in growth and root tissue than support-seeker seedlings, similar to the biomass trade off that is usually shown for pioneer versus understory plant species (Gilbert, Wright, Muller-Landau, Kitajima, & Hernandéz, 2006).

As I already mentioned, rainfall does not seem to affect liana density or diversity in my study. Nevertheless, it is conceivable that better drainage of limestone than of lateritic soil favors lianas because they have deeper roots than the surrounding vegetation (Restom & Nepstad, 2004; Schnitzer, 2005). Because lianas can tap water from deep sources and because a low canopy and LAI on limestone sites allow high light availability, this will provide liana seedlings with an advantage. So their population density is higher than at the laterite sites where the liana seedlings do not have these advantages over the surrounding vegetation.

My general conclusions are that rainfall fails as a predictor of liana seedling abundance and diversity along the gradient that I studied, but it does influence the distributions of freestanding and support-seeker seedlings. Limestone soil has a stronger effect than rainfall pattern on the abundance of liana seedlings.

Table 2.1. Environmental characteristics for the six study sites used in this study. UTM coordinates correspond to zone 17. The mean canopy height was measured parallel to the census transects and is given as a mean ± 1 SD, n= 190 for all study sites, significance symbols (a,b) indicate that those means followed by the same letter do not differ by Tukey´s HSD pairwise comparisons. All significant differences are at $p < 0.001$ (ANOVA $F_{5,\,1062}$= 24.8, p<0.001). *Sources:* 1. Smithsonian Tropical Research Institute, Environmental Science Program; 2. Panama Canal Authority, Meteorology and Hydrology Branch; 3. Pyke, Condit, Aguilar, & Lao, 2001; 4. Center for Tropical Forest Science

	Atlantic Wet Side		Middle		Pacific Dry Side	
Environmental Characteristic.	LA-W1	LS-W2	LA-M1	LS-M2	LA-D1	LA-D2
Precipitation (mm/year)	3140.041	3140.041	2130 2	23782	1797.42	1865.711
Soil type[1]	Laterite	Limestone	Laterite	Limestone	Laterite	Laterite
Dry Season Length (Days)[3]	106	106	118	118	129	129
Elevation (mamsl)[4]	20	100	70	109	64	300
Coordinates (UTM)4						
Easting	614856.9	613985.4	637861	653822	660188	651373
Northing	1031786.4	1030725.4	1012976	1018532	994526	987031
Site Topography[4]	Level	Irregular	Level	Level	Irregular	Slopped
Canopy Height (m)	22.02±7.33a	15.79±7.43b	21.32±7.57^a	15.92±8.55^b	20.49±6.28^a	21.93±8.07^a
Stand Age[4]	Primary	Secondary	Mature Secondary	Mature Secondary	Secondary	Mature Secondary
Stems ≥ 50 mm/Ha[4]	570	605	663	585	412	358

Table 2.2. Biodiversity values for each of the six study sites, including biological classification of lianas, freestanding and support-seeker data and diversity indexes.

	Pacific Dry Side		Middle		Atlantic Wet Side	
	LA-D2	LA-D1	LS-M2	LA-M1	LS-W2	LA-W1
Individuals	131	147	388	190	479	141
Species	27	26	30	31	26	29
Genera	23	22	25	24	20	21
Families	11	11	14	12	13	14
Seedlings/m^2	0.44	0.49	1.29	0.63	1.6	0.47
Freestanding	93	85	341	178	429	132
Support-seeker	38	62	47	12	50	9
Dominance D	0.07	0.09	0.3	0.09	0.2	0.1
Shannon H	2.88	2.71	1.85	2.88	2.07	2.82
exp(H)	17.89	15	6.33	17.76	7.96	16.73
Simpson 1-D	0.93	0.91	0.7	0.91	0.8	0.9
1/D	13.39	10.65	3.36	10.82	5.11	10.27
Evenness (e^H/S)	0.66	0.58	0.21	0.57	0.31	0.58
Equitability J	0.88	0.83	0.54	0.84	0.64	0.84
Fisher alpha	10.54	9.37	7.67	10.54	5.96	13.16

Table 2.3. Species name, species and family code, and abundance in each of the study sites. Species family codes: Acanthaceae (Acan), Apocynaceae (Apoc), Asclepiadaceae (Ascl), Asteraceae (Aste), Bignoniaceae (Bign), Celastraceae (Cela), Combretaceae (Comb), Connaraceae (Conn), Convulvulaceae (Conv), Dilleniaceae (Dill), Fabaceae-caesalpinioideae (F.Ca), Fabaceae-mimosoideae, (F. Mi), Fabaceae-papilionoideae (F.Pa), Lamiaceae (Lami), Loganiaceae (Loga). Malpighiaceae (Malp), Menispermaceae (Meni), Polygonaceae (Poly), Sapindaceae (Sapi), Smilacaceae (Smil), Solanaceae (Sola), Verbenaceae (Verb).

			Atlantic Wet Side		Middle		Pacific Dry Side	
Scientific Name	Specie Code	Family Code	LA-W 1	LS-W 2	LA-M 1	LS-M 2	LA-D 1	LA-D 2
Abuta racemosa	ABUTRA	Meni	2	0	2	10	0	0
Acacia hayesii	ACACHA	F.Mi	0	0	0	0	1	0
Aegiphila cephalophora	AEGICE	Lami	0	4	0	0	1	0
Anthodon panamense	ANTHPA	Cela	52	0	191	0	0	0
Arrabidaea verrucosa	ARRAVE	Bign	0	5	0	0	2	12
Bauhinia guianensis	BAUHGU	F.Ca	0	7	0	1	0	0
Callychlamys latifolia	CALLLA	Bign	0	0	1	0	5	0
Ceratophytum tetragonolobum	CERATE	Bign	0	0	0	0	0	1
Chondodendron tomentosum	CHONTO	Meni	0	0	0	3	0	0
Clitoria javitensis	CLITJA	F.Pa	1	0	0	2	0	0
Cnestidium rufescens	CNESRU	Conn	2	2	1	1	7	9
Coccoloba parinensis	COCCP1	Poly	0	4	0	2	3	0
Combretum laxum	COMBLA	Comb	0	0	2	0	0	2
Connarus panamense	CONNPA	Conn	4	1	4	13	0	1
Connarus turckzaninowi	CONNTU	Conn	146	4	2	10	0	0
Davilla nitida	DAVINI	Dill	0	0	0	2	1	2
Doliocarpus decandrum	DOLIDE	Dill	0	1	0	0	0	0
Doliocarpus major	DOLIMA	Dill	35	26	0	15	3	9
Doliocarpus olivaceus	DOLIOL	Dill	4	1	2	1	0	6

			Atlantic Wet Side		Middle		Pacific Dry Side	
Scientific Name	Specie Code	Family Code	LA-W 1	LS-W 2	LA-M 1	LS-M 2	LA-D 1	LA-D 2
Forsteronia viridescens	FORSVI	Apoc	0	0	0	0	0	1
Hippocratea volubilis	HIPPVO	Cela	123	9	14	0	22	1
Hiraea faginea	HIRAFA	Malp	0	0	0	1	0	0
Hiraea smilacina	HIRAQU	Malp	0	1	0	0	0	0
Hiraea reclinata	HIRARE	Malp	1	0	2	0	9	0
Justicia graciliflora	JUSTGR	Acan	0	0	0	0	0	1
Macfadenya unguis-cati	MACFUN	Bign	13	0	0	0	0	0
Machaerium pittieri	MACHAR	F.Pa	9	0	0	0	0	3
Machaerium kegelii	MACHKE	F.Pa	1	0	0	0	0	0
Machaerium isadelphum	MACHM1	F.Pa	0	0	1	0	4	0
Machaerium milleflorum	MACHM2	F.Pa	0	0	0	0	0	4
Machaerium seemanii	MACHSE	F.Pa	0	0	0	0	0	1
Mansoa aliacea	MANSAL	Bign	1	0	37	0	0	0
Maripa panamense	MAR2PA	Conv	2	11	2	46	7	1
Marsdenia crassipes	MARSCR	Apoc	2	1	3	0	0	0
Mascagnia hiraea	MASCHI	Malp	3	0	0	2	2	0
Mascagnia ovatifolia	MASCNE	Malp	0	0	55	2	6	1
Mendoncia literalis	MENDLI	Acan	0	1	0	0	1	7
Mendoncia graciliflora	MENGR	Acan	0	1	0	0	0	0
Mikania leiostachya	MIKALA	Aste	0	0	1	0	0	0
Paragonia pyramidata	PAR1PY	Bign	0	2	1	4	9	28
Paullinia baileyi	PAULBA	Sapi	0	2	2	10	0	0
Paulinia bracteosa	PAULBR	Sapi	1	2	1	0	12	0
Paulinia fibrigera	PAULFI	Sapi	0	0	5	6	10	0
Paulinia glomerulosa	PAULG2	Sapi	1	1	3	4	2	0
Paulinia pterocarpa	PAULPT	Sapi	0	0	0	3	8	0
Paulinia rugosa	PAULRU	Sapi	0	1	0	1	0	0

			Atlantic Wet Side		Middle		Pacific Dry Side	
Scientific Name	Specie Code	Family Code	LA-W 1	LS-W 2	LA-M 1	LS-M 2	LA-D 1	LA-D 2
Paulinia turbacensis	PAULTU	Sapi	0	0	30	0	0	0
Petrea aspera	PETRAS	Verb	10	6	2	10	3	0
Phryganocydia corymbosa	PHRYCO	Bign	16	4	2	4	1	19
Pithecoctenium crucigerum	PIT2CR	Bign	0	0	0	0	3	0
Pleonotoma variabilis	PLEOVA	Bign	0	1	4	6	1	3
Prionostema asperum	PRI1AS	Cela	0	0	1	13	0	2
Rourea glabra	ROURGL	Conn	0	0	1	1	0	0
Serjania paucidentata	SERJPA	Sapi	1	0	0	0	0	0
Serjania mexicana	SERJME	Sapi	1	1	2	2	1	15
Serjania rhombea	SERJRH	Sapi	0	1	0	0	0	1
Smilax mollis	SMILMO	Smil	0	1	0	0	0	0
Solanum adhaerens	SOLALA	Sola	0	2	0	0	0	0
Stizophyllum riparium	STIZRI	Bign	0	0	1	3	1	5
Strychnos brachistantha	STRYBR	Loga	23	1	0	5	0	1
Strychnos panamense	STRYPA	Loga	2	0	0	0	0	0
Tetracera portobellensis	TET1PO	Dill	5	0	1	2	1	5
Thinouia myriantha	THINMY	Sapi	0	0	0	4	0	0

Table 2.4. Table of species abundances (species names are given in Table 3) across the gradient; species in sites under the same rainfall and seasonality pattern were grouped together, i. e., LA-W1 and LS-W2 are together in the Wet column, LA-M1 and LS-M2 under the Mid column and LA-D1 is grouped together with LA-M2 in the Dry column.

Species	Wet	Mid	Dry
MACFUN	13		
SOLALA	2		
STRYPA	2		
DOLIDE	1		
HIRAQU	1		
MACHKE	1		
MENGR	1		
SERJGL	1		
SMILAX	1		
CONNTU	150	12	
ANTHPA	52	191	
BAUHGU	7	1	
MARSCR	3	3	
ABUTRA	2	12	
PAULBA	2	12	
CLITJA	1	2	
MANSAL	1	37	
PAULRU	1	1	
HIPPVO	132	14	23
DOLIMA	61	15	12
STRYBR	24	5	1
PHRYCO	20	6	20
PETRAS	16	12	3
MAR2PA	13	48	8
CONNPA	5	17	1
DOLIOL	5	3	6
TET1PO	5	3	6
CNESRU	4	2	16
COCCP1	4	2	3
MASCHI	3	2	2
PAULBR	3	1	12
PAR1PY	2	5	37
PAULGL	2	7	2
SERJME	2	4	16
HIRARE	1	2	9
MENDLI	1	0	8
PLEOVA	1	10	4

Species	Wet	Mid	Dry
AEGICE	4		1
ARRAVE	5		14
MACHAR	9		3
SERJRH	1		1
PAULTU		30	
THINMY		4	
CHONTO		3	
ROURGL		2	
HIRAFA		1	
MIKALA		1	
CALLLA		1	5
COMBLA		2	2
DAVINI		2	3
MACHM1		1	4
MASCNE		57	7
PAULFI		11	10
PAULPT		3	8
PRI1AS		14	2
STIZRI		4	6
MACHM2			4
PIT2CR			3
ACACHA			1
CERATE			1
FORSVI			1
JUSTGR			1
MACHSE			1

Table 2.5**.** Table of species abundances (species names are given in Table 3) on the two soils surveyed. Species in sites on the same soil type are grouped together, i. e., LS-W2 and LS-M2 are together in the Limestone column, and LA-W1 and LS-M1 are together under the Laterite column. Because there is no limestone soil in the dry area, the species of the two dry plots, LA-D1 and LA-D2, are not included in this tabulation.

Species	**Limestone**	**Laterite**
ANTHPA	243	
MANSAL	38	
PAULTU	30	
MACFUN	13	
MACHAR	9	
HIRARE	3	
COMBLA	2	
STRYPA	2	
CALLLA	1	
MACHKE	1	
MACHM1	1	
MIKALA	1	
SERJGL	1	
CONNTU	148	14
HIPPVO	137	9
MASCNE	55	2
DOLIMA	35	41
STRYBR	23	6
PHRYCO	18	8
PETRAS	12	16
CONNPA	8	14
DOLIOL	6	2
TET1PO	6	2
MARSCR	5	1
PAULFI	5	6
ABUTRA	4	10
MAR2PA	4	57
PAULGL	4	5
PLEOVA	4	7
CNESRU	3	3
MASCHI	3	2
SERJME	3	3
PAULBA	2	12
PAULBR	2	2
CLITJA	1	2

Species	**Limestone**	**Laterite**
PAR1PY	1	6
PRI1AS	1	13
ROURGL	1	1
STIZRI	1	3
BAUHGU		8
COCCP1		6
ARRAVE		5
AEGICE		4
THINMY		4
CHONTO		3
MENDLI		3
PAULPT		3
DAVINI		2
PAULRU		2
SOLALA		2
DOLIDE		1
HIRAFA		1
HIRAQU		1
MENGR		1
SERJRH		1
SMILAX		1

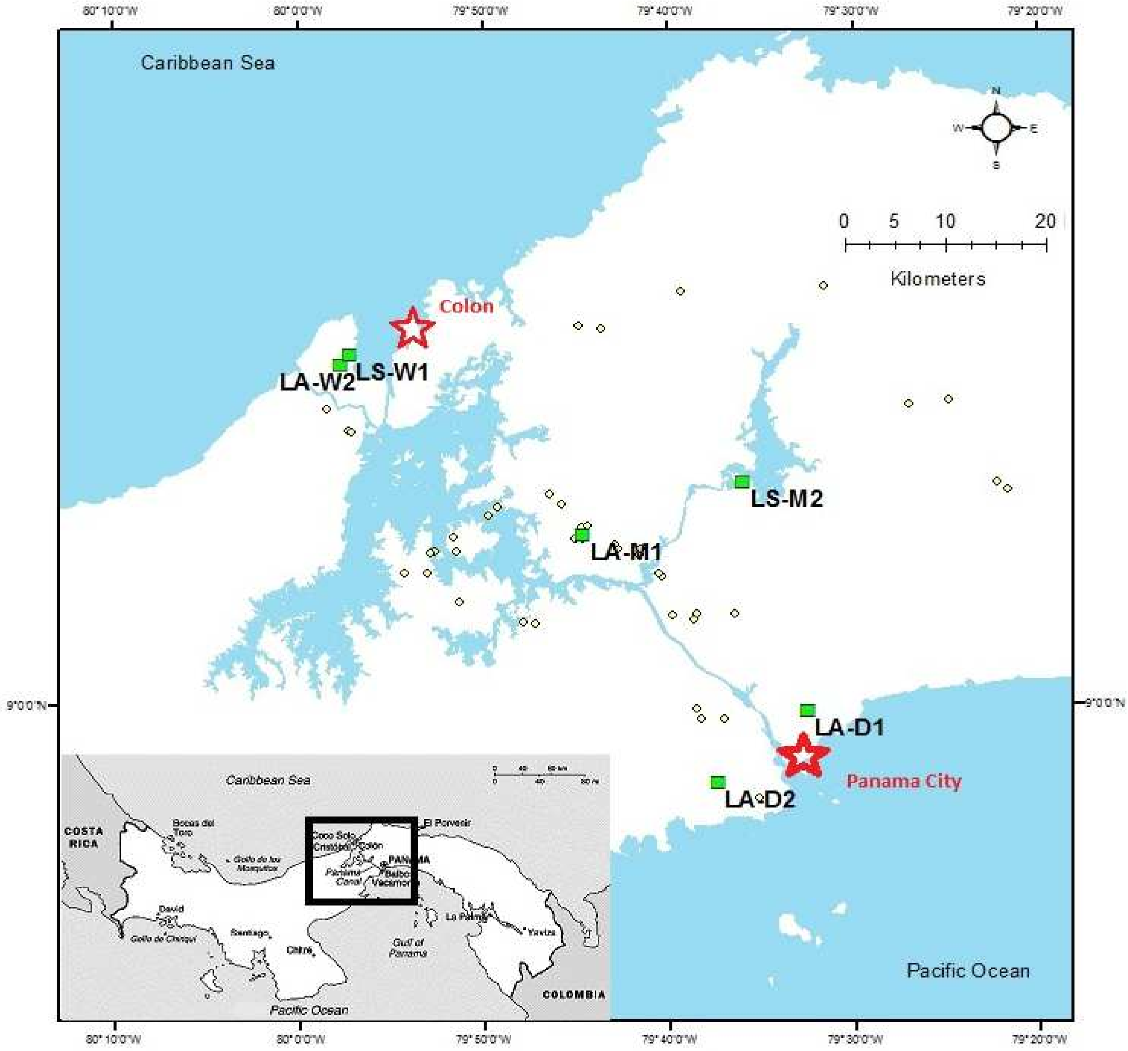

Figure 2.1. Locations of CTFS plots, small diamonds, and the study sites, green squares, across the Panama Isthmus. Insert shows Panama with the square indicating the location of the large map

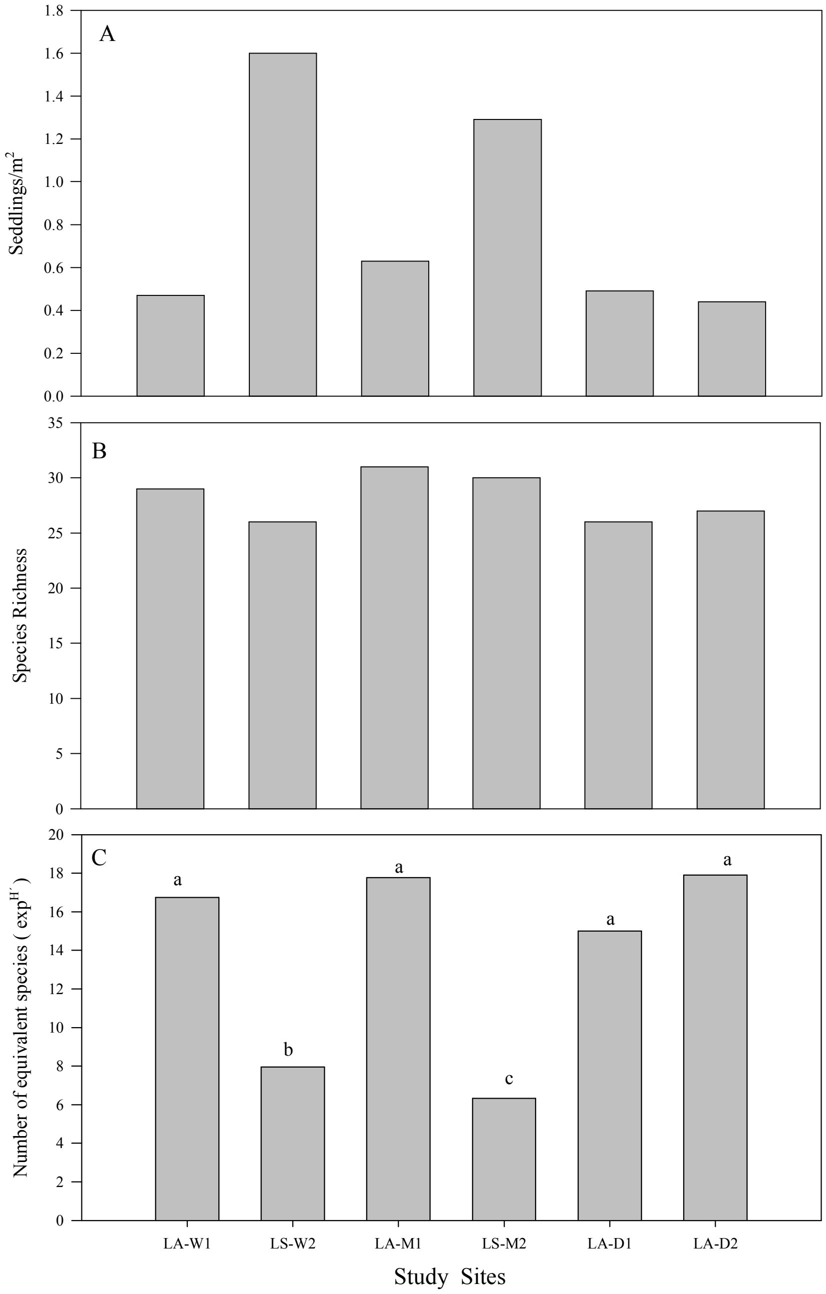

Figure 2.2. (**A**)Liana seedling density in each of the six study sites (site codes as in Fig. 1), (**B**)Species richness for the six study sites (**C**) Number of equally common species that would produce the same Shannon diversity index as was calculated using (N_1)= $e^{(H)}$ (Krebbs 1998, Joust 2006). Significant differences between sites in **C** were calculated using bootstrap analysis (Hammer et al 2001). Bars topped by the same letter do not differ significantly

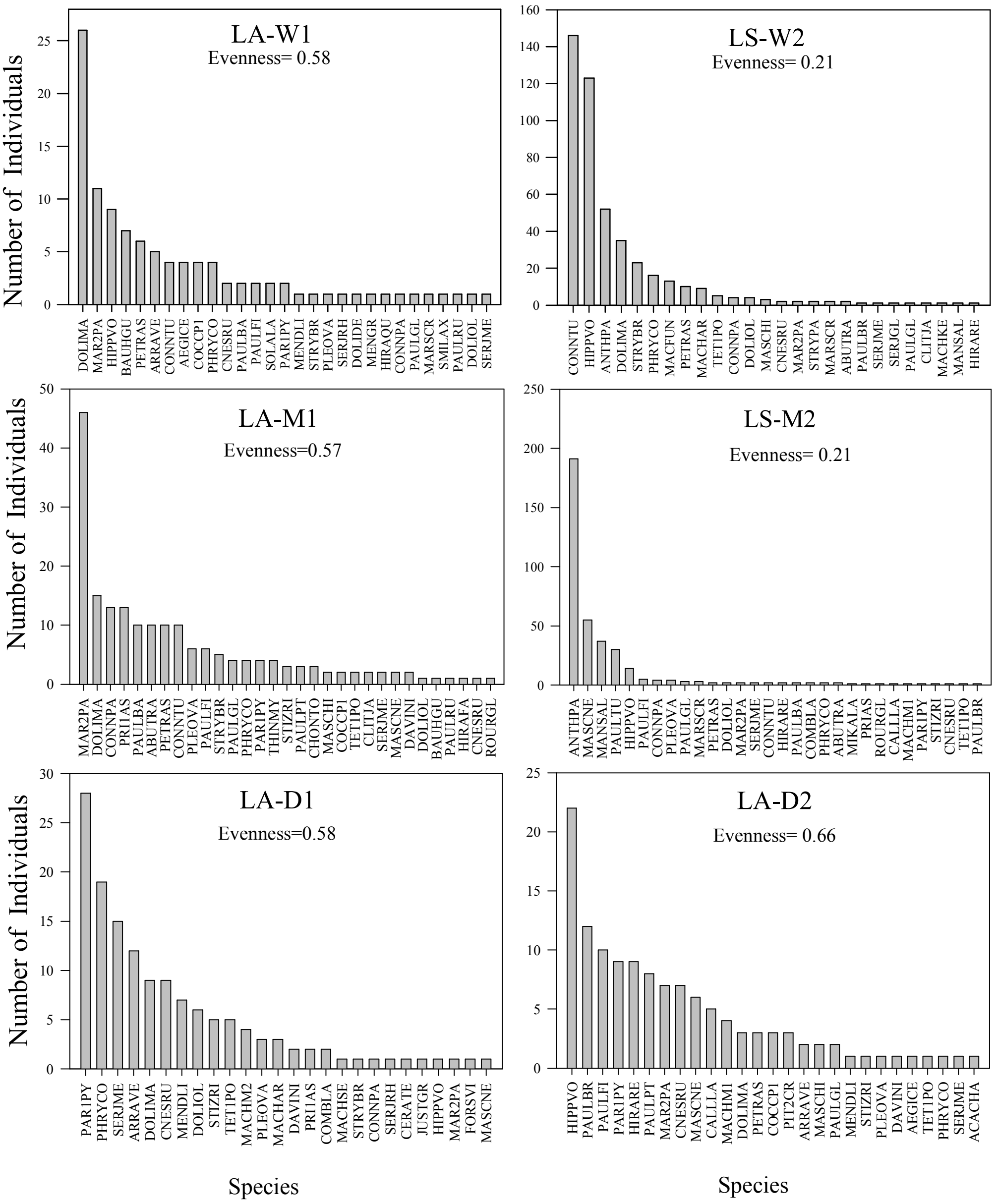

Figure 2.3. Number of individuals by species in each study site and the evenness (e^H/S) value for each site. Total number of individuals per species is shown on the y-axis and species name, using the CTFS code (Table 2.3) (first four letters of the genus and the two first letters of the species), is shown on the x-axis. Site codes are as in Fig. 2.1; sites LS-W2 and LS-M2 were sites with limestone substrate.

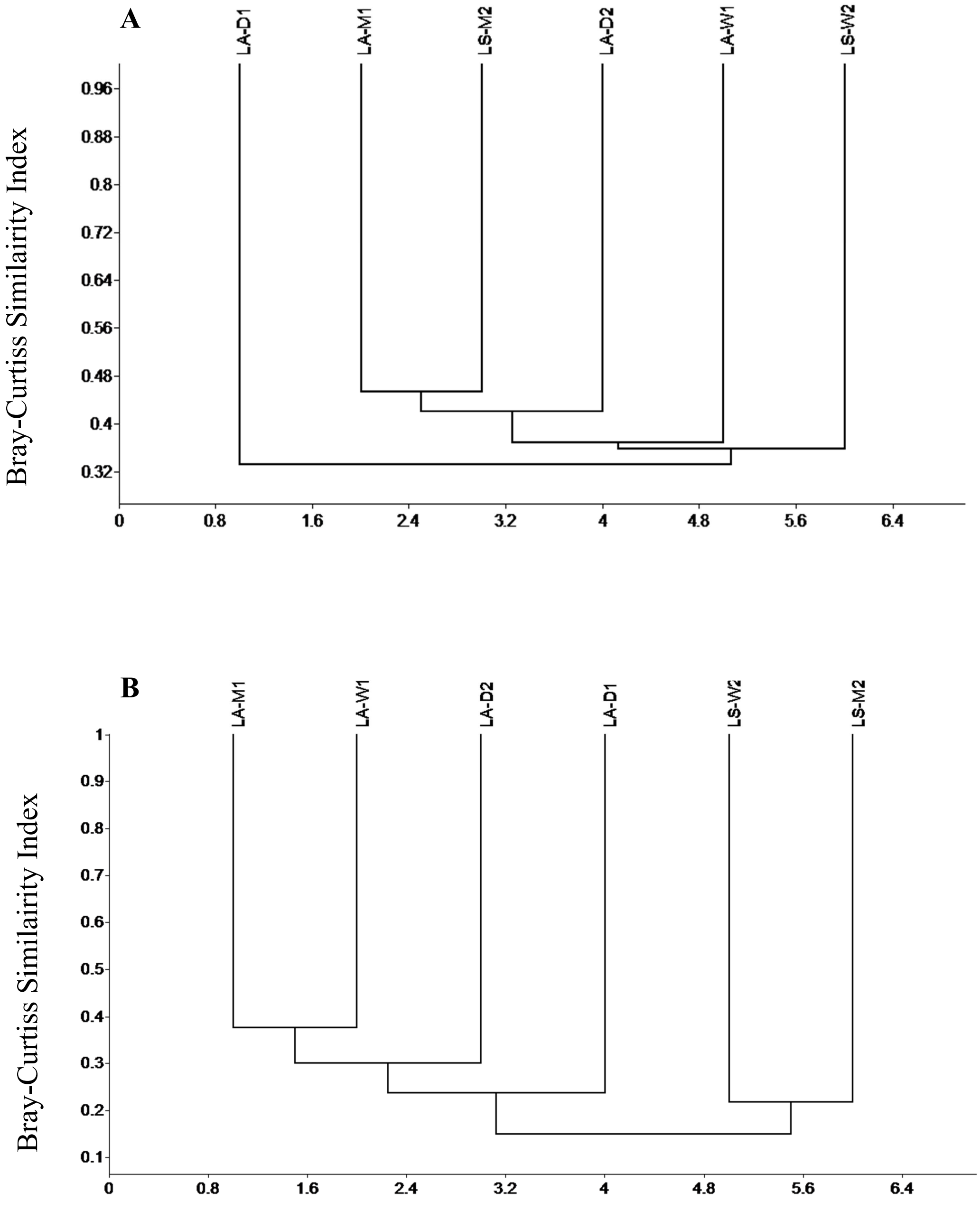

Figure 2.4. Results of a Bray-Curtis similarity index cluster analysis based on (A) presence/absence data (B) species abundance data.

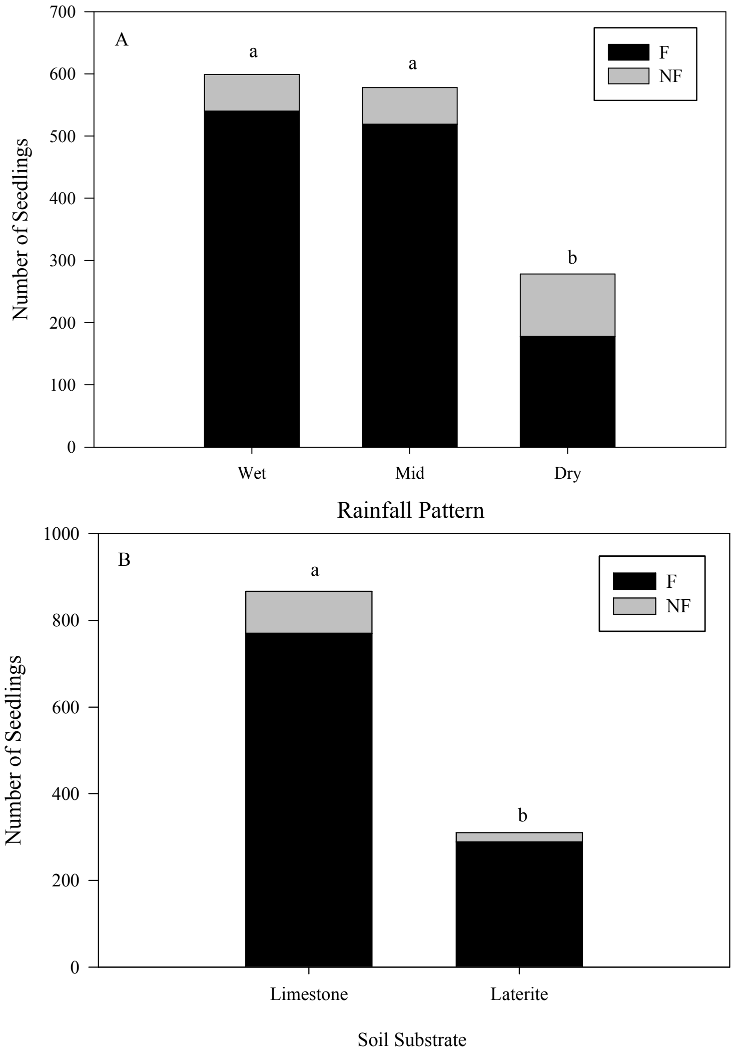

Figure 2.5. (A) Number of freestanding (F) and support-seeker (SS) seedlings for both sites combined at the ends and middle of the rainfall gradient, and (B) on the limestone versus the laterite soils**.** Statistical significance was calculated using a log-linear model over the proportion of each seedling category at the sites. For A the six study sites were grouped according to their position on the rainfall gradient ($df=2$, $X^2=99.486$,$p>0.001$). For B, the dry sites were excluded because they lacked limestone soil ($df=1$, $X^2 = 5.3103$, $p=0.0212$). Proportions of freestanding versus support-seeker seedlings in bars marked with the same letter do not differ significantly.

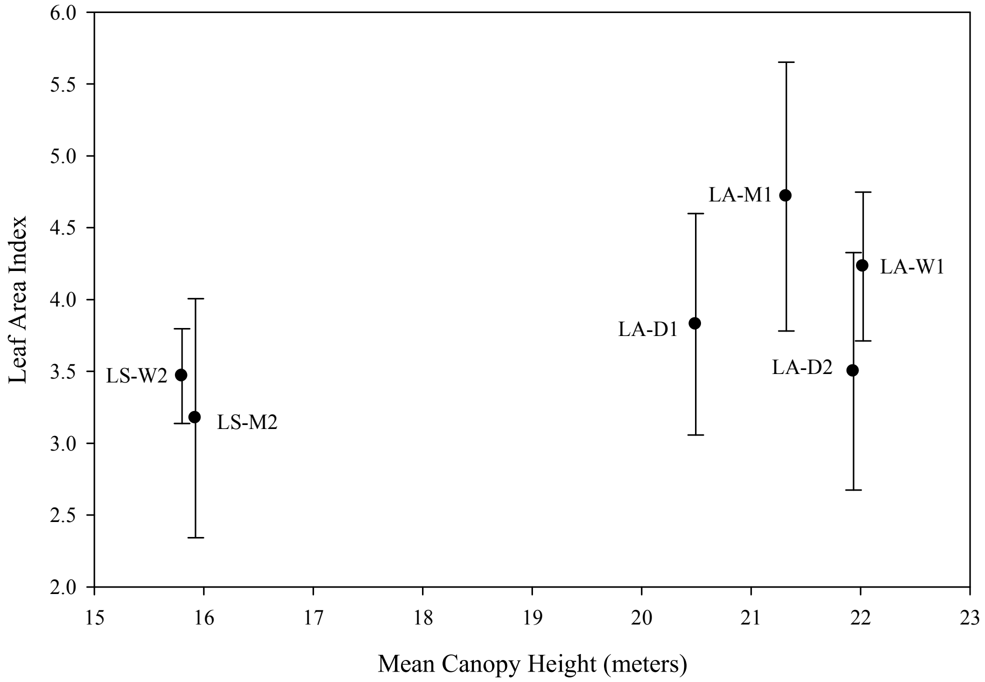

Figure 2.6. Relationship between leaf area index and mean canopy height across the six study sites. Error bars represent plus or minus one standard error of the mean.

Chapter 3

Soil nutrients and forest understory influences on the population dynamics of liana seedlings in a Neotropical lowland forest.

The seedling is a critical stage in the life cycle of plants. In this early stage of development, plant species are especially prone to exhibit high mortality due to factors such as density-dependent mortality and parent tree's pathogens (Augspurger, 1984; Comita, Aguilar, Perez, Loo de Lao, & Hubbell, 2007). Seedlings are particularly sensitive to small changes in environmental conditions such as droughts (Engelbrecht et al., 2006, 2005). The successful establishment of seedlings can lead to the colonization of new areas, affecting the diversity and distribution of the species at local and regional levels (Garwood, 2009). The ecology of some species seedlings currently is poorly understood, although its knowledge is crucial for determining plant distribution at maturity (Garwood, 2009).

The liana life cycle starts with the germination of a seed. The seedlings grow and may eventually reach the canopy with the help of trees or other established lianas as mechanical hosts. Liana seedlings constitute from20 % to 30 % of seedlings present in the tropical forests understory (Putz, 1983, 1984). Liana seedling density and liana density in general seems to be increasing in the tropics (Swaine & Grace, 2007; Wright, Calderón, Hernandéz, & Paton, 2004). Most seedling ecology studies have focused on tree seedlings, leaving a gap in knowledge on the ecology and demography of liana seedlings in particular (Comita et al., 2007; Engelbrecht, Wright, & De Steven, 2002;

Goldsmith, Comita, Morefield, Condit, & Hubbell, 2006; Harms, Condit, Hubbell, & Foster, 2001).

Lianas can affect several ecological processes. For example, they can reach high densities in forest gaps and consequently may delay succession and gap-phase regeneration processes (Dewalt et al., 2000; Schnitzer & Carson, 2001). Lianas also can compete for resources with surrounding trees, especially for water resources. Because liana seedlings have relatively deep roots, they can acquire water from deeper sources than tree seedlings (Restom & Nepstad, 2004; Schnitzer et al., 2005). Liana seedlings also have been shown to have an advantage due to future predicted increases in ambient CO_2, and they can respond positively to nutrient-enriched soils, not only at a local scale (Hättenschwiler, 2002) but also at a regional scale (DeWalt et al., 2006).

Liana seedlings can be classified in two different groups (i) freestanding, those seedlings that can remain as small shrubs without external support for a long period of time before starting to climb into the canopy, and (ii) Support-seekers which are those seedlings that need to use an external support to grow and reach the canopy very early in their developmental stage.

Adult lianas can increase the mortality of trees by entangling their canopies and limiting the light availability by shading their leaves (Perez-Salicrup & Meijere, 2005; Putz, 1984; Pérez-Salicrup et al., 2001). If the liana seedling population is increasing in number, then the number of adult lianas probably will increase and thus the negative effects of adult lianas on canopy tree dynamics will be enhanced.

Barro Colorado Island (BCI) is an island located in the middle of the Panama Canal that is the remnant of a hill that becomes separated from the mainland with the formation of the Gatun Lake, an artificial lake in the middle section of the Panama Canal. BCI have been a center for studies in tropical biology for decades, and the rich biodiversity of the site has been extensively documented (Leigh, 1999). BCI was selected because is the first of a series of permanent forest plots established by the Center for Tropical Forest Science, CTFS, as a part of a study called the Forest Dynamics Project (Leigh et al., 2004)

Lianas have been increasing in importance in the BCI forests (Wright et al., 2004), hence I expect faster year-to-year increases in the total number of liana seedlings than for tree and shrub seedling populations. Also, I expect that among liana seedlings, the support-seekers will have a relatively rapid increase in their population size compared to freestanding liana seedlings. Lianas can respond to different levels of soil nutrients (DeWalt et al., 2006) I predict that their recruitment rate will be positively correlated with high soil nutrient availability, while mortality rates will be highest in low nutrient availability sites.

Methods

Field site

Barro Colorado Island (BCI: 9°10'N, 79°51'W) is the remnant of a small mountain peak that became an island when the waters of the Chagres River was dammed. It is the largest island in the Gatun Lake and has been separated from the mainland for over one hundred years. It has been under conservation status for over 85 years, and is part of the Smithsonian Institution since 1946 (E. G. Leigh et al., 2004; E. G. Leigh, 1999). The BCI forest is a tropical lowland forest with an average of 2623 mm of rain per year; this rainfall is seasonal with a dry season that lasts an average of 3.5 months from late December to early April, receiving on average of 285 mm precipitation during this period. The wet season lasts from April to December and on average receives over 90 % of the annual rainfall (http://stri.si.edu/sites/esp/description_bci.htm) (Condit et al., 2000; Leigh, 1999).

Field Study

The study site was the Center for Tropical Forest Science CTFS 50-ha plot located in the central plateau roughly at the center of BCI (Figure 3.1). The Forest Dynamic Plot (FDP) was established in 1980. This area has an elevation between 120 and150 m asl, and the topography consists of a central plateau surrounded by gentle slopes to the south and west. The vegetation is predominantly an old forest with a small patch of young forest (<100 years) on the north east side of the plot. The plot is divided into 20 x 20 meter for a total of 1250 quadrats; each one of these 20 x 20 m quadrates is divided into sixteen 5 x 5 m subplots; these divisions were made to help with the field work inside the 50 Ha plot, and particularly for the mapping of the plants. The first census was conducted between 1982-1983: all trees and shrubs ≥ 1 cm DBH were measured, tagged, mapped, identified to species and subsequently re-measured together with recruits every 5-year starting in 1985 (Hubbell & Foster 1983, Condit 1998, Condit, Hubbell, & Foster, 1992).

In 2001 Liza Comita set up a network of 1 x 1 meter plots that were located in the center of each 5 x 5 m subplot, and every seedling or sapling larger than 20 cm tall and smaller than 1 cm DBH was measured, tagged, mapped and identified to species if possible, leaving fewer than 0.5 % of individuals without a species identification (Comita, Aguilar, et al., 2007; Comita, Condit, & Hubbell, 2007). Together with that information, for each seedling the following measurements were taken: seedling length, number of leaves, basal diameter, and if the liana seedling was attached to a host or not. This resulted in a total of 20,000 one square meter subplots, but 344 of these plots were excluded from the project, thereby decreasing the number to 19,634 one square meter subplots. After the first census in 2001, these subplots were censed again in 2002, 2003 and 2004; while in the 2003 census all the data was taken for old seedlings and recruits as well, the 2002 and 2004 census that information was taken just for the recruits, and the mortality was the only information recorded for previous censed seedlings. Although these censuses included all types of woody seedlings, for my component of the project, I tended to focus more on the liana seedlings.

Data analysis

In this study seedling population sizes per hectare for trees, shrubs and lianas were calculated for each of the four censuses to estimate whether the populations were decreasing or increasing in size. For lianas, the total number of seedlings in each year was calculated by adding the number of new seedling recruits (recruitment) in a given year to the previous population and subtracting the number of death seedlings (mortality).

I used the total number of liana seedlings of each year to analyze species diversity with the statistical package PAST, (Hammer et al 2001), available on line at http://folk.uio.no/ohammer/past/. I calculated the different species index were and their confidence intervals using a bootstrap procedure of 1000 random samples, each with the same total number of individuals as in each original sample for each year (Hammer et al, 2001). Then I calculated the combined mean of the different indexes across the four year period, but I omitted the plants not identified to species level. I used these indices to compare the diversity of liana seedlings with that from other forests.

Liana seedlings were divided into two groups: freestanding (F) and support-seekers (SS). A third category, undetermined (U), became necessary because some seedlings were not recorded as either F or SS.

Soil data, collected by Jim Dalling, (Department of Plant Biology, University of Illinois) were available for each 20 x 20 m subplot of the 50 ha plot. These soil data include information on available aluminum, boron, calcium, copper, iron, magnesium, manganese, phosphorus, zinc, nitrate, ammonium nitrate and pH. To reduce the effect of co-linearity among nutrient variables, I exclude highly correlated variables in favor of those mineral nutrients assumed to be the most relevant for plant functions. Additionally, soil variables were centered and standardized to allow comparable estimations of the effects of each retained variable. I performed multiple linear regressions to analyze relationships between each response variable (the density of lianas, recruitment, mortality, and the transitions from a unsupported liana seedling to a host-attached liana plant in each 20 x 20 m subplot in 2003) and the level of each of the mineral nutrients (Al, B, Ca, Fe, Mg, Zn, and pH) and all possible interactions among them. Analyses were performed using the software package R, version 2.0.1(R Development Core Team, 2010). Finally a PCA was performed to reduce the dimensionality of the soil data and test the principle components for an effect on each response variables for year 2003. The 2003 census was selected to perform this analysis, because it was the only year were not only the recruits were measured, tagged, mapped and identified, but the also the already censed seedlings from previous years were measured for, seedling length, number of leaves, basal diameter, and if the liana seedling was attached to a host or not. Meanwhile, the 2002 and 2004 census were only mortality and recruitments census, in which, those measurements were performed only in recruits, while the old plants were censed just for alive or death status.

For each response variable, a fully-crossed model was fitted (full interaction), a model with all interactions excluded (additive model) was fitted, and backward, stepwise variable selection was used to find the 'best' combination of variables. Significant model fit along with significance of all included factors were used as criteria for the best model for each demographic variable.

Canopy data that were collected in 2001, 2003 and 2004 also were available courtesy of the CTFS. Canopy cover was estimated at the corner of each 5 x 5 m subplot as the percentage cover in eight height classes: 0-1m, 1-2m, 2-5m, 5-10m, 10-20m, 20-30m, and >30m. For each of these height classes the percent canopy cover was estimated to fall within the following categories: 0 = 0-10%, 10 = 10-25%, 25 = 25-50%, 50 = 50-75% and 75 = 75-100%.

I chose to use the three lowest height classes as indicators of understory heterogeneity to test for differences in seedling demography in response to understory structure. The highest cover was assumed to provide the highest probability of a liana seedling to find a suitable host. Plots with high understory cover were expected to have low density, low recruitment, moderate mortality, and highest rate of liana seedlings attaching to a host. Combining cover for the three lower height classes, I used linear regression to test the effect of understory structure on demography (density, recruitment, mortality, and the number of new liana seedling connected to their host).

Results

Out of a total of 15,055 liana seedlings counted by Comita´s field crew in the four censuses, individuals that were identified only to the genus level or the family level were discarded, reducing the number to 14,430 individuals including plants that died during the study period. These seedling populations including lianas, shrubs and trees contained in the 19,634 subplots of 1m^2 were 10,218 seedlings in the 2001 census, 10,750 in the 2002 census, 11,445 seedlings in 2003 and 11,933seedlings in 2004, which indicate that the total number of seedlings increased by 1715 seedlings during a 4 year period in the sampled area. Out of 95 liana species (Table 3.1), the most common species was *Mascagniahiraea* with 1326 seedlings in the four combined censuses. *Paullinia* was the genus with most species (10), and the family with most genera was the Sapindaceae (15). The density of lianas on average was 0.76 seedlings m^{-2}. The mean Shannon diversity index of the seedlings sampled in each of the four censuses 2001 to 2004 was 3.60. Simpson's diversity index and Fisher’s alpha also are provided (Table 3.2). The evenness index was 0.39, and the equitability was 0.79 (Table 3. 2).

The liana seedling population grew from a starting population of 5109 seedlings ha^{-1} in 2001 to a final population of 5746 seedlingsha^{-1} in 2004; a total increase of 637 seedlings ha^{-1} (Figure 3. 2A). The population of shrub seedlings also increased but at a faster pace than the liana seedlings: Shrubs started with a population of 6018 seedlings

ha^{-1} and grew to a final population of 6895 seedlings ha^{-1}; a net increase of 877 seedlings ha^{-1}(Figure 3.2B). For the tree seedlings the trend was opposite to the previous two seedlings type with a decrease in the total number of seedlings from 18,780 seedlings $ha^{-1}$to 17,261.5 seedlings ha^{-1}; a total decrease of 1518.5 seedlings ha^{-1}(Figure 3.2C).

Support-seekers liana seedlings contributed more to the aforementioned increase of the liana seedling population than did the freestanding seedlings. This is evident when one compares the increase in population size of the top ten most abundant species of each group (Figures 3.3 and 3.4). Almost all the support-seekers are increasing in numbers in a year to year basis (Figure 3.3) while the freestanding seedlings tended to increase at slower rates with some species even decreasing in population size (Figure 3.4).

The two liana seedling type, support-seekers versus freestanding showed significant differences in the mean of the yearly growth rates (increase in yearly population sizes) (Mann-Whitney pair wise comparison on Kruskall-Wallis test$H$=4.939, p=0.1763) (Figure 3.5)

The PCA was successful in facilitating variable reduction for the soil nutrients, with the first two components representing 82% of the variance (Table 3.3). In the first component Ca, Mg, B, and Zn have highest correlation with it, and Al and Fe are highly correlated with the second component. These two components, however, were not good predictors of the demographic variables. The fourth principle component, in which Fe and Mg showed higher correlation, was a significant predictor of seedling density ($F_{1,\,1248} = 11.12$, $p < 0.001$, $R^2 = 0.0088$) and the sixth, Mg, B, and Zn correlated, and seventh, Ca and Mg correlated, components were significant predictors of mortality ($F_{2,\,1228} = 11.12$, $p < 0.01$, $R^2 = 0.0079$).

In the multiple regression analysis the total number of liana seedlings increased from 2001 to 2004 (Figure 3.2A) with a consistent growth rate indicated by a high coefficient of determination in the multiple regression analysis (Table 3.4). In this analysis assessing the effect of soil nutrients on density, recruitment, mortality, and transition from seedling to a host attached plant was difficult because statistically significant results were coupled with very low coefficients of determination. The density of liana seedlings was better predicted by soil Al, Fe, and Mg levels (Table 3.4). Mortality was predicted by soil with higher Al, B, Ca, Zn, and pH levels (Table 3.4). No combination of soil variables significantly predicted recruitment and transition from free living seedling to a host attached plant (Table 3.4). Understory cover had a significant effect on all four demographic variables, but again the explained variance was very low (Table 3.4). Liana seedling density (slope of the relationship ± SE = 0.015 ± 0.0024), recruitment (0.019 ± 0.0025), mortality (0.001 ± 0.0006) and transition from unsupported to an attached (0.002 ± 0.0002) all increased with increasing understory cover, but again the effect was negligible (Table 3.4).

Discussion

Liana seedlings in the BCI 50 ha plot constitute 30 % of the total seedling population (Comita et al., 2007) indicating that lianas are likely to make a large contribution to the total dynamics of the forest. The calculated liana seedling diversity Fisher's alpha index of 12.6 in this study is very similar to a Bornean tropical forest ($\alpha \approx 12$) (DeWalt et al., 2006) and to a Costa Rican forest ($\alpha \approx 13.1$) (Mascaro, Schnitzer, & Carson, 2004).The index for the BCI 50 Ha plot is low, however, compared to an Ecuadorian forest (α ≈ 36.9) (Burnham, 2002). Similarly, the total number of liana species in the 50 Ha plot is lower than for the Ecuadorian forest but similar to the Bornean and Costa Rican forests.

The total population size of lianas shows a steady increase during the four-year period studied. This pattern agrees with previous results from other Tropical forests suggesting that liana populations are increasing worldwide (Swaine & Grace, 2007; Wright et al., 2004). Although the causes of this pattern remain unknown, many ecologists suggest that global climate change is partially responsible for the increase in liana population size. Additionally, extended dry seasons and lower total rainfall can contribute to successful colonization and rapid growth by liana seedlings (Clinebell et al., 1995; Körner, 2009; Phillips et al., 2002).

Previous studies had shown that not only population size but also the biomass of adult lianas is increasing (Wright et al., 2004) . In this study, I show that the number of liana seedlings is increasing as well, which might lead to an increased number of adult lianas and consequently total biomass. Longer dry seasons favor lianas in general because they can grow quickly and perhaps increase their density compared to trees (Restom & Nepstad, 2004; Schnitzer, 2005), and because liana seedlings can delay the closing of tree fall gaps, thereby retarding tree establishment during gap succession(Dewalt et al., 2000; Schnitzer et al., 2000). Adult lianas can increase tree mortality(Perez-Salicrup & Meijere, 2005; Putz, 1984) which will have an impact on the dynamics of the whole forest. More research is needed to assess that this trend of increasing liana abundance holds for different tropical forests.

My results did not support the hypothesis regarding interactions of liana seedling abundance with soil nutrients. I found significant relationships for example between recruitment of liana seedlings and soil nutrient characteristics, but all the models had a very low predictive power. Although a positive response to an increase in soil fertility, due to soil fertilization, was found in another liana seedling study (Hättenschwiler, 2002), and differences in general soil factors can affect liana population growth patterns (DeWalt et al., 2006), in my study, soil factors even though having a statistical significant relationship with recruitment and mortality, the predictive power of such relationships are very low to imply a cause-effect interaction between soil and demography. Perhaps the difference in nutrient availability across the 50 ha plot is not large enough to have an effect on the liana seedling population dynamics and spatial distributional pattern. Additional studies in other plots with larger variations in soil properties may help to corroborate the potential impact of soil characteristics on seedling demography.

Similar to soil mineral nutrients, understory structure of the forest measured at canopy cover is a very poor predictor for seedling mortality and recruitment. This unexpected result is contrary to results of a previous study that suggests that forest structure seems to be a strong predictor of liana abundance, even stronger than climate or soil (van der Heijden & Phillips, 2008). It is also contrary to my own results along the rainfall, rainfall seasonality gradient and soil types. The intervals for the percentage canopy cover may have been too broad and may have failed to accurately capture differences in understory structure.

Because both soil mineral nutrients and understory structure can be used to predict liana populations, I propose several ways to improve the accuracy of the prediction. First, for the soil data set, a larger sample area should be used, and instead of using the whole 50 ha plot as a sample unit, a random subsample using the 20 by 20 m plots as sample units should be used. For the understory and canopy structure it would be useful to collect quantitative data with the help of a fisheye lens to measure canopy openness or with the cheaper, but still reliable, densitometer instead of subjective categorization obtained by different observers.

My results show not only a steady increase in the liana seedling population, but also show that support-seeker liana seedlings are increasing at higher rate than are freestanding ones. Support-seeker lianas which thrive under high light conditions have been found to outgrow trees in forest gaps, and not only to delay forest succession but also to reduce tree growth rates which may affect their consequent ability to capture solar radiation (Dewalt et al., 2000). The reason for this increase in lianas in general still is unknown, and although lianas apparently can benefit from elevated CO_2 (Granados & Körner, 2002) or the increasing dry conditions predicted by global climate change models for tropical wet forests (Swaine & Grace, 2007). Lianas can affect several processes at the ecosystem level (DeWalt et al., 2006; Phillips et al., 2002; Schnitzer et al., 2000), and consequently I may expect that any change in liana populations will have a high impact on processes determining structure and function of the forests. At the seedling level, because liana seedlings can grow faster than tree seedlings(Cai, Poorter, Cao, & Bongers, 2007), lianas seedlings, especially the support-seekers that grow the fastest, can dominate seedling communities.

In this study, I have shown that the liana seedling bank of the 50 hectare plot on BCI is as diverse as those are in other tropical forests. I cannot relate liana seedling demography to soil nutrients or canopy characteristics; however, more work is needed to determine what controls species seedling distributions at this scale. Nonetheless, most important is that liana seedlings are increasing in number compared to trees which are decreasing, and among liana seedlings, the support-seekers are increasing in number faster than the freestanding ones. All of these events that occur at an early stage of the plants life cycle are of outmost importance for understanding the ecology of tropical forests.

Acknowledgements: I thank Liza Comita and Stephen Hubbell, the responsible persons of the seedling census. Canopy data collection from 2003-2007 was funded by NSF grant DEB-0075102 to Steve Hubbell. Soil data were graciously provided by Jim Dalling with funding from NSF DEB021104, 021115, 0212284, 0212818 and OISE 0314581to the STRI Soils Initiative and CTFS.

Table 3.1. Abundance of seedlings by species in the 50 hectare plot from the first census in 2001 (initial population) to the last one (2004) utilized for this study. Information included is the species name, species code, family, and the seedling type: support-seeker (SS) or freestanding (F); those species without enough information to be classified in one of the two groups are designated undetermined (U).

Species Name	Species Code	Family	Seedling Type	Initial Population	Population 2002	Population 2003	Population 2004
Abuta racemosa	ABUTRA	Menispermaceae	SS	300	353	436	503
Acacia hayesii	ACACHA	Fabaceae-Mimosoideae	SS	282	292	305	310
Aegiphila cephalophora	AEGICE	Verbenaceae	U	158	169	149	124
Aegiphila elata	AEGIEL	Verbenaceae	U	86	103	121	133
Aristolochia cordiflora	ARISGI	Aristolochiaceae	SS	0	0	0	1
Aristolochia tonduzii	ARISTO	Aristolochiaceae	SS	1	1	2	4
Arrabidaea verrucosa	ARRAVE	Bignoniaceae	SS	8	9	12	11
Byttneria aculeata	BYTTAC	Bignoniaceae	U	1	0	1	1
Callichlamys latifolia	CALLLA	Bignoniaceae	F	338	362	380	356
Celtis iguanaea	CELTIG	Ulmaceae	SS	31	28	31	30
Ceratophytum tetragonolobum	CERATE	Bignoniaceae	SS	55	53	39	34
Chiococca alba	CHIOAL	Rubiaceae	U	5	5	6	5
Chomelia barbellata	CHOMAT	Rubiaceae	U	2	2	3	3
Chondrodendron tomentosum	CHONTO	Menispermaceae	SS	30	29	32	44
Clitoria javitensis	CLITJA	Fabaceae-Papilionoideae	F	60	56	53	55
Cnestidium rufescens	CNESRU	Connaraceae	F	65	72	63	66
Coccoloba parimensis	COCCP1	Polygonaceae	F	338	345	360	369
Combretum decandrum	COMBDE	Combretaceae	SS	8	8	10	8
Combretum laxum	COMBLA	Combretaceae	SS	33	32	34	35
Connarus panamensis	CONNPA	Connaraceae	F	5	5	6	6
Connarus turczaninowii	CONNTU	Connaraceae	F	334	341	338	337
Davilla nitida	DAVINI	Dilleniaceae	SS	24	24	34	40

Species Name	Species Code	Family	Seedling Type	Initial Population	Population 2002	Population 2003	Population 2004
Desmodium axillare	DESMAX	Fabaceae-Papilionoideae	SS	37	37	43	41
Doliocarpus dentatus	DOLIDE	Dilleniaceae	SS	1	0	2	2
Doliocarpus major	DOLIMA	Dilleniaceae	SS	725	811	919	1027
Doliocarpus multiflorus	DOLIMU	Dilleniaceae	SS	11	15	20	31
Doliocarpus olivaceus	DOLIOL	Dilleniaceae	SS	285	294	342	362
Fischeria blepharopetala	FISCBL	Asclepiadaceae	U	3	6	4	4
Forsteronia myriantha	FORSMY	Apocynaceae	SS	16	13	8	6
Forsteronia viridescens	FORSVI	Apocynaceae	SS	17	21	23	26
Heteropterys laurifolia	HETELA	Malpighiaceae	SS	18	19	16	15
Hippocratea volubilis	HIPPVO	Hippocrateaceae	F	347	422	501	545
Hiraea faginea	HIRAFA	Malpighiaceae	F	13	16	18	19
Hiraea grandifolia	HIRAGR	Malpighiaceae	F	90	88	92	92
Hiraea smilacina	HIRAQU	Malpighiaceae	F	36	42	47	53
Hiraea reclinata	HIRARE	Malpighiaceae	F	975	982	1017	1044
Hylenaea praecelsa	HYLEPR	Hippocrateaceae	U	0	1	1	1
Justicia graciliflora	JUSTGR	Acanthaceae	SS	137	128	103	97
Macfadyena unguis-cati	MACFUN	Bignoniaceae	SS	186	205	237	250
Machaerium pittieri	MACHAR	Fabaceae-Papilionoideae	F	65	64	69	70
Machaerium floribundum	MACHFL	Fabaceae-Papilionoideae	F	1	2	3	3
Machaerium isadelphum	MACHM1	Fabaceae-Papilionoideae	F	12	10	12	12
Machaerium milleflorum	MACHM2	Fabaceae-Papilionoideae	F	91	103	103	101
Machaerium seemannii	MACHSE	Fabaceae-Papilionoideae	F	9	9	11	11
Maripa panamensis	MAR2PA	Convolvulaceae	SS	290	326	414	350
Marcgravia nepenthoides	MARCNE	Marcgraviaceae	U	1	0	0	0

Species Name	Species Code	Family	Seedling Type	Initial Population	Population 2002	Population 2004	Population 2003
Marsdenia crassipes	MARSCR	Asclepiadaceae	SS	2	5	2	3
Mascagnia hiraea	MASCHI	Malpighiaceae	SS	842	948	1136	1062
Mascagnia ovatifolia	MASCNE	Malpighiaceae	SS	169	205	218	221
Mendoncia gracilis	MENDGR	Acanthaceae	SS	18	8	7	4
Mendoncia litoralis	MENDLI	Acanthaceae	SS	3	3	4	3
Mikania leiostachya	MIKALE	Asteraceae	U	17	13	5	5
Odontocarya tamoides	ODO2TA	Menispermaceae	U	1	2	2	2
Omphalea diandra	OMPHDI	Euphorbiaceae	F	16	14	13	15
Paragonia pyramidata	PAR1PY	Bignoniaceae	F	183	198	223	224
Passiflora ambigua	PASSAM	Passifloraceae	SS	3	7	11	8
Passiflora vitifolia	PASSVI	Passifloraceae	SS	0	2	3	3
Paullinia baileyi	PAULBA	Sapindaceae	F	260	278	358	329
Paullinia bracteosa	PAULBR	Sapindaceae	F	93	90	97	97
Paullinia fibrigera	PAULFI	Sapindaceae	F	133	140	150	153
Paullinia fuscescens var. glabrata	PAULG1	Sapindaceae	F	3	1	4	4
Paullinia glomerulosa	PAULG2	Sapindaceae	SS	28	31	25	27
Paullinia pinnata	PAULPI	Sapindaceae	SS	2	12	12	12
Paullinia pterocarpa	PAULPT	Sapindaceae	F	154	159	161	162
Paullinia rugosa	PAULRU	Sapindaceae	F	45	44	49	44
Paullinia turbacensis	PAULTU	Sapindaceae	SS	535	555	614	593
Petrea volubilis	PETRAS	Verbenaceae	F	336	336	300	318
Phryganocydia corymbosa	PHRYCO	Bignoniaceae	F	292	303	322	306
Piper aristolochiaefolium	PIPEA2	Piperaceae	SS	2	4	0	1
Pisonia aculeata	PISOAC	Nyctaginaceae	U	2	3	6	6

Species Name	Species code	Family	Seedling Type	Initial Population	Population 2002	Population 2004	Population 2003
Pithecoctenium crucigerum	PIT2CR	Bignoniaceae	SS	98	113	100	109
Pleonotoma variabilis	PLEOVA	Bignoniaceae	SS	34	34	36	35
Prestonia obovata	PRESOB	Apocynaceae	U	18	22	30	29
Prionostema aspera	PRI1AS	Hippocrateaceae	SS	480	503	553	536
Rhynchosia pyramidalis	RHYCPY	Papilionoideae	SS	64	70	82	80
Rourea glabra	ROURGL	Connaraceae	F	29	31	29	28
Serjania circumvallata	SERJCI	Sapindaceae	SS	71	81	115	102
Serjania mexicana	SERJME	Sapindaceae	SS	10	16	23	21
Serjania rhombea	SERJRH	Sapindaceae	SS	38	41	36	38
Smilax mollis	SMILMO	Smilacaceae	SS	4	3	3	3
Smilax spinosa	SMILS1	Smilacaceae	SS	3	3	10	5
Smilax spissa	SMILS2	Smilacaceae	SS	0	2	2	2
Solanum adhaerens	SOLALA	Solanaceae	SS	13	14	10	12
Stizophyllum riparium	STIZRI	Bignoniaceae	SS	9	11	12	10
Strychnos brachistantha	STRYBR	Loganiaceae	F	73	77	76	81
Strychnos darienensis	STRYDA	Loganiaceae	F	1	1	1	1
Strychnos panamensis	STRYPA	Loganiaceae	F	18	20	16	17
Strychnos toxifera	STRYTO	Loganiaceae	F	0	0	3	0
Tetracera hydrophila	TET1HY	Dilleniaceae	SS	1	1	0	1
Tetracera portobellensis	TET1PO	Dilleniaceae	SS	50	54	65	66
Tetrapterys goudotiana	TET3MA	Malpighiaceae	SS	33	35	41	41
Thinouia myriantha	THINMY	Sapindaceae	SS	165	184	194	198
Tournefortia hirsutissima	TOURHI	Boraginaceae	U	1	1	0	1
Uncaria tomentosa	UNCATO	Rubiaceae	U	1	0	0	0

Table 3.2**.** Means of the diversity indices calculated using the means in each of the census years, from 2001 to 2004, and bootstrapped 95 % confidence intervals for liana seedlings of the 50 Ha plot.

	BCI	Lower	Upper
Species	95	89	95
Individuals	14430	14430	14430
Dominance D	0.03988	0.03906	0.04095
Shannon's H	3.602	3.58	3.616
Simpson's 1-D	0.9601	0.959	0.9609
Evenness e^H/S	0.386	0.3851	0.4115
Equitability J	0.791	0.7899	0.8026
Fisher's alpha	13.64	12.64	13.47

Table 3.3. Principal components analysis for soil variables, correlations (loadings) coefficients between soil variables and each component, eigenvalues, and the cumulative percent of variation explained by each additional component.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Al	0.245	-0.662	0.616	-0.284	0.192		
B	-0.423		0.252	-0.34	-0.493	-0.573	-0.264
Ca	-0.445	-0.102	-0.11	-0.233			0.842
Fe	-0.324	-0.549		0.693	-0.308		
Mg	-0.425	-0.144	-0.186	-0.426		0.614	-0.447
Zn	-0.424			0.117	0.777	-0.425	
pH	-0.311	0.47	0.709	0.273		0.311	
Eigenvalue	4.653	1.103	0.534	0.328	0.207	0.121	0.055
Cumulative % of Variance	0.665	0.822	0.899	0.945	0.975	0.992	1.000

Table 3.4. Results of multiple regression models using either liana seedling population size, recruitment, mortality, or transition as the response variables, and years, soil factors and understory structure as predictor variables. The first column indicates which variables were tested. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.

Multiple regression	*F*	Df	*p*	Multiple R^2	Residual SE	Df
Total population from year 2001 to 2004	207	1, 2	0.004799*	0.9904	0.05346	2
Full interaction model, effect of soil factors on recruitment in 2003	1.29	127, 122	0.02263*	0.1271	0.6526	1122
Additive model, effect of soil factors on recruitment in 2003	1.24	7 , 1242	0.2772	0.00694	0.6616	1242
Full interaction model, effect of soil factors on the total population in 2003	1.87	127, 1122	1.34E-07***	0.1743	0.6138	1122
Additive model, effect of soil factors on the total population in 2003	6.47	3, 1246	0.000242**	0.01533	0.6361	1246
Effect of understory openness on the total population in 2003	40.1	1, 1248	3.40E-10***	0.03112	0.6305	1248
Effect of understory openness on the mortality in 2003	3.94	1, 1229	0.04748*	0.00319	0.1489	1229
Effect of understory cover on transitioning to SS in 2003	36.8	1, 1226	1.73E-09***	0.02915	0.0757	1226
Effect of soil factors on mortality in 2003	1.28	117, 1113	0.02976**	0.1185	0.1472	1113
Effect of soil factors on transitioning to SS in 2003	1.21	109, 1118	0.07759*	0.1056	0.07609	1118

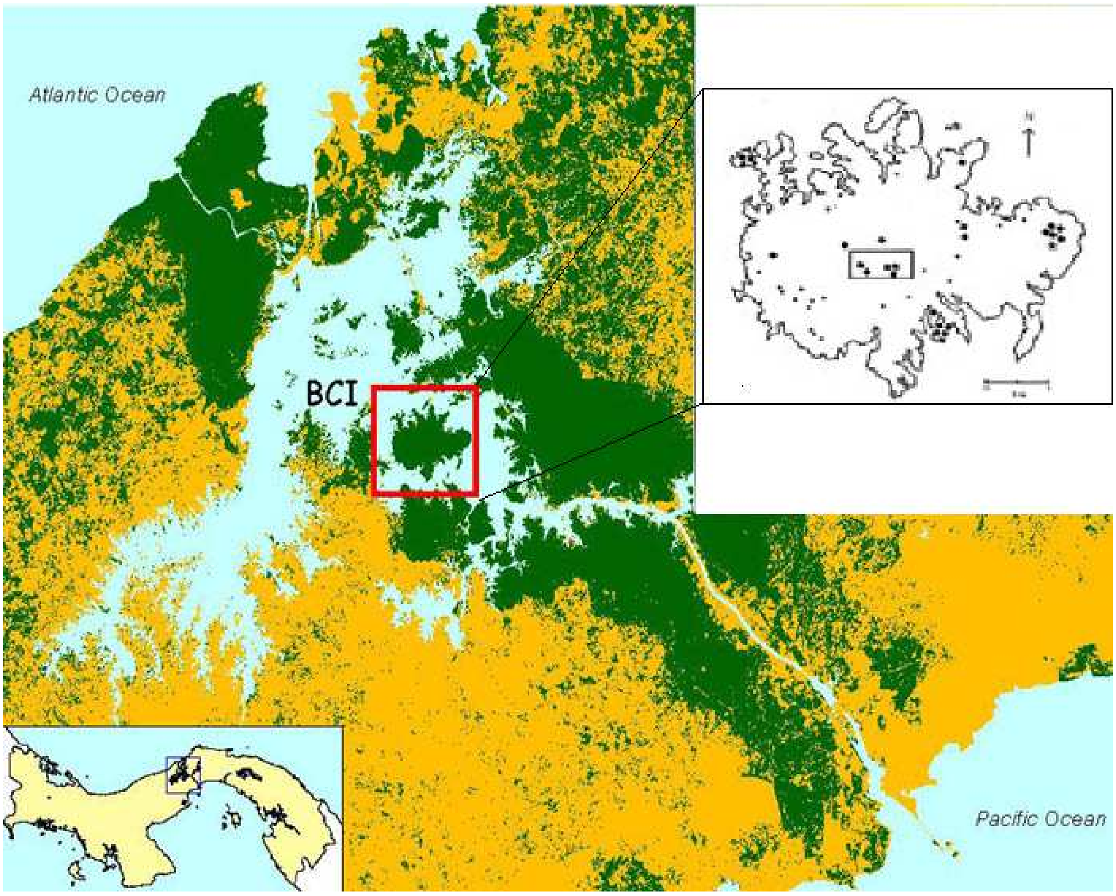

Figure 3.1. The 50 hectare plot (central rectangle on right insert) on Barro Colorado Island, Panama (left insert), Areas colored in green represent continuous forest cover and in yellow deforested areas with predominance of grasslands and urban areas.

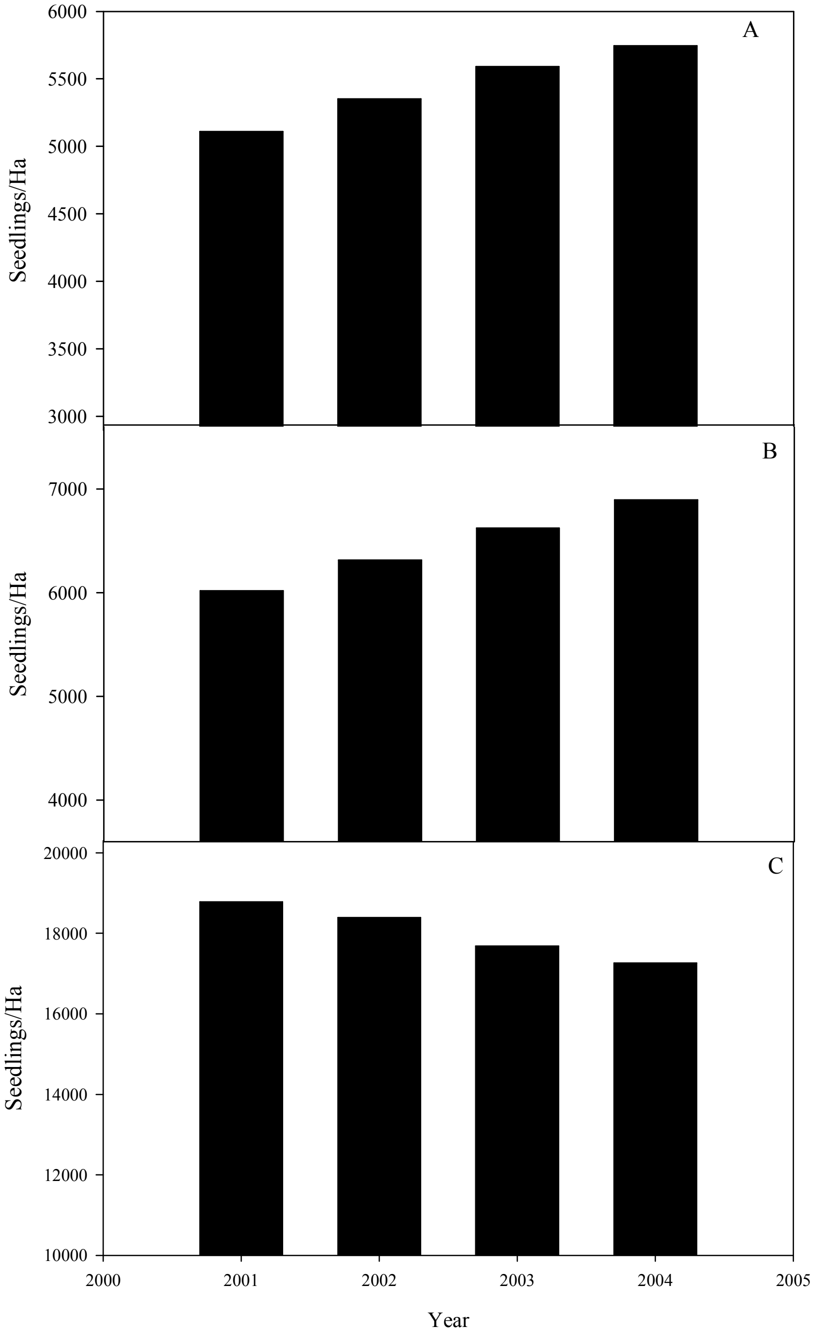

Figure 3.2. Changes in the numbers of seedlings per ha for: (A) lianas (B) shrubs and (C) trees.

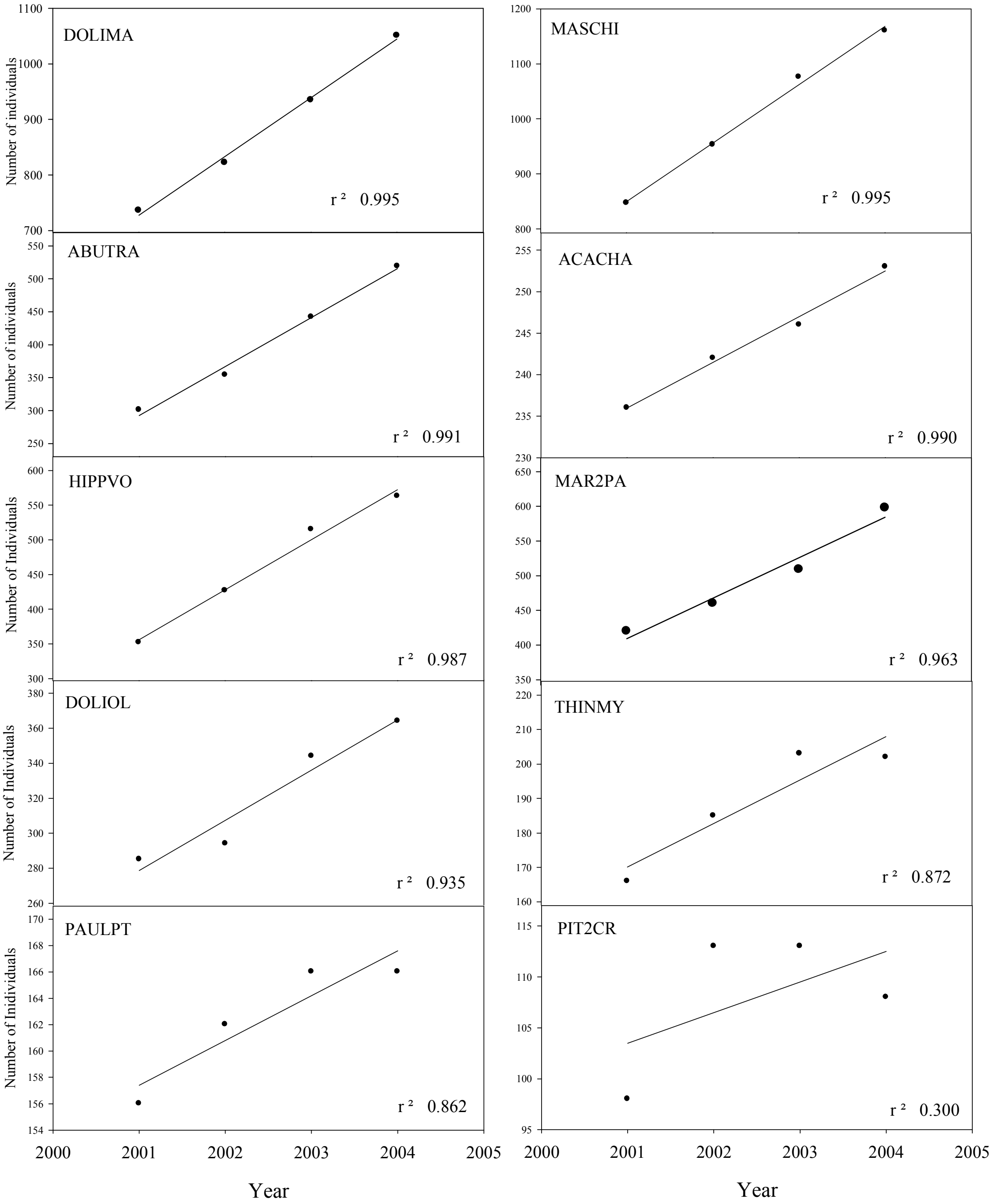

Figure 3.3. Changes in the population sizes of the ten most common species (species codes as in Table 3.1) of support-seeker liana seedlings with best-fit, least-squares regression lines and coefficients of determination (r^2). The species are ordered from the best-determined positive to the most poorly determined and negative relationships.

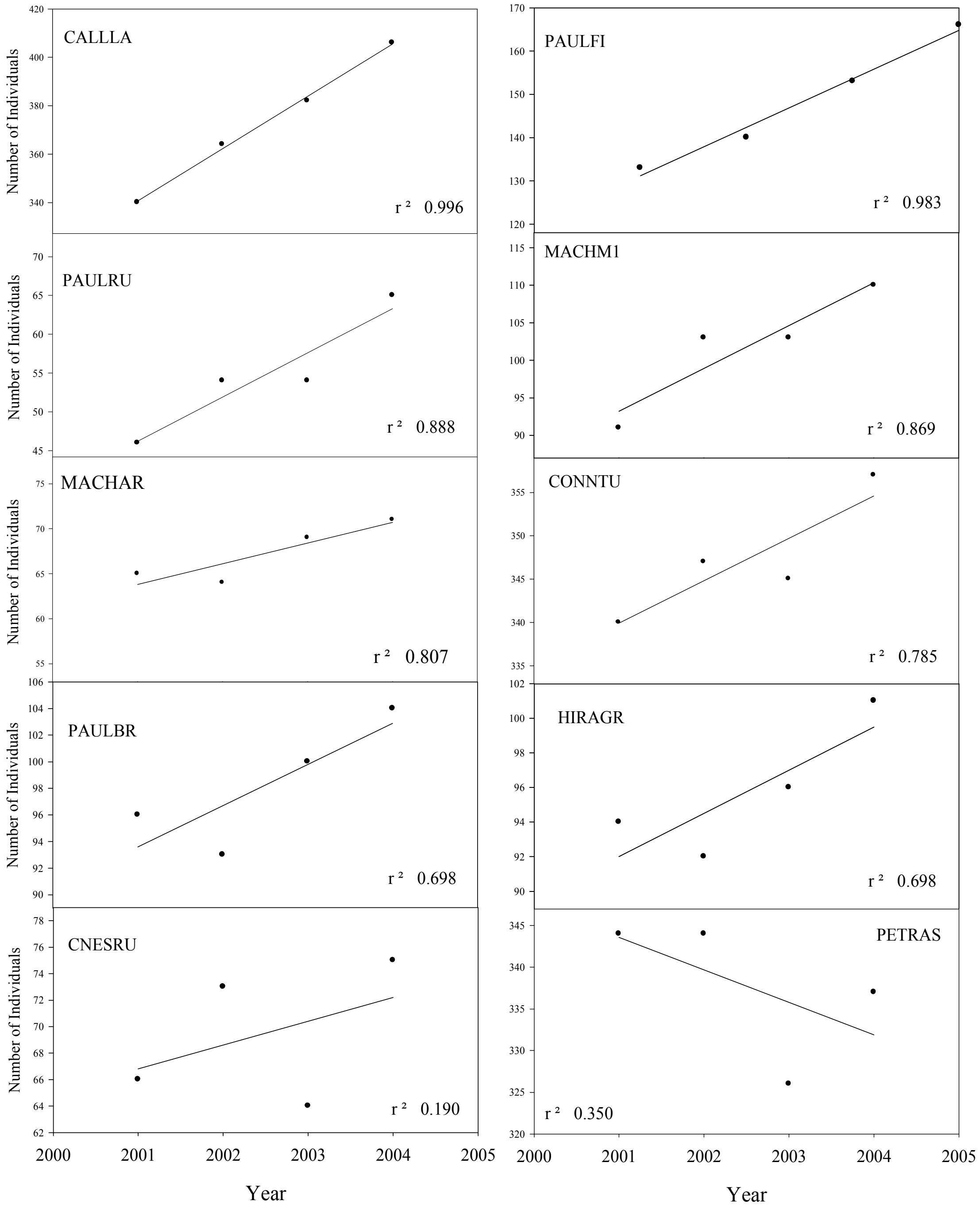

Figure 3.4. Changes in the population sizes of the ten most common species (species codes as in Table 3.1) of freestanding liana seedlings with best-fit, least-squares regression lines and coefficients of determination (r^2). The species are ordered from the best-determined to the most poorly determined.

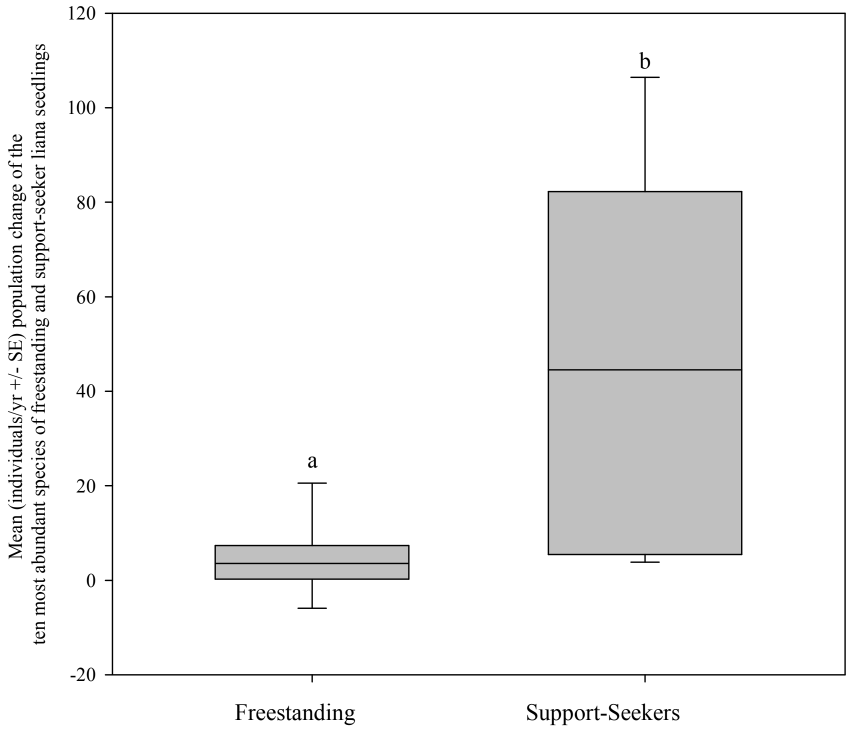

Figure 3.5. Mean population change (slope of the population sizes from 2001 to 2004) for the ten most common species of freestanding and support-seekers liana seedlings, boxes with different letters showed significative differences (Mann-Whitney pairwise comparison Kruskall-Wallis, H:4,939, *p*=0.1763)

Chapter 4

Life history traits and physiology of freestanding and support-seekers seedlings

In Ecophysiology, a trade-off is an important conceptual framework that can be broadly characterized as the costs and benefits for an organisms having any given trait (Lambers, Chapin, & Pons, 2008), or as a negative functional relationships between traits (Kneitel & Chase, 2004). Physiological trade-offs in carbon allocation have a direct impact on life history traits, and may help to understand how different species can have different responses and adaptations to limiting resources, and its impact on structure and function at the ecosystem level (Bonsall, Jansen, & Hassell, 2004; Gilbert et al., 2006; Kneitel, Chase, & Letters, 2004; Stearns, 1989).

Lianas are a common and important component of tropical and subtropical forests. Plants of this polyphyletic group (Gentry, 1991) start their life cycle on the forest floor and use the surrounding vegetation to climb up to the upper canopy (Gentry, 1991; Putz & Windsor, 1987; Schnitzer & Bongers, 2002). Seedlings of lianas have not been systematically studied, despite being an important stage on the plant life cycle. Despite lianas having a distinct ontogenetic behavior after germination and seedling emergence, little information is known on the physiology and trade-offs of liana seedlings (Schnitzer & Bongers, 2002). For the development of liana seedlings it is particularly critical that they find structural support before they can fully develop to maturity and reach the upper canopy of the forest. Because lianas do not invest on their own support tissue as much as canopy trees, they can invest more in growth, producing long slender stems, and might have a relatively small leaf surface area per individual.

Lianas, In general, have two different ontogenetic stages; first they can grow independently as a freestanding organism before they make contact with the host; Secondly, they reach the upper tree canopy with the help of an external support. Even though all liana seedlings exhibit these two life cycle stages, some of them can grow as freestanding for a relatively long period of time and maintain the stems in an upright position such that they resemble more the architecture of a shrub (freestanding seedlings) (Kennard, 1998, Gallenmuller, Rowe, & Speck, 2005; Putz, 1984). Other lianas grow as freestanding for a short period of time searching at the same time for an appropriate host support earlier in their life cycle than the freestanding, (Gerwing, 2004; Putz, 1984). We call this group, support-seekers seedling. Most of the liana studies have focused on the abundance of liana seedlings (Gerwing, 2004; Gerwing & Farias, 2000; Kennard, 1998; Putz, 1984) or on their biomechanics of these two groups (Gallenmuller et al., 2005; Rowe et al., 2004; Rowe & Speck, 1996). However, there is no study that elucidates the physiological differences between the different growth patterns of both liana seedling groups

These two seedling growth patterns might be related to tradeoffs in resource allocation and life history traits. I am hypothesizing that freestanding lianas will grow slower than support-seekers lianas and invest more in self-support tissue, while the support-seekers seedlings will invest more resources in rapid growth. The differences between both groups of liana seedlings might reflect a trade-off in terms of capturing light limiting resource in the forest understory (Gilbert et al., 2006; Montgomery, 2004;

Swaine & Whitmore, 1988). The freestanding seedlings that grow relatively slow might be more shade tolerant than support-seekers seedling species which may be more similar in some aspects to the fast growing, light demanding pioneer species.

Most of the studies on hydraulic architecture of lianas were related to comparisons between lianas and trees; usually lianas have some of the widest xylem vessels in nature and thus being very efficient in long distance water transport (Ewers & Fisher, 1989; Ewers et al., 1989) compared to shrubs or trees of a comparable stem diameter (Ewers & Fisher, 1989; Gartner et al., 1990; Gartner, 1991a).

I will analyze the physiology of these two groups of liana seedlings, and in particular some aspects of their photosynthetic rates and hydraulic architecture. I expect physiological differences such as higher photosynthetic rates and more leaf surface area per individual in freestanding liana seedlings and higher hydraulic conductivity and slender stems in non-free-standing liana seedlings. Additionally, since freestanding lianas apparently allocate more resource to support tissue I will expect them to have thicker stems, and lower specific hydraulic conductivity (Ks) at comparable age.

Finally, another physiological aspect in which I expect both functional groups of liana seedlings to differ is in photosynthetic rates. I developed photosynthetic light curves using seedlings that have been growing under gap and understory light conditions and estimate electron transport rates (ETR), a proxy to photosynthetic rates (Beer et al., 1998; Ralph & Gademann, 2005), at different light levels. I expect that the support-seekers lianas will have higher ETRs, than the freestanding ones when both types of seedlings grow in a high light environment.

Methods

Plant material and experimental design

I collected seeds of eight species of lianas from 4 to 5 individuals of each species, in Barro Colorado Island (BCI) and along the Pipe Line road and planted them in individual containers in a shade house of the Smithsonian Tropical Research Institute (STRI), located in the town of Gamboa next to the Panama Canal. The eight species and their proposed functional group are indicated in Table 4.1.

The seeds were allowed to germinate and grow in a shade house where the mean maximum Photosynthetic Photon Flux Density (PPFD) was 55.70 μmol m^{-2} s^{-1}. I measured PPFD during five consecutive days in the dry season using a Li-190 SA Quantum sensor (LiCor, NE, USA) connected to a data logger (CR10X, Campbell Scientific, Logan, UT, USA). Each seedling was numbered and after reaching 20 cm height each one was randomly assigned to the different treatments.

For one of the experiments I grew 50 seedlings per species in the shade house (55.70 μmol m^{-2} s^{-1}) without any structural support for a period of 12 months. The percentage of the seedlings that bent more than 45 degrees form the vertical (upright) position was recorded to determine the species-specific potential to be free or support-seeker. After 12 month, I randomly harvested ten plants from each species and oven-dried leaves, stems and roots of each seedling to obtain the biomass fraction that each seedling allocated to the different tissues.

For another experiment, ten seedlings per species were assigned in the greenhouse to either under low or high light levels: 172.47μmol m^{-2} s^{-1} and 530 μmol m^{-2} s^{-1}, simulating the understory and gap light conditions respectively. The seedlings were also measured every month for a period of 12 months. The maximum stem length after that period of time (t) was recorded and the change in length was used to estimate Relative Growth Rate (RGR):

$$RGR = \frac{[ln(final\ plant\ length) - ln(initia\square\ plant\ length)]}{t}$$

Hydraulic Architecture

Hydraulic architecture studies consisted of vessel length, hydraulic conductivity (Kh), specific conductivity (Ks), leaf-specific conductivity (Kl). Hydraulic conductivity (Kg s-1MPa^{-1} m) is the rate of water flow (F) in Kg s^{-1} divided by the pressure gradient (Δp) in MPa that is the driving force of the flow across the length of the stem segment Δl(m):

$$Kh = \frac{F(Kg\ s^{-1})}{((\Delta P(Mp))/\Delta l(m))}$$

The diameter of any given stem was used to calculate Specific Hydraulic Conductivity (Ks), which is defined as the volume of water through the cross sectional area of stem xylem:

$$Ks = \frac{kh}{(A\ xylem\ )}$$

Where *A xylem* is the active xylem area of each of the segments used to measured Kh. This is an estimate of the specific efficiency of water transport of the liana stem for each one of the seedlings species.

I used the leaf area of the seedling distal to the stem used to measure Ks to obtain an estimate of the Leaf-specific hydraulic conductivity (Kl):

$$Kl = \frac{Kh}{A\ leaf}$$

where *A leaf* is the leaf area distal to the stem. This is an estimate of how efficient a stem is in supplying water the leaves distal to that given stem segment or plant.

Plants were harvested from the greenhouse; each seedling was cleaned of soil from its roots. I cut the stem segment under water, to avoid embolisms in the xylem. Each segment was then attached to a water filled hydraulic apparatus system that consisted of a series of tubing connected to a reservoir: The reservoir was 70 cm higher above the samples. The solution in the system was a 0.5 mmol^{-1} KCL solution of distilled, degasified and filtered water. At the distal end of each segment, I attached a 5 ml, divided in 0.1 ml sections, serological pipette using latex tubing to volumetrically measure water flow.

At the beginning of each trial the initial volume, *Vo*, was recorded and then the water solution was allowed to run for 20 min. At the end of this period of time the final volume, *Vf*, was recorded, and the difference, was used against the time (in seconds) to find the Flow, *F*, through the system.

The xylem area was measured using digital images obtained with a digital camera attached to a binocular microscope, and the Image J software was used to measured xylem area (Abramoff, Magalhães, & Ram, 2004). Leaves were dried for a 48 hour period in an oven and kept at 60 °C to determine the leaf mass per area (LMA). The leaf area (fresh leaves) was calculated by scanning the leaves after excision and using the same software, image J system (Abramoff, Magalhães, & Ram, 2004). Leaves were dried for a 48 hour period in an oven kept at 60 °C to determine the leaf mass per area (LMA).

I tested for significant differences in the means and between species of the same family using the Past software (Hammer, Harper, & Ryan, 2001).

Fluorescence kinetics

I use an instrument that measure fluorescence kinetics (ETR) to build the photosynthetic light response curves for the lianas species, since it has been proven that ETR derived from light curves can be used as a measure of overall photosynthetic efficiency (Beer et al., 1998; Maxwell & Johnson, 2000; Ralph & Gademann, 2005; White & Critchley, 1999). The light curves were obtained for seedlings that grew under gap and understory light conditions and were used to estimate electron transport rates (ETR). After growing the seedlings at these light levels for three months, I measured photosynthesis fluorescence with a MINI-PAM (Heinz Walz GmbH, Effeltrich, Germany).

The fluorescence response of each plant to different light levels was recorded using eight values of PPFD starting at 5 μmol m^{-2} s^{-1} and ending around 1800 to 2000 μmol m^{-2} s^{-1}. At each light level, a saturation pulse of 0.8 s was applied to the leaf surface followed by a recovery period of 30 second to one minute to create a light response curve (LRC) for plants growing under each type of light environment. Each plant was covered with a black plastic bag to avoid external light influence throughout the measurement period. Values of ETR, for each light level were recorded to build the LRC and the PPFD value at which each plant reach the maximum ETR was recorded.

I tested for significant differences between the physiological and life history traits of the two functional groups using ANOVA tests. In addition a PCA multivariate analysis was performed. The following orthogonal variables were used: leaf area, electron transport rate, maximum length, and stem cross sectional area, specific hydraulic conductivity and leaf specific hydraulic conductivity.

Results

After three months, three of the liana seedling species grown under similar environmental conditions started to bend naturally without the presence of any structural support (Figure 4.1). After 12 months of growth, 30-60% of the individuals of these 3 species deviated substantially from the vertical position. These three species were members of the support-seekers liana seedlings group. None of the proposed freestanding seedlings had bent after 12 months of growth (Figure 4.1). Consistent with the natural bending behavior, the three support-seekers liana seedlings at 12 month age, had smaller stem cross sectional area than the freestanding liana seedlings (one way ANOVA $F_{7,72}= 50.36, p>0.01$) (Figure 4.2).

Total leaf area per seedling was substantially lower in the four support-seekers seedling species compared to the freestanding seedling species (Figure 4.3). The four support-seekers liana species had an average of total leaf surface area per plant of 350 cm^2, while the four freestanding lianas species had a leaf surface area per plant of $850cm^2$. However, only the two species that behaved as support-seekers, (PIT2CR and ACACHA) showed statistical difference in leaf surface area compared to the other seedlings (one way ANOVA $F_{7,32}= 5.798, p>0.005$). A linear functional relationship was observed between stem cross sectional area and total leaf surface area per plant (Figure 4.4). The four freestanding liana seedlings had higher leaf and cross sectional stem areas compared to the support-seekers liana seedlings. Leaf mass per area (LMA) tended to be lower in the four support-seekers seedling species showing substantially lower LMA than the freestanding seedling species (Figure 4.5).

Liana seedling length of one support-seekers was substantially longer after 12 months of growth under high light conditions, and the statistical difference was especially large for the support-seeker PIT2CR (one way ANOVA $F_{7,56}$= 60.74, p>0.05, (Figure 4.6 A). The four free-standing liana seedlings length was substantially shorter compared with the support-seekers seedlings for plants growing under the low light, conditions with the exception of SERJAT (one way ANOVA $F_{7,56}$= 65.68, p>0.05) (Figure 4.6 B).

Relative growth rates of seedlings grown under high light conditions varied across species (Fig 4.7 A). However one support-seekers seedling species appears to grow substantially faster than the other liana seedling species (one way ANOVA $F_{7,61}$= 7.84, $p>0.001$) (Figure 4.7 A), The RGR did not show statistical differences among species when grown under low light conditions (Figure 4.7 B). Differences in biomass allocation between roots stem and leaves between support-seekers and freestanding seedling species was not observed (results not shown).

Specific hydraulic conductivity tended to be higher in the support-seekers liana seedlings, PIT2CR, ACACHA and MACHM2, with the exception of SERJAT that had the lowest Ks (Figure 4.8 A). Three of the freestanding seedlings, PETRAS, CALLLA and TONTOV, were in the same group, with the exception of CNESRU that was grouped with the support-seekers seedlings (one way ANOVA $F_{7,32}$= 36.34, p>0.01, Figure 4.8 A). Leaf species-specific hydraulic conductivity showed significant differences between seedlings (one way ANOVA $F_{7, 32}$= 59.46, p>0.001), and the freestanding lianas seem to have closest values than the support-seekers (Figure 4.8 B).

Species specific maximum ETR differed across species under different growing lights (Figure 4.9 A). Under high light levels three support-seekers seeding species (PIT2CR, ACACHA and SERJAT) had lower ETR compared to the other species and only SERJAT showed significant differences in ETR when compared to the freestanding seedling species (one way ANOVA $F_{7,32}$= 17.86, p>0.001). CALLLA and PIT2CR where in the same group with three freestanding species, and TONTOV was grouped with the support-seekers MACHM2, under low light levels max ETR’s across species (Figure 4.9 B) showed statistical significances (one way ANOVA $F_{7,32}$= 4.23, p>0.05*,* Tukey’s HSD test).

Results of the Principal Components Analysis indicate that the two liana seedling functional groups tended to be separated in different areas of the ordination plots (Figure 4.10). Two support-seekers liana species (PIT2CR and ACACAHA) are located on the right of the PC1.CALLLA, CNESRU and TONTOV and PETRAS are located on the left of the PC1. MACHM2 and SERJAT are intermediates. The first three PCA´s explained 56.35 18.11% and 14.63 % of the variation for a total of 89.9 % of the cumulative variation (Table 4.2). The eigenvectors, that is the values of the coefficients in the linear combinations of each one of the variables making up PCA, are shown in Table 4.3.

Discussion

This research investigates the physiological traits of liana seedlings and attempts to identify the characteristics of two functional groups based on their growth and physiological traits. The results of the study support the idea that some species of liana seedlings are more prone to bend at an earlier age than others. The first group is the support-seekers and the second group of seedlings (freestanding) includes those seedlings that do not bend during the early stages of their life cycles and remains as small shrubs for a relatively long period of time. In the absence of a physical support, the support-seekers liana seedlings bent, which suggest that it is a biomechanical behavior helping them to search for a mechanical support. Consistent with the lack of structural stiffness, the stem cross sectional area of the support-seekers liana seedlings was significant smaller than the stem of freestanding seedlings which means that the freestanding are more mechanically stable than the support-seekers seedlings.

The support-seekers seedlings exhibited not only longer stem length than the freestanding seedlings but also higher relative grow rates, in particular when growing under high light environments. Two previous studies, compared the structural stability of shrub and liana forms of *Toxicodendrum diversilobium* in California and *Croton nuntians* in Guyana. For *C. nutians* the liana form had lower stem cross sectional area (Gallenmuller et al., 2005; Gartner, 1991b) and *T. diversilobium* liana form grew longer than the shrub growth form (Gartner, 1991b). In my study, I compared not only some biomechanical and morphological traits but also physiological traits of eight different species of lianas. Although my first idea was that there were clearly two seedling groups, the support-seekers species which include PIT2CR, ACACHA, MACHM2 and SERJAT, and the freestanding CALLLA, PETRAS, CNESRU and TONTOV, my results characterized PIT2CR, ACACHA as support-seekers, while CALLLA, PETRAS, CNESRU, TONTOV as freestanding seedlings. However, MACHM2 and SERJAT which I expected to behave as a support-seekers seedling exhibited intermediate characteristics between both groups. Previous studies show that the congeneric species of MACHM2, *M. cuspidatum*, in Ecuador grows well under low light environments and attach to a host early in their life cycle (Nabe-Nielsen, 2002), and are associated with early successional stages of vegetation dynamics (Gerwing, 2004).

Adult lianas showed high RGR in gaps than in the forest understory (Avalos & Mulkey, 1999). My study indicates that PIT2CR, a support-seekers lianas seedling, showed the highest RGR across all seedlings studied in high light environment, but interestingly, plants of this species acclimate to the low light environment as well in the greenhouse. Under these low light conditions I did not find any significant difference among seedlings of different species, whether they were free or support-seekers liana seedlings. This results suggests a plastic response to changes in light environment, previously observed in other liana species (Avalos & Mulkey, 1999)

Freestanding lianas show higher leaf area together with higher stem cross sectional area, and when both morphological characteristics are plotted in a regression the freestanding are at the high end on both variables, total leaf area and cross sectional area, suggesting higher biomass investments in those two structures. Meanwhile the support-seekers lianas grow consistently longer and have higher RGR than the freestanding; faster growing rates with subsequent rapid increase in length are associated to light demanding plants (Swaine & Whitmore, 1988). It is noteworthy that most of the species were located close to the regression line suggesting that stem cross sectional area y and total leaf area are functionally related but the species of the two groups were located in different portions of the functional relationship. I can use this patter as another evidence of a gradient in physiological traits between two extremes of seedling growth forms.

Understory shade tolerant plants produce more leaves and retain them for more time than light demanding plants (Coley & Kursar, 1999; Dalling et al., 2001; Kursar & Coley, 1993) consistent with the suggested shade tolerance ecological behavior of the freestanding seedlings which had the highest leaf surface area at similar age as observed in the functional relationship depicted in Figure 4.4 and had relatively low RGRs as well. The hydraulic architecture of the seedlings did not allow us to distinguish a clear pattern. However, in terms of specific hydraulic conductivity, Ks, three of the support-seekers seedling PIT2CR, ACACHA and MACHM2 had higher values, contrasting with other support-seekers, SERJAT, that had lower Ks. Freestanding seedlings tended to have lower Ks values. Lianas usually are very efficient in long distance water transport when compared to trees (Ewers, 1985; Ewers et al., 1989; Gartner et al., 1990). When comparing lianas and shrubs of the same species, the lianas form have higher Ks (Chiu & Ewers, 1992; Gartner, 1991a) similar to the support-seekers in my study.

Previous studies of leaf specific hydraulic conductivity, Kl, show no differences between trees and lianas of different species, or between lianas and shrub forms of the same species (Chiu & Ewers, 1992; Ewers et al., 1989; Gartner et al., 1990; Gartner, 1991a), (but see Ewers, 1985). I found that the support-seekers seedlings, with the exception of MACHM2 had higher values of Kl, and the freestanding seedlings showed consistent lower Kl, and this result coincides with the higher total leaf area value observed for freestanding seedlings, more surface are per unit of active water transport tissue. Freestanding seedlings invest in large leaf area perhaps because they are better adapted to the understory light conditions. In contrast, support-seekers seedling tend to grow in gaps with high light intensity and, will need only a fraction of that leaf area to capture the same amount of incident light.

Lianas can exhibit a wide range of photosynthetic response that helps them to cope with the ever changing light environment of the forest canopy and understory. Previous studies of climbing plants for temperate zones in southern Chile and subtropical Brazilian forests suggest that these species can adjust their photosynthetic rates to cope with to different light environment (Valladares, Gianoli, & Saldaña, 2011) or ((Sanches & Válio, 2008). The freestanding liana seedlings had lower maximum ETR in the shade compared to the ETR values under high light levels in the greenhouse experiment. This suggests an adaptation to down regulate the photosynthetic processes under conditions where light is limited, which may be typical of shade tolerant plants. MACHM2 a support-seeker seedling had higher ETR rates in high or low light environment than almost all other liana seedlings, an unexpected result indicating that this species does not have physiological responses consistent with the other three support-seeker species.

The two liana seedling growth forms, freestanding and support-seekers, in my study, even though had some distinct life history traits, they can also be analyzed as a gradient of species specific traits where some species can be located at the extremes, and other species can be in different positions along the gradient. The results of my PCA show that free standing species being similar to each other from the physiological and life history traits stand point. The support-seekers seedlings had a wider spread range of separation among them. Freestanding lianas also show convergence in leaf area, stem diameter and maximum ETR, traits that could be associated with these plants being better adapted to grow under low light conditions.

I found separation in life history and physiological traits in the eight species. This is consistent with the liana habit having evolved independently in numerous taxa, from shrubby or tree ancestors (Alcantara & Lohmann, 2011; Gentry, 1991; Gianoli, 2004; Lahaye, Civeyrel, Speck, & Rowe, 2005; Lohmann, 2006). My results partially support my hypothesis that both groups of lianas are clearly distinct functional groups characterized by different physiological and life history traits. Alternatively, it is possible to analyze the species-specific trait ins terms of a gradient of liana seedling characteristics that ranges from the ones that are mainly freestanding (CALLLA, TONTOV, PETRAS and CNESRU) which are most successful in the forest understory, to ones that are support-seekers (PIT2CR and ACACHA), which are most successful in open forest or forest gaps. Two seedling species were in the middle portion of the gradient between the two groups (SERJAT and MACHM2).

I have shown that a gradient in liana life history traits exist and that this gradient could be correlated with different patterns of resource allocation: for example more allocation to leaf surface area rather than stem elongation, that is typical of the free standing seedlings, are in one extreme of the gradient while the support-seekers invest less in leaf surface and grow faster and are in the other extreme of the gradient. In conclusion there was clustering in life history and physiological traits in freestanding and support-seekers with some outliers, but at the same time we can analyze the species specific variation in terms of functional relationships or a gradient of liana seedling characteristics that ranges from the ones that are mainly freestanding to those that are mainly support-seekers.

Table 4.1. Species used for the experiments, including species name, species code, family and the proposed functional group for each one.

Specie and species code	**Family**	**Functional group**
Acacia hayesii (ACACHA)	Fabaceae-mimosoideae	SS
Pithecoctenium crucigerum (PIT2CR)	Bignoniaceae	SS
Serjania atrolineata (SERJAT)	Sapindaceae	SS
Machaerium milleflorum (MACHM2)	Fabaceae-papilionoideae	SS
Petrea aspera (PETRAS)	Verbenaceae	F
Cnestidium rufescens (CNESRU)	Connaraceae	F
Callychlamys latifolia (CALLLA)	Bignoniaceae	F
Tontelea ovalifolia (TONTOV)	Celastraceae	F

Key: SS= support-seekers, F= freestanding

Table 4.2. Eigenvalues, percentage of variation explained and cumulative % of the variation explained for the principal component analysis.

PCA	Eigenvalues	%Variation	Cum.%Variation
1	4.5082	56.35	56.35
2	1.44	18.11	74.46
3	1.17	14.63	89.09
4	0.52	6.5	95.67
5	0.28	3.6	99.29
6	0.04	0.6	100

Table 4.3. Eigenvectors (Coefficients in the linear combinations of variables making up PC's) for each of the variables used in the PCA analysis.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
LMA	-0.417	-0.242	0.004	-0.077	-0.651	0.21
STEM DIAM	-0.422	-0.237	-0.019	0.197	0.568	0.195
LA	-0.43	-0.112	0.092	-0.474	-0.192	-0.39
MAXh	0.33	-0.531	0.251	0.052	-0.183	0.561
KS	0.156	0.427	0.714	0.184	-0.192	-0.099
Kl	0.3	-0.613	0.079	0.207	-0.008	-0.656
ETR	-0.31	-0.179	0.641	-0.134	0.323	0.027
RGR	0.38	-0.034	0.035	-0.796	0.205	0.099

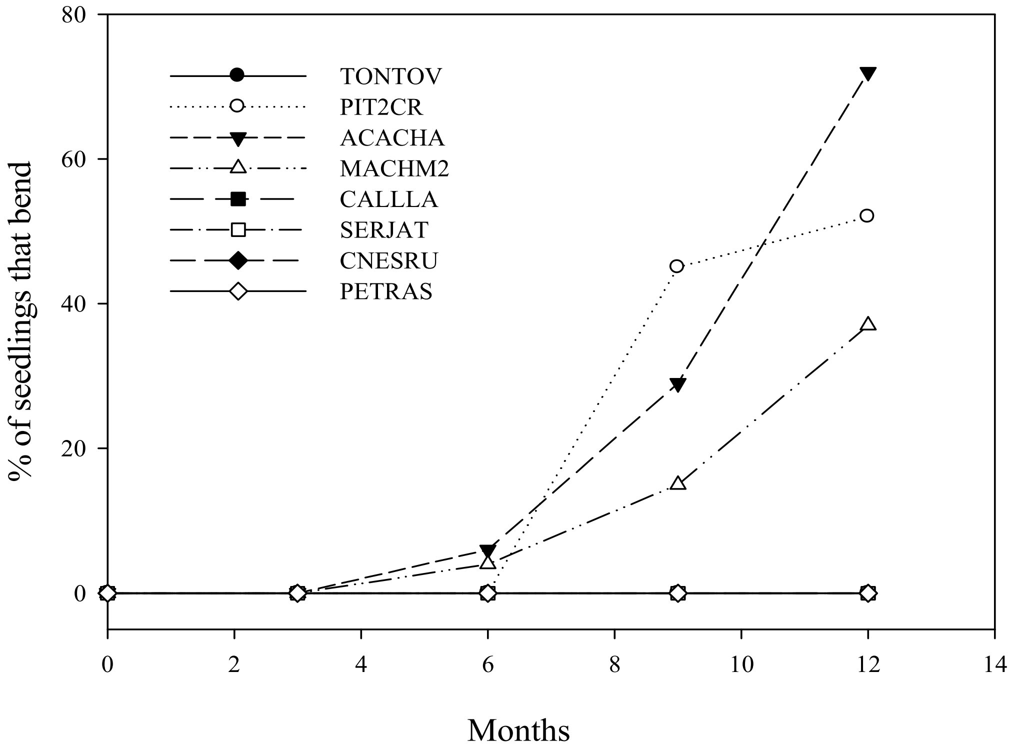

Figure 4.1. Percent of seedlings per species growing in a greenhouse under similar environmental condition (55 μmol m^{-2} s^{-1}) for 12 months that bend without the help of any target support. Three support-seekers seedling species (filled symbols) bent and one support-seekers and all freestanding seedling species grow vertically without bending. One support-seeker and the four freestanding seedling species did not bend (horizontal line with overlapping symbols)

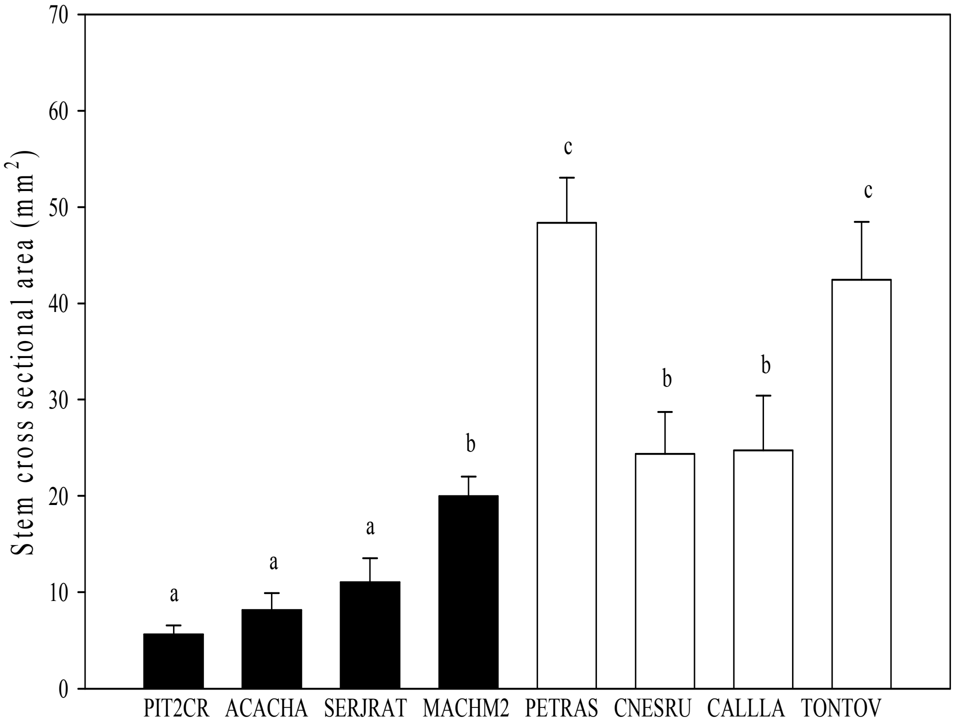

Figure 4.2. Stem cross sectional area of liana seedlings. The first four species on the left are support-seekers (dark bars) while the four species on the right (open bars) are freestanding, after 18 months of growth in a greenhouse under 55 µmol m-2s-1PPFD .Bars topped with the same letter do not differ significantly at *p*< .05, one way ANOVA test with a subsequent Tukey HSD, bars are means + SE (n=10)

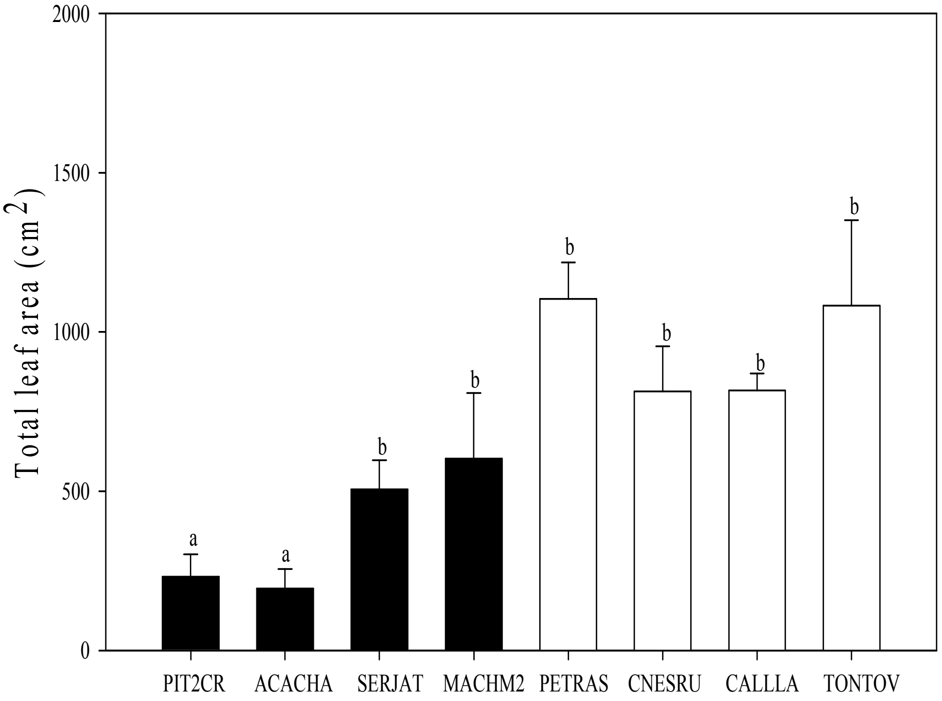

Figure 4.3. Total leaf surface area per plant of the support-seekers and freestanding liana seedlings after 18 months of growth in a greenhouse under 55 µmol m^{-2}s^{-1}PPFD. Bars topped with the same letter do not differ significantly at p<0.05, one way ANOVA test with a subsequent Tukey HSD, bars are means + SE (n=5).

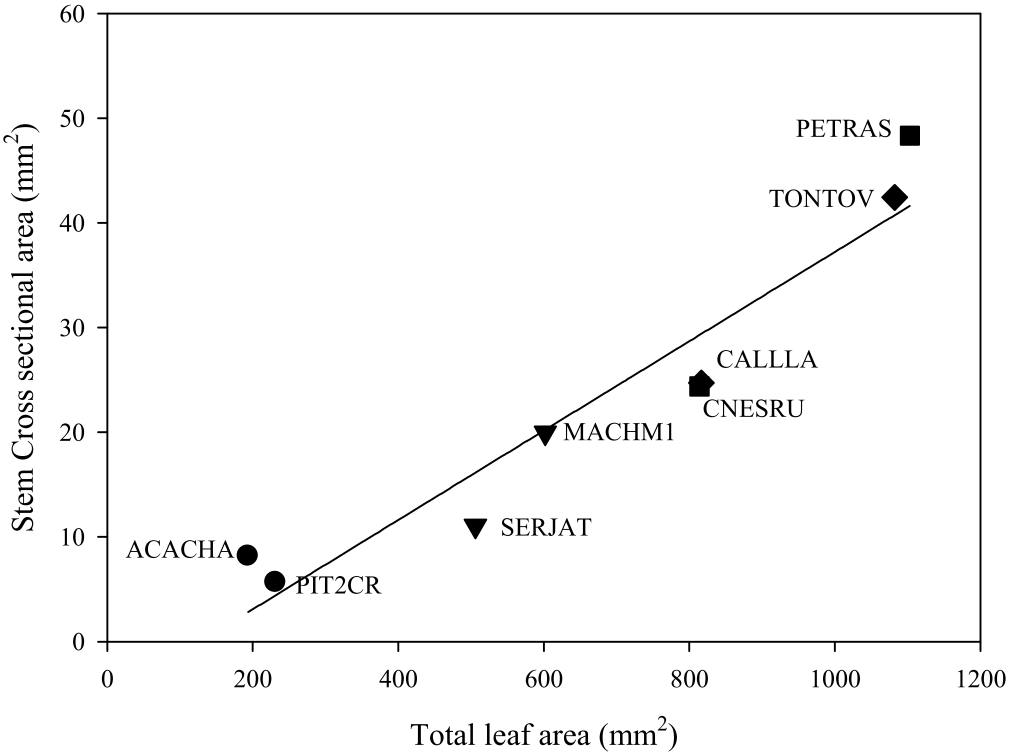

Figure 4.4. Correlation between stem cross sectional area and total leaf surface area per plant, r= 0.95, p=0.0002.

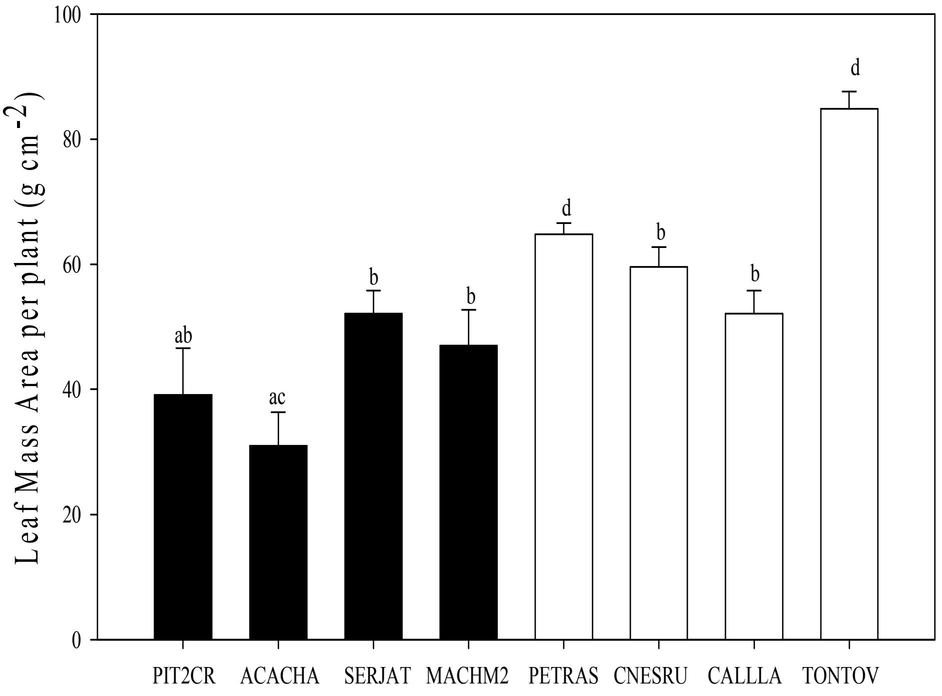

Figure 4.5. Leaf mass per area (LMA, g cm^{-2}) of the support-seekers and freestanding liana seedlings after 18 months of growth in a greenhouse under 55 μmol m^{-2}s^{-1} PPFD. Open bars are freestanding and black bars are support-seekers. Bars topped with the same letter do not differ significantly at p<0.05, one way ANOVA test with a subsequent Tukey HSD test, bars are means + SE (n=5).

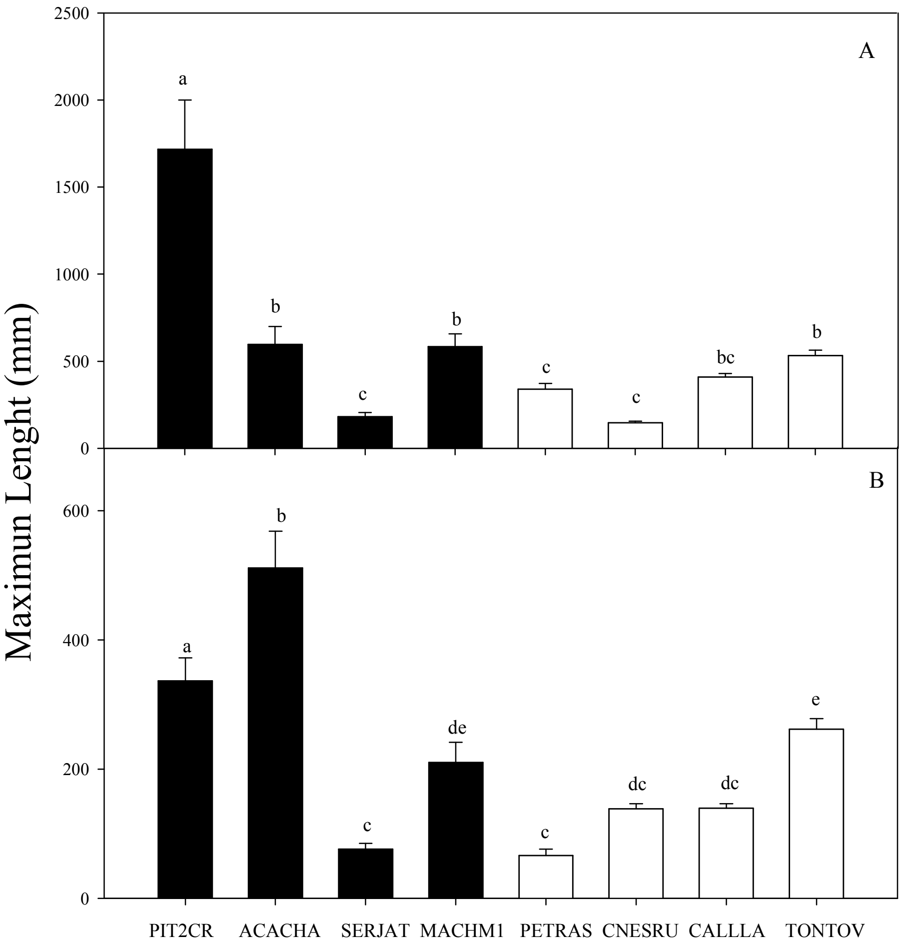

Figure 4.6. Length of liana seedlings attained after 12 months of growth in a greenhouse under (A) high light conditions (530 µmol $m^{-2}s^{-1}$) and under low light conditions (170 µmol $m^{-2}s^{-1}$). Open bars are freestanding and black bars are support-seekers. Bars topped with the same letter do not differ significantly at $p<0.05$, one way ANOVA test with a subsequent Tukey HSD test, bars are means + SE (n=7)

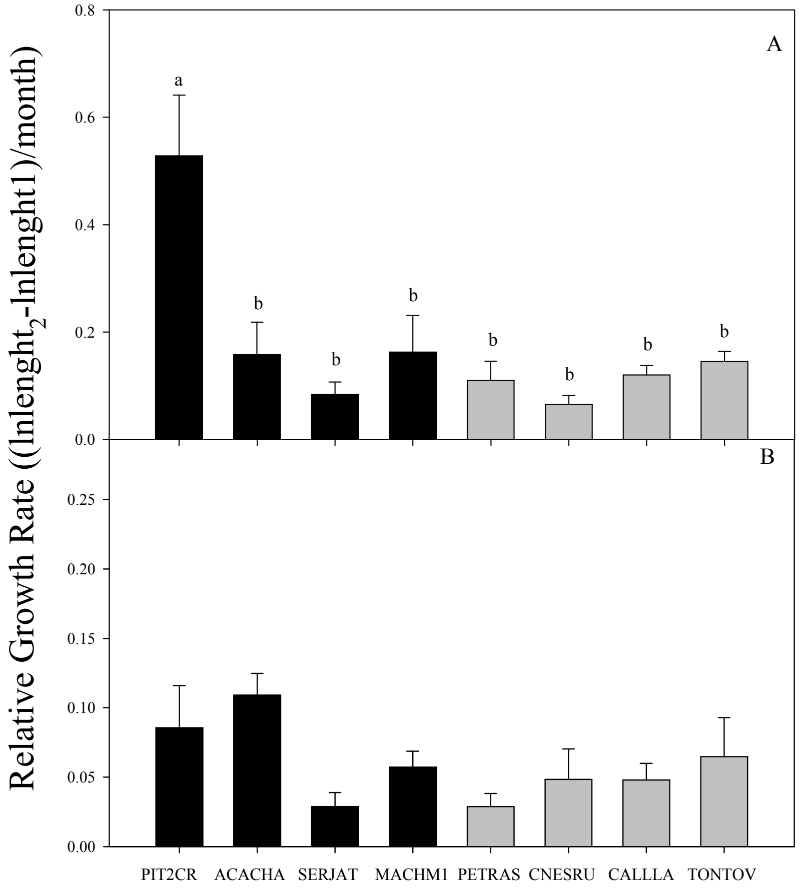

Figure 4.7. Relative growth rate in height (mm month^{-1} (ln final height-ln initial height/time) of support-seekers and freestanding liana seedling under (A) high light conditions (530 μmol m^{-2}s^{-1}) and under low light conditions (170 μmol m^{-2}s^{-1}). Open bars are freestanding and black bars are support-seekers. Bars topped with the same letter do not differ significantly at $p < 0.05$, one way ANOVA test with a subsequent Tukey test, bars are means + SE (n=7), bars are means + SE (n=10)

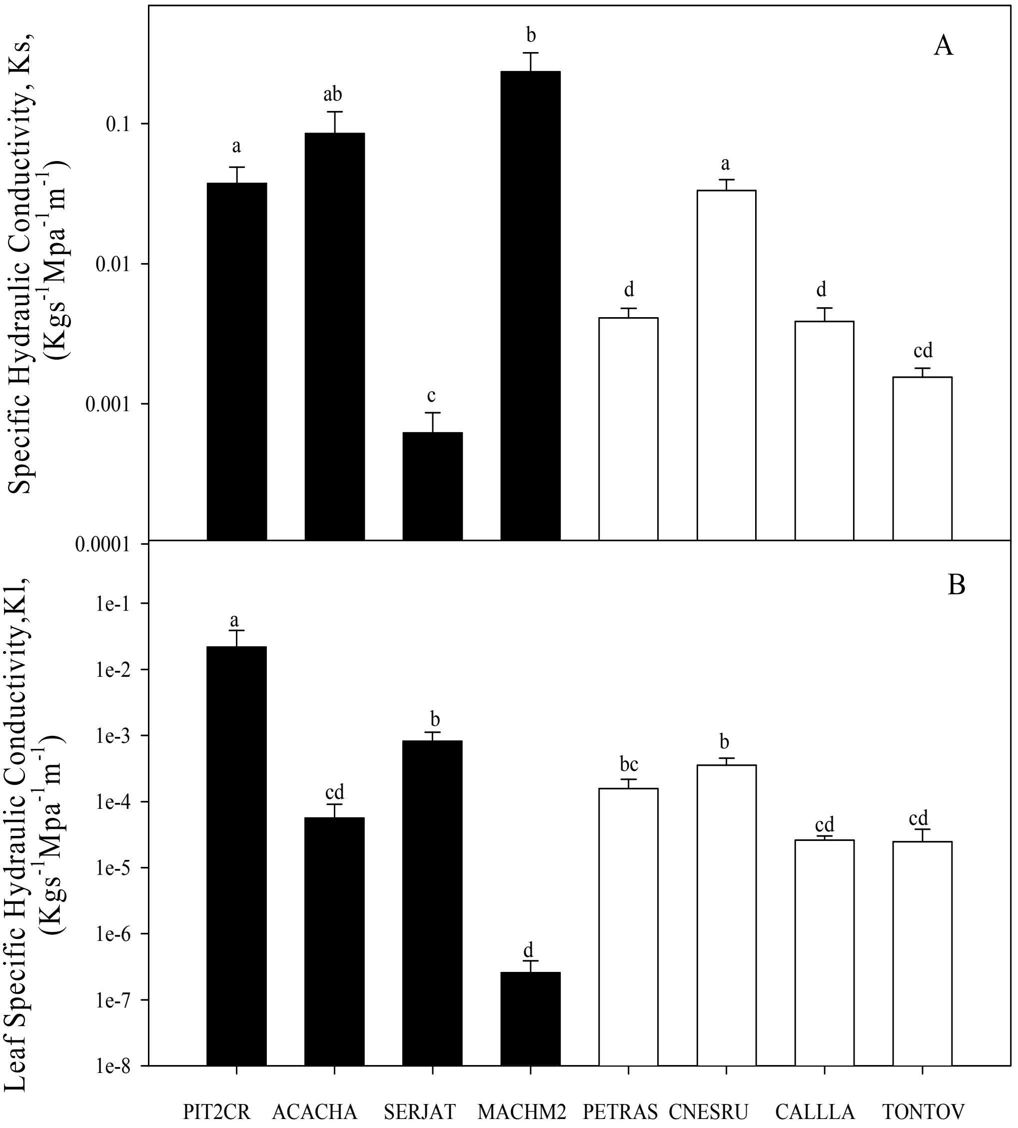

Figure 4.8. Specific hydraulic conductivity, Ks (A), and leaf specific hydraulic conductivity, Kl,(B) of support-seekers and freestanding liana seedlings growing under 50 μmol m^{-2}s^{-1} PPFD. Open bars are freestanding and black bars are support-seekers. Bars topped with the same letter do not differ significantly at $p<0.05$, one way ANOVA test with a subsequent Tukey HSD test, bars are means + SE (n=5).

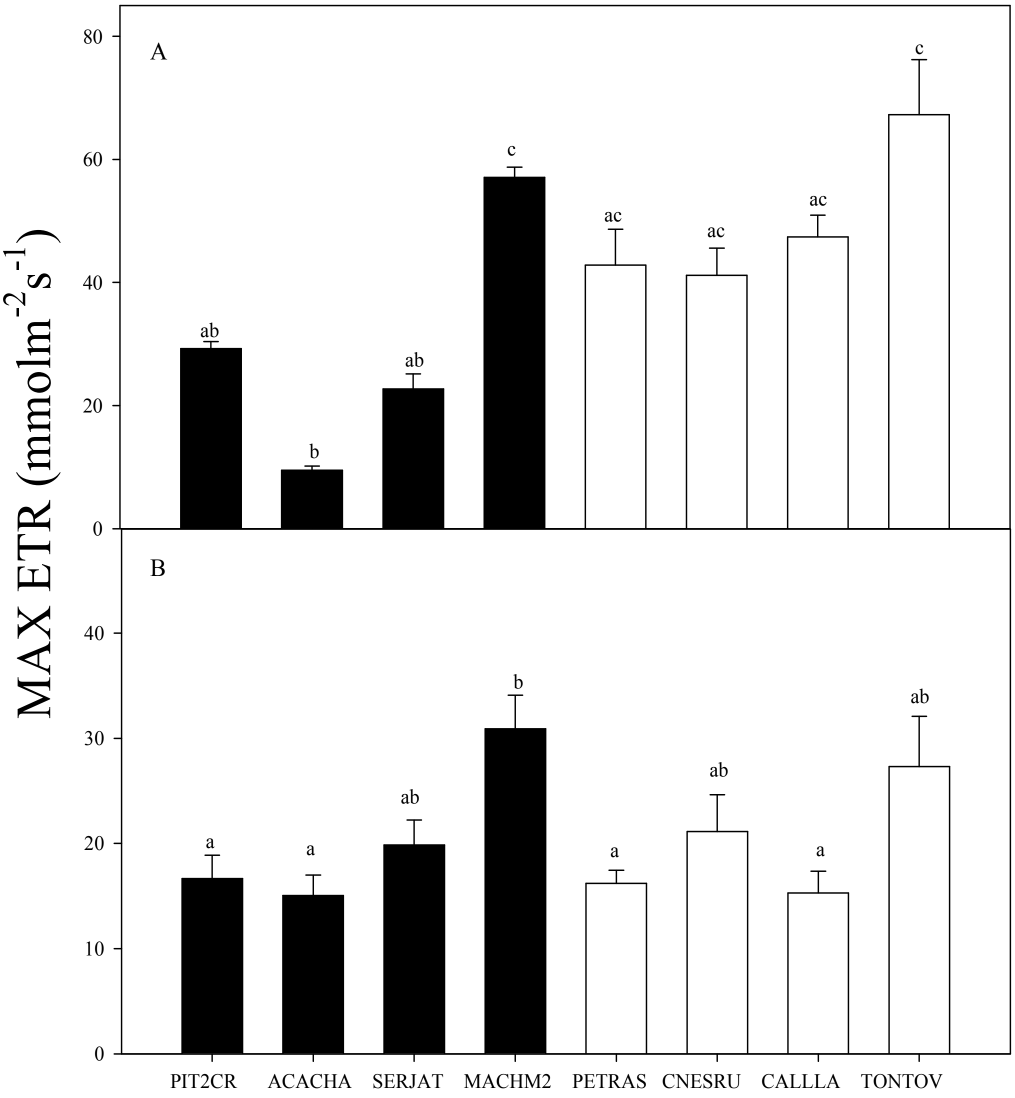

Figure 4.9. Maximum Electron transport rate (ETR at light saturation) of support-seekers and freestanding liana seedlings under (A) high light conditions (530 µmol m^{-2}s^{-1}) and (B) under low light conditions (170 µmol m^{-2}s^{-1}). Open bars are freestanding and black bars are support-seekers. Bars topped with the same letter do not differ significantly at $p<0.05$, one way ANOVA test with a subsequent Tukey HSD .Bars are means + SE (n=5).

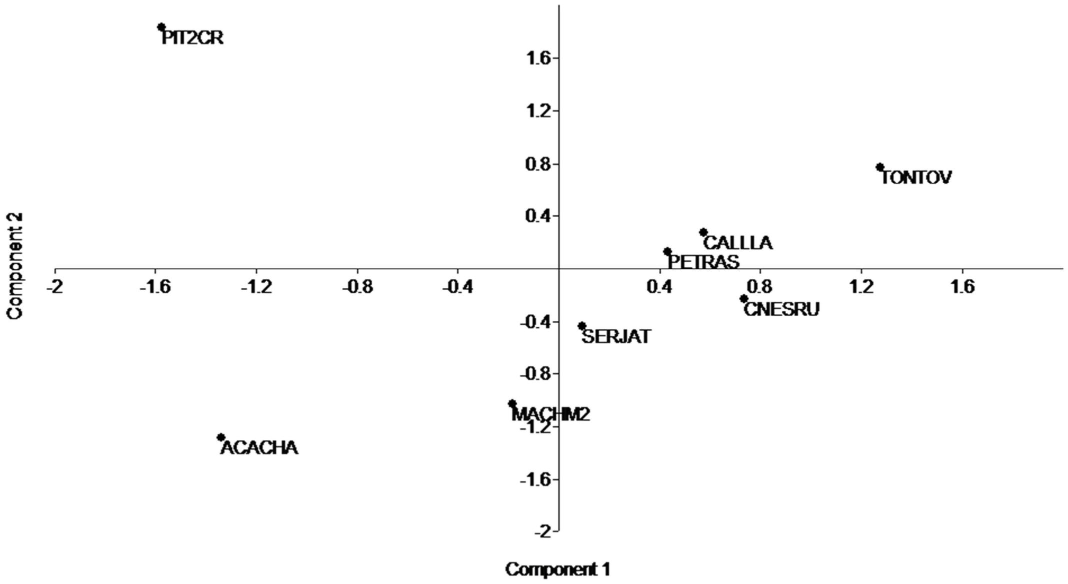

Figure 4.10. Principal component analysis (PCA) plot, showing the ordination of the eight lianas species using the first two PCA axes. Filled symbols are support-seeker seedlings and open symbols are freestanding seedlings

Chapter 5

Conclusions

The results of my research shows that there are two liana seedling groups, freestanding and support-seekers, with different life history traits, however those groups are not completely distinct functional groups. The different species can be organized conceptually along a gradient of physiological and morphological traits from completely freestanding to completely support-seeker liana seedling. Those traits reflect differences in carbon allocation, photosynthetic rates and hydraulic architecture. Furthermore, the physiological differentiation has an effect on seedling ecology resulting in different patterns in the distribution and density of the lianas seedlings across tropical forests in Panama. This is the first study that has shown that liana seedlings can be described as freestanding and support-seeker and tested the effect of the observed differences at the physiological and ecological level and its pattern of ecological distribution.

Across the rainfall gradient in the Panama Isthmus, I found that the diversity and density of liana seedlings is strongly correlated to the forest structure. Although the rainfall pattern has an effect on density and diversity, this effect was overshadowed by the effects of soil types. Lianas seedling were more abundant in the limestone soils and their density was especially high in the limestone soil site located in the wettest side of the rainfall gradient.

The distribution pattern of freestanding and support-seeker sites across the rainfall gradient was close to predictions, with higher proportion of freestanding in the wet part of the gradient and higher proportion of support-seeker in the dry part of the gradient. This pattern can be explained by higher canopy and leaf area index in the wettest forest stands. These two factors produce a darker understory than the dry side of the gradient. This habitat type is not suitable for liana seedlings that need support early in their life cycle, particularly for the support-seeker lianas. However, liana seedlings, mainly freestanding liana seedlings, can persist for a long period of time as small shrubs and survive in this type of habitat. The dry sites, with lower canopy and lower leaf area index, have higher incoming light in the understory; this allows a higher numbers of sapling and shrubs to grow which can be used as trellises by the support-seeker lianas. This group will have an advantage in this environment, and therefore will be more abundant in sites with these characteristics.

In the 50 Ha plot the overall number of lianas seedlings is increasing. The mortality rate for liana seedlings in the censuses was always smaller than the recruitment of seedlings between censuses, which results in a net increase in the number of lianas. But not only liana seedlings are incrementing in numbers, also shrubs, which are increasing in an even a higher rate than liana seedlings. Meanwhile tree seedlings seem to be decreasing in numbers during the study period. The reason for this three population temporal patterns is still unknown. Interestingly the liana species that have support-seeker seedlings seems to be increasing at a faster rate than the liana species that have freestanding seedlings. Furthermore liana recruitment, mortality and density do not seem to respond strongly to any of the soil nutrients variables or understory structure variable measured. The environmental conditions across the 50 Ha plot were fairly uniform which make it more difficult to find environmental determinants of spatial patterns of species distribution and temporal patterns of population dynamics.

The original hypothesis of two distinct functional groups of lianas, freestanding and support-seekers was partly supported by the morphological and physiological studies. The freestanding and support-seeker groups exists but at the same time the two different functional groups; liana seedlings can be organized in a gradient of traits with species being either in one or the other of the endpoints of the gradient. The freestanding species consistently exhibited lower grow rates, higher leaf area per individual, larger stem cross sectional area, lower specific and leaf specific hydraulic conductivity, and higher max ETR than the support seeker liana seedlings. My study provides novel evidences of the existence of this two liana seedling groups, freestanding and support-seekers. The species in each group share similar life history traits

Future Research

In order to obtain a better understanding of the proposed gradient in growth functional strategies, I will need to provide answer to questions that my dissertation did not address. At the regional scale level it may be useful to increase both the number of sites to be sampled and the species sample size. New sample sites should include a wide variety of soil types with more points across the rainfall gradient.

At a more local scale, it is necessary to elucidate if the freestanding liana seedlings are effectively more abundant in the understory while support seeker liana seedlings are more abundant in gaps because the information on canopy cover is not as good as expected for the analysis that I did. This can be a done using transects from the understory to the gap centers. If possible, new gaps should be included.

The seedlings population trends for lianas trees and shrubs, should be revisited and if new data is available, this can probe if those trends are an effect of a cycle in population density or a more consistent long temporal trend. The increment in liana and shrub seedlings and decrease in tree seedlings should be investigated taking in account the effects that such trend can have in the ecology of the forests.

Finally a larger sample size, in terms of the number of species, may be useful for the study of physiological traits. Including more species in a study will lead us to clarify the extension of the gradient in resource allocation. This study can be coupled with a comparative biomechanics study that will show the difference in biomechanics between free and support-seeker seedlings, at different stage in their development. Also a common garden experiment in which freestanding and support-seeker species can be subjected to different levels of light, and support availability will show how this species respond to these environmental cues, and perhaps will elucidate which is the main factor driving the change from a freestanding seedling to a climbing liana.

References

Abramoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International*, *11*(7), 36–42.

Alcantara, S., & Lohmann, L. (2011). Contrasting phylogenetic signals and evolutionary rates in floral traits of Neotropical lianas. *Biological Journal of the Linnean Society*, 378–390.

Andrade, J. L., Meinzer, F. C., Goldstein, G., & Schnitzer, S. A. (2004). Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees*, *19*(3), 282–289.

Augspurger, C. K. (1984). Seedling survival of tropical tree species : Interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, *65*(6), 1705–1712.

Avalos, G., & Mulkey, S. S. (1999). Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest canopy. *Oecologia*, *120*(4), 475–484.

Beer, S., Vilenkin, B., Weil, A., Veste, M., Susel, L., & Eshel, A. (1998). Measuring photosynthetic rates in sea grasses by pulse amplitude modulated (PAM) fluorometry. *Marine Ecology Progress Series*, *174*, 293–300.

Bonsall, M. B., Jansen, V. A. A., & Hassell, M. P. (2004). Life history trade-offs assemble ecological guilds. *Science (New York, N.Y.)*, *306*(5693), 111–4.

Burnham, R. (2002). Dominance, diversity and distribution of lianas in Yasuní, Ecuador: who is on top? *Journal of Tropical Ecology*, *18*(06), 845–864.

Cai, Z.-Q., Poorter, L., Cao, K.-F., & Bongers, F. (2007). Seedling growth strategies in *Bauhinia* species: comparing lianas and trees. *Annals of Botany*, *100*(4), 831–8.

Campanello, P. I., Garibaldi, J., Gatti, M. G., & Goldstein, G. (2007). Lianas in a subtropical Atlantic Forest: Host preference and tree growth. *Forest Ecology and Management*, *242*(2-3), 250–259.

Chen, J. M., Rich, P. M., Gower, S. T., Norman, J. M., & Plummer, S. (1997). Leaf area index of boreal forests: Theory, techniques, and measurements. *Journal of Geophysical Research*, *102*(D24), 29429–29443.

Chiu, S.-T., & Ewers, F. W. (1992). Xylem structure and water transport in a twiner, a scrambler, and a shrub of *Lonicera* (Caprifoliaceae). *Trees*, *6*(4), 216–224.

Clark, D. A., & Clark, D. B. (1992). Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs*, *62*(3), 315.

Clinebell, R. R., Phillips, O. L., Gentry, A. H., Stark, N., & Zuuring, H. (1995). Prediction of Neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, *4*(1), 56–90.

Coley, P. D., & Kursar, T. A. (1999). Modes of light acclimation in two species, contrasting of the rainforest understory. *Ecology*, *121*(4), 489–498.

Comita, L. S., Aguilar, S., Perez, R., Loo de Lao, S., & Hubbell, S. P. (2007). Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *Journal of Vegetation Science*, *18*(2), 163.

Condit, R. (1998). Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climatic Change*, 413–427.

Condit, R., Aguilar, S., Hernandéz, A., Perez, R., Loo de Lao, S., Angehr, G., Hubbell, S. P., et al. (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season. *Journal of Tropical Ecology*, *20*(1), 51–72.

Condit, R., Watts, K., Bohlman, S. A., Perez, R., Foster, R. B., & Hubbell, S. P. (2000). Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*, *11*(5), 649–658.

Dalling, J. W., Winter, K., Nason, J. D., Hubbell, S. P., Murawski, D. A., & Hamrick, J. L. (2001). The unusual life history of *Alseis blackiana* : A shade-persistent pioneer tree ? *Ecology*, *82*(4), 933–945.

DeWalt, S. J., Ickes, K., Nilus, R., Harms, K. E., & Burslem, D. F. R. P. (2006). Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecology*, *186*(2), 203–216.

Denslow, J. S., Ellison, A. M., & Sanford, R. E. (1998). Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology*, *86*(4), 597–609.

Dewalt, S. J., Schnitzer, S. A., & Denslow, J. S. (2000). Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology*, *16*(1), 1–19.

Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, *447*(7140), 80–2.

Engelbrecht, B. M. J., Dalling, J. W., Pearson, T. R. H., Wolf, R. L., Gálvez, D. a, Koehler, T., Tyree, M. T., et al. (2006). Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia*, *148*(2), 258–69.

Engelbrecht, B. M. J., Kursar, T. A., & Tyree, M. T. (2005). Drought effects on seedling survival in a tropical moist forest. *Trees*, *19*(3), 312–321.

Engelbrecht, B. M. J., Wright, S. J., & De Steven, D. (2002). Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical Ecology*, *18*(04), 569–579.

Ewers, F. W. (1985). Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *International Association of Wood Anatomists Bulletin*, *6*(4).

Ewers, F. W., & Fisher, J. B. (1989). Variation in vessel length and diameter stem of six subtropical lianas. *American Journal of Botany*, *76*(10), 1452–1459.

Ewers, F. W., Fisher, J. B., & Chiu, S.-T. (1989). Water transport in the liana *Bauhinia fassoglensis* (Fabaceae). *Plant Physiology*, *91*(4), 1625–31.

Gallenmuller, F., Rowe, N., & Speck, T. (2005). Development and growth form of the Neotropical liana *Croton nuntian*s: The effect of light and mode of attachment on the biomechanics of the stem. *Journal of Plant Growth Regulation*, *23*(2), 83–97.

Gartner, B. L. (1991a). Stem hydraulic properties of vines vs . shrubs of western poison oak, *Toxicodendron diversilobum*. *Oecologia*, *72*(6), 180–189.

Gartner, B. L. (1991b). Structural stability and architecture of vines vs . shrubs of poison oak , *Toxicodendron diversilobum*. *Ecology*, *72*(6), 2005–2015.

Gartner, B. L., Bullock, S. H., Mooney, H. A., By Brown, V., Whitbeck, J. L., & Brown, B. (1990). Water tranport properties of vines and tree stems in a tropical decidious forest. *American Journal of Botany*, *77*(6), 742–749.

Garwood, N. C. (2009). *Seedlings of Barro Colorado Island and the Neotropics* (First Edit., p. 656). Comstock Publishing Associates.

Gentry, A. H. (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, *75*(1), 1–34.

Gentry, A. H. (1991). The distribution and evolution of climbing plants. In F. E. Putz & H. A. Mooney (Eds.), *The Biology of vines.* (p. 526). Cambridge University Press.

Gentry, A. H. (1992). Tropical forest biodiversity : Distributional patterns and their conservational significance. *Oikos*, *63*(1), 19–28.

Gerwing, J. J. (2004). Life history diversity among six species of canopy lianas in an old-growth forest of the eastern Brazilian Amazon. *Forest Ecology and Management*, *190*(1), 57–72.

Gerwing, J. J., & Farias, D. L. (2000). Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology*, *16*(3), 327–335.

Gianoli, E. (2004). Evolution of a climbing habit promotes diversification in flowering plants. *Proceedings Biological sciences*, *271*(1552), 2011–5.

Gilbert, B., Wright, S. J., Muller-Landau, H. C., Kitajima, K., & Hernandéz, A. (2006). Life history trade-offs in tropical trees and lianas. *Ecology*, *87*(5), 1281–8.

Goldsmith, G. R., Comita, L. S., Morefield, L. L., Condit, R., & Hubbell, S. P. (2006). Long-term research impacts on seedling community structure and composition in a permanent forest plot. *Forest Ecology and Management*, *234*(1-3), 34–39.

Granados, J., & Körner, C. (2002). In deep shade, elevated CO 2 increases the vigor of tropical climbing plants. *Global Change Biology*, 1109–1117.

Harms, K. E., Condit, R., Hubbell, S. P., & Foster, R. B. (2001). Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology*, *89*(6), 947–959.

Harms, K. E., Wright, S. J., Calderón, O., Hernandéz, A., & Herre, E. A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, *404*(6777), 493–5.

Hubbell, S. P. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, *283*(5401), 554–557.

Hättenschwiler, S. (2002). Liana seedling growth in response to fertilization in a Neotropical forest understory. *Basic and Applied Ecology*, *143*, 135–143.

Ibarra-Manríquez, G., & Martínez-Ramos, M. (2002). Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology*, *160*(1), 91–112–112.

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375.

Kennard, D. K. (1998). Biomechanical properties of tree saplings and free-standing lianas as indicators of susceptibility to logging damage. *Forest Ecology and Management*, *102*(2-3), 179–191.

Kneitel, J. M., Chase, J. M., & Letters, E. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, *7*(1), 69–80.

Kull, O. (1995). Light interception, nitrogen and leaf mass distribution in a multilayer plant community. *Functional Ecology*, *9*(4), 589.

Kursar, T. A., & Coley, P. D. (1993). Photosynthetic induction times in shade-tolerant species with long and short-lived leaves. *Oecologia*, *93*(2), 165–170.

Körner, C. (2009). Responses of humid tropical trees to rising CO 2. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 61–79.

Lahaye, R., Civeyrel, L., Speck, T., & Rowe, N. (2005). Evolution of shrub - like growth forms in the secamonoideae (apocynaceae) of Madagascar: Phylogeny, biomechanics and development. *American journal of botany*, *92*(8), 1381–1396.

Lambers, H., Chapin, F. S., & Pons, T. L. (2008). *Plant Physiological Ecology* (Second Edi., p. 610). New York: Springer.

Leigh, E. G. J. (1999). *Tropical Forest Ecology. A view from Barro Colorado Island.* Oxford University Press.

Leigh, E. G. J., Loo de Lao, S., Condit, R., Hubbell, S. P., Foster, R. B., & Perez, R. (2004). Barro Colorado Island Forest Dynamics Plot, Panama. In E. Losos & E. G. J. Leigh (Eds.), *Tropical Forest Diversity and Dynamism: Findings from a large-scale plot network.* (pp. 451–463). Chicago: University of Chicago Press.

Lohmann, L. (2006). Untangling the phylogeny of neotropical lianas (Bignonieae, bignoniaceae)1. *American Journal of Botany*, *93*(2), 304–318.

Mascaro, J., Schnitzer, S. A., & Carson, W. P. (2004). Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica. *Forest Ecology and Management*, *190*(1), 3–14.

Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence--a practical guide. *Journal of Experimental Botany*, *51*(345), 659–68.

Molina-Freaner, F., Castillo Gámez, R., Tinoco-Ojanguren, C., & Castellanos V., A. E. (2004). Vine species diversity across environmental gradients in northwestern México. *Biodiversity and Conservation*, *13*(10), 1853–1874.

Montgomery, R. (2004). Relative importance of photosynthetic physiology and biomass allocation for tree seedling growth across a broad light gradient. *Tree Physiology*, *24*(2), 155–67.

Nabe-Nielsen, J. (2002). Growth and mortality rates of the riana *Machaerium cuspidatum* in relation to light and topographic position. *Biotropica*, *34*(2), 319–322.

Nabe-Nielsen, J. (2004). Demography of *Machaerium cuspidatum*, a shade-tolerant Neotropical liana. *Journal of Tropical Ecology*, *20*(5), 505–516.

Perez-Salicrup, D., & Meijere, W. D. (2005). Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas , Mexico 1. *Biotropica*, *37*(1), 153–156.

Phillips, O. L., Vásquez Martínez, R., Arroyo, L., Baker, T. R., Killeen, T., Lewis, S. L., Malhi, Y., et al. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature*, *418*(6899), 770–4. 6

Putz, F. E. (1983). Liana biomass and leaf area of a "Tierra Firme " forest in the Rio Negro basin , Venezuela. *Biotropica*, *15*(3), 185–189.

Putz, F. E. (1984). The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, *65*(6), 1713–1724.

Putz, F. E. (1990). Liana stem diameter growth and mortality rates on Barro Colorado Island, Panama. *Biotropica*, *22*(1), 103.

Putz, F. E., & Windsor, D. M. (1987). Liana phenology on Barro Colorado Island , Panama. *Biotropica*, *19*(4), 334–341.

Pyke, C. R., Condit, R., Aguilar, S., & Loo de Lao, S. (2001). Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, *12*(4), 553–566.

Pérez-Salicrup, D. R., Sork, V. L., & Putz, F. E. (2001). Lianas and trees in a liana forest of Amazonian Bolivia1. *Biotropica*, *33*(1), 34.

Ralph, P. J., & Gademann, R. (2005). Rapid light curves: A powerful tool to assess photosynthetic activity. *Aquatic Botany*, *82*(3), 222–237.

Reddy, M. S., & Parthasarathy, N. (2003). Liana diversity and distribution in four tropical dry evergreen forests on the Coromandel coast of south. *Biodiversity and Conservation*, (12), 1609–1627.

Restom, T., & Nepstad, D. (2004). Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management*, *190*(1), 109–118.

Rowe, N., Isnard, S., & Speck, T. (2004). Diversity of mechanical architectures in climbing plants: An evolutionary perspective. *Journal of Plant Growth Regulation*, *23*, 108–128.

Rowe, N., & Speck, T. (1996). Biomechanical characteristics of the ontogeny and growth habit of the tropical liana *Condylocarpon guianense* (Apocynaceae). *International Journal of Plant Science*, *1*(1, 57), 406–417.

Sanches, M. C., & Válio, I. F. M. (2008). Photosynthetic response of two tropical liana species grown under different irradiances. *Photosynthetica*, *46*(4), 557–566.

Sautu, A., Baskin, J. M., Baskin, C. C., & Condit, R. (2006). Studies on the seed biology of 100 native species of trees in a seasonal moist tropical forest, Panama, Central America. *Forest Ecology and Management*, *234*(1-3), 245–263.

Schnitzer, S. A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, *166*(2), 262–76.

Schnitzer, S. A., & Bongers, F. (2002). The ecology of lianas and their role in forests. *Trends in Ecology & Evolution*, *17*(5), 223–230.

Schnitzer, S. A., & Carson, W. P. (2001). Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, *82*(4), 913.

Schnitzer, S. A., Dalling, J. W., & Carson, W. P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, *88*(4), 655–666.

Schnitzer, S. A., Kuzee, M. E., & Bongers, F. (2005). Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, *93*(6), 1115–1125.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*(3), 259–268.

Swaine, M. D., & Grace, J. (2007). Lianas may be favored by low rainfall : Evidence from Ghana. *Plant Ecology*, *192*(2), 271–276.

Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, *75*(1-2), 81–86.

Valladares, F., Gianoli, E., & Saldaña, A. (2011). Climbing plants in a temperate rainforest understorey: searching for high light or coping with deep shade? *Annals of Botany*, *108*(2), 231–9.

van der Heijden, G. M. F., & Phillips, O. L. (2008). What controls liana success in Neotropical forests? *Global Ecology and Biogeography*, *17*(3), 372–383.

White, A. J., & Critchley, C. (1999). Rapid light curves : A new fluorescence method to assess the state of the photosynthetic apparatus. *Photosynthesis Research*, 63–72.

Whitmore, T. C. (1989). Canopy gaps and the two major groups of forest tree. *Ecology*, *70*(3), 536–538.

Wright, S. J., Calderón, O., Hernandéz, A., & Paton, S. (2004). Are lianas increasing in importance in tropical forests? a 17-year record from Panama. *Ecology*, *85*(2), 484–489.