COMPARING THE FUNCTIONAL TRAITS OF LIANAS AND TRESS IN A LOWLAND TROPICAL FOREST: GETTING TO THE "ROOT" OF THE ISSUE

by

COURTNEY GRACE COLLINS

(Under the Direction of Nina Wurzburger)

ABSTRACT

Over the past 30 years, lianas (woody vines) have become more dominant in Neotropical rainforests. The objective of this study was to compare root functional traits of Neotropical liana and tree communities to delineate traits associated with increasing liana abundance. Fine roots (<2mm diameter) were sampled from 6 liana and 6 tree species (paired by family) on Barro Colorao Island (BCI), Panama with n=10 individuals per species, and chemical, morphological, and symbiont root functional traits were quantified. Liana roots had a higher specific root length (SRL) (cm/g), lower C/N, C/P, and N/P ratios, lower tissue density (g/cm3), and higher branching (forks/cm) than those of trees. Mycorrhizal colonization was significantly different between trees and lianas after excluding the family Fabaceae. Our results suggest that lianas may use a suite of specialized root functional traits to gain an ecological advantage over co-occurring trees, providing insight into the current increase in liana abundance.

INDEX WORDS: liana; tree; functional trait; root; belowground; tropical

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DEDICATION

I would like to dedicate this thesis to the furthering of climate science and to the men and women who are dedicated to finding real solutions to the pressing issues of climate change facing our world today.

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CHAPTER 1

INTRODUCTION

Global change may have substantial impacts on the ecological functioning of tropical forests, including the ability of these ecosystems to act as carbon (C) sinks due to shifts in vegetation composition and structure (Cramer et al. 2001). One major shift in vegetation structure evidenced in the last several decades is a steady increase in the abundance of lianas, or woody vines, relative to trees (Phillips et al. 2002, Benitez-Malvido and Martinez-Ramos 2003, Wright et al. 2004b, Schnitzer 2005, Cai et al. 2009, Ingwell et al. 2010, Zhu and Cao 2010). Phillips et al. (2002) documented a 1.78-4.03% increase in liana stem density and nearly a two fold increase in liana basal area relative to trees from 1979-2002 in western Amazonia. More recently, Ingwell et al. (2010) reported a 65% increase in liana infestation of tree canopies on Barro Colorado Island, Panama from 1996-2007. Overall nearly a dozen studies have been published within the last 10 years documenting the trend of liana increase in neotropical forests.

A major theory proposed to explain this trend is that lianas are favored by global change factors, including increased temperature, atmospheric CO_2, disturbance and/or fragmentation of the forested landscape, and drought severity. For example, lianas were more prevalent in disturbed forest patches and edges as opposed to intact interior forest in the central Amazon and were over 200% more abundant in previously logged forests than old growth forests in southern China (Laurance et al. 2001, Ding and Zang 2009). Biomass of liana species *Ipomoea cairica* increased 69.6% under temperatures increased from 22-30°C (Wang et al. 2011). Lianas also grew nearly seven times greater in height and accessed significantly deeper water resources than did trees during seasonal droughts in central Panama (Andrade et al. 2005, Schnitzer 2005). Finally the temperate liana species *Toxicodendron radicans* increased in annual growth by 149% under artificially elevated CO_2 conditions, as compared to plants growing under ambient CO_2 conditions (Mohan et al. 2006) and in the tropics liana biomass increased 23-48% and height increased 5.5-7.1 times under increased CO_2 conditions (Condon et al. 1992, Granados and Korner 2002). These and numerous other studies highlight the striking correlation between liana increase and global change conditions (Schnitzer and Bongers 2011).

Although it is clear that lianas are changing the plant community structure of tropical forests, it is less clear what specific mechanisms are facilitating the increase in lianas relative to trees in these areas. There is a need to improve our ecological understanding of lianas, and in particular, how their functional traits differ relative to trees (Cai 2007, Zhu and Cao 2010, Schnitzer and Bongers 2011). Functional traits are measurable organismal properties that influence ecological performance (McGill et al. 2006). They reflect long term adaptations to environmental conditions through investment of resources to different plant tissues and functions (Lavorel and Garnier 2002). There is growing consensus that functional traits provide insight into the diverse ecological strategies among species (Diaz and Cabido 2001, Lavorel and Garnier 2002, Westoby and Wright 2006, Wright et al. 2010, Lavorel and Grigulis 2012). Numerous empirical studies have emphasized this viewpoint, with the recognition that plants are unable to simultaneously achieve both resource acquisition and conservation (Wright et al. 2004a, Freschet et al. 2010). Rather, there are unavoidable trade-offs in resource acquisition strategies, where plants display a unique suite of functional traits that place them along a continuum between rapid acquisition and conservation of resources (Bloom et al. 1985, Grime et al. 1997, Reich et al. 1997, Wahl and Ryser 2000, Grime 2001, Diaz et al. 2004).

Comparing functional traits across species in the framework of competitive growth strategies was highlighted by the seminal “Worldwide Leaf Economics Spectrum” paper (Wright et al. 2004a). This study quantified plant investment of nutrients and dry mass (C) to leaves and the potential growth (photosynthate) return on these investments. Using these parameters, they established an “economic” spectrum from quick to slower rates of return on investment, along which species would fall depending on key chemical, structural and physiological properties of their leaves. Further, these properties (traits) were strongly related to one another depending on a species' position along the spectrum (Fig 1). At the quick-return end were species with leaf traits including high nutrient concentrations, high photosynthetic and respiration rates, short leaf life spans, and high Specific Leaf Area (SLA) (leaf area per unit dry mass). At the slow-return end are species with long leaf life spans, low SLA, low nutrient concentrations, and low rates of photosynthesis and respiration. Additionally, these trait relationships stayed surprisingly consistent across different biomes and vegetation types, showing that leaf trait syndromes are largely independent of the influence of local climate (Reich et al. 1997, Wright et al. 2004a).

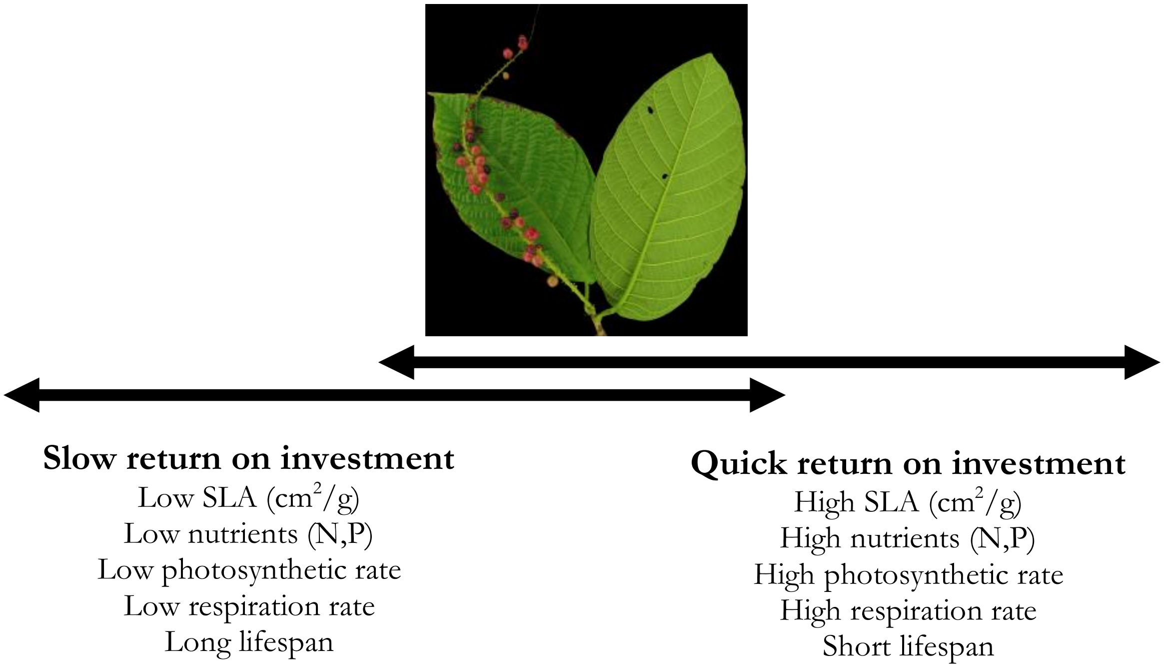

Figure 1

This perspective has also been applied on a whole plant level, including both above and belowground functional traits, and a consideration for linkages among traits. For example, Wahl and Ryser (2000) observed a negative correlation between plant relative growth rate (RGR) and root tissue mass density (TMDr) and a positive correlation between TMDr and leaf dry matter content in

19 perennial grass species. This suggests that there may be relationships between tissue structure and growth strategies at the whole plant level. In addition, Tjoelker et al. (2005) highlighted "leaf and root trait syndromes" that consisted of a positive relationship between leaf and fine root C and N concentrations, tissue longevity (lifespan) and respiration rates among 39 grassland and savanna species. However, in contrast, Craine et al. (2005) observed a weak correlation between leaves and roots traits with the exception that root nitrogen (N) concentrations increased with increasing leaf N concentrations. While this study observed little direct coupling between roots and leaves on a per-trait basis, relationships among traits were evidenced in both leaves and roots. Specifically, roots or leaves that had low concentrations of N also had high tissue density, high lignin contents, and low soluble biomass, and vice-versa. More recently, Freschet et al. (2010) observed a "plant economic spectrum" for subarctic flora, in which suites of traits were consistent across leaves, roots, and stems and represented the trade-offs between rapid resource acquisition and resource conservation strategies. Percent C, N, and lignin, pH, and tissue dry matter content (DMC) were all positively correlated between leaves and stems and between leaves and roots. Percent C and lignin, and DMC were also positively correlated between stems and roots. These studies all suggest that the concepts of the leaf economic spectrum may also be applicable to roots, however aboveground and belowground traits are not consistently linked to each other across different plant functional groups and ecosystems and require further study (Westoby and Wright 2006).

Relating the concepts of the leaf economic spectrum to lianas has demonstrated that liana leaf traits may be more responsive to the environmental conditions associated with global change (Andrade et al. 2005, Selaya et al. 2008, Cai et al. 2009, Zhu and Cao 2010). Cai et al. (2009) found that liana leaves had higher CO_2 assimilation per unit dry mass, higher N concentration, higher $\delta^{13}C$ values, and higher SLA than trees. These findings demonstrate that lianas have higher assimilation rates per unit leaf mass and higher water-use efficiency, but lower leaf structural investments relative to trees. Additionally, Selaya et al. (2008) observed that lianas have a higher light interception per unit leaf mass and area relative to long-lived pioneer trees, and liana traits were similar to short- lived pioneer trees such as *Cecropia* spp. Finally, Zhu and Cao (2010) demonstrated that lianas tend to fall on the quick-return end of the leaf economic spectrum as compared to co-occurring trees and thus exhibited traits such as higher SLA, higher photosynthetic rates, higher photosynthetic N and phosphorus (P) use efficiencies, lower leaf construction cost per unit leaf area and a shorter leaf life span. Overall, the leaf functional traits of lianas promote the highest potential return of water and nutrients on investment of dry mass which would prove very competitive during increased drought and atmospheric CO_2 concentrations, and other projected global change conditions.

These findings provide important insight into how lianas may be gaining an advantage under current global change conditions (elevated $CO_{2,}$ drought, habitat fragmentation, etc.). However the vast majority of functional trait research has examined above ground traits (leaves and stems) with much less consideration given to belowground traits (roots); particularly in the case of lianas. In order to fully understand the growth strategies employed by lianas in the context of global change, we must consider both above and belowground mechanisms (van der Heijden and Phillips 2009).

The objective of this study was to compare the root functional traits of the liana and tree communities in a neotropical forest to determine trait patterns that may be associated with the observed increase in liana abundance. To date, the roots of liana communities have been poorly studied and information regarding their chemical and morphological properties, symbiont relationships, and how their functional traits might differ from those of trees is scant. Focus on the fine root functional traits of lianas and trees would help to clarify whether lianas are investing nutrients and C to their roots differently than trees, and if so, are effectively acquiring limiting resources from the soil that maximize their competitive potential for growth. If present, these differences would likely be expressed as a unique suite of root functional traits for the liana community.

If functional traits of lianas reflect a rapid resource acquisition strategy, it is necessary to consider both the costs and benefits of this growth tactic. One major trade-off of rapid growth and resource acquisition is decreased lifespan in tissues, as is evidenced in short lived pioneer tree species and lianas (Whitmore 1989, Chapin et al. 2002, Zhu and Cao 2010). Another trade-off of this strategy is decreased resistance to environmental and biological stressors including herbivores, pathogens, and drought (Eissenstat et al. 2000, Wahl and Ryser 2000, Chapin et al. 2002), which is highly correlated with decreased lifespan in tissues (Eissenstat et al. 2000, Chapin et al. 2002). It has also been proposed that tree species that exhibit rapid growth and resource acquisition do so at the cost of reduced mechanical stability in their trunks (Putz 1983, 1984, Niklas 1992). Lianas however, do not likely experience this trade-off because they rely on trees for structural support (Putz 1983, 1984, Tyree and Ewers 1991, Cernusak et al. 2008, Selaya et al. 2008). Therefore, compared to trees, lianas may have functional traits that are more highly characterized by strategies for rapid resource acquisition, without suffering from reduced mechanical stability. This potential competitive advantage may provide insight into specific root mechanisms behind the current increase in liana abundance. For this study, we tested the hypothesis that: **root functional traits of lianas are more strongly characterized by strategies for rapid resource acquisition than those of co-occurring trees. (H1).**

We examined morphological, chemical, and symbiont traits of liana and tree roots. Morphological functional traits can serve as valuable proxies for the trade-off between growth and structural investment in plant roots and how this relates to a plant's resource acquisition strategy. For example, one of the most widely used parameters of fine roots, specific root length (SRL), *i.e.*, root length per unit dry mass, considers the cost/benefit ratio of root production with length representing the amount of soil exploited for resource acquisition (benefit), and mass representing the construction and maintenance cost to the plant (Fitter et al. 1991, Eissenstat and Yanai 1997, Ostonen et al. 2007). Plants with high SRL can access a greater soil volume by constructing thinner or less dense roots per unit C (Chapin et al. 2002, Cornelissen et al. 2003). High SRL can improve rates of nutrient and water uptake, at the expense of a shorter-lived roots and reduced protection against belowground herbivores, pathogens and soil desiccation (Eissenstat and Yanai 1997, Reich et al. 1998, Chapin et al. 2002). Tissue density is another key trait affecting the trade-offs present in a resource acquisition strategies (Ryser 1996, Wahl and Ryser 2000). Low tissue density in roots is characteristic of fast growing species with high resource acquisition capacities and short root lifespans (Ryser 1996, Wahl and Ryser 2000). Conversely, roots with a higher tissue density are more energetically and C costly to create but have longer lifespan and greater protection against herbivores and pathogens (Eissenstat and Yanai 1997, Ryser 1998). Finally, root branching intensity is an aspect of topology (pattern of root branching) that affects the absorption of resources from a spatially heterogeneous soil environment (Fitter et al. 1991). This trait quantifies the frequency of fine lateral roots (branches, *i.e.*, forks) per length of primary root (Klepper 1987). Fine lateral roots are involved in direct nutrient and water uptake and therefore their frequency may greatly influence a plant's resource acquisition strategy (Fitter et al. 1991, Robinson et al. 2003), and increase the foraging ability of roots for nutrients and water in discrete soil resource hot spots (Robinson 1994, Hutchings and John 2003). Highly branched roots may even offset the demand for mycorrhizal symbionts as evidenced in the negative relationship between root branching and mycorrhizal colonization (Steeves and Sussex 1989, Hetrick et al. 1991). However, high branching intensity also increases the proportion of the lowest root orders and therefore tends to reduce the lifespan of the root system as fine roots turn over more quickly than coarse roots (Hendrick and Pregitzer 1993, Eissenstat and Yanai 1997). Morpohological functional traits including SRL, tissue density, and branching intensity are important considerations for the trade-offs in a plant's belowground resource acquisition strategy (Fitter et al. 1991).

Chemical functional traits are also useful in considering trade-offs within plant growth strategies including how plants differentially distribute Carbon (C) and nutrients (*e.g.*, N,P) to their root tissue. C is a key structural element for roots, with typically 40% of the C entering a growing root being allocated to the creation of new root biomass (Farrar and Jones 2003). C is also vital for the release of root exudates in response to environmental stressors (organic acids, allelochemical defenses, etc.) as is evidenced in ^{14}C tracer studies that show most root exudation occurring at the root apex and lateral branching sites where the largest C sinks are located (McDougal.Bm and Rovira 1970). Nitrogen (N) and Phosphorus (P) are important nutrients for growth because of their role in metabolic processes and cellular development (Vitousek 1982, Chapin et al. 1986). Specifically, N is primarily incorporated into proteins which function in metabolism and respiration in plant tissues is highly correlated to tissue N content (Chapin et al. 1986, Schlesinger 1997, Chapin et al. 2002). P, on the other hand, is most commonly assimilated into high energy molecules including ATP and phospholipids and ribosomal RNA required for growth (Chapin et al. 1986, Agren 2004). Therefore the C:N:P stoichiometry in root tissues can give insight into the biochemical control over the creation of structural compounds (C), the investment in N-rich proteins, and the use of P-rich energy sources (Sterner and Elser 2002, Agren 2004). In general, lower C:N, C:P, and N:P ratios can promote more rapid growth in root tissues due to the increased investment in RNA to create proteins necessary for growth (Agren 2004). However, high root nutrient concentrations (N, P) and low C content may also result in decreased root longevity and resistance to herbivory and pathogens (Eissenstat and Yanai 1997, McCormack et al. 2012). Fine root lifespan has been shown to decrease as N content increases (Hendrick and Pregitzer 1993, Tjoelker et al. 2005) and root herbivory has also been linked to high root N concentrations (Mattson 1980, Seastedt and Murray 2008).

Furthermore, lower C reserves in root tissue may decrease the potential creation of root exudates including chemical defenses against herbivores and pathogens and organic compounds to stimulate microbial breakdown of nutrients. (Eissenstat and Yanai 1997, Farrar and Jones 2003). Overall C:N:P ratios of root tissues provide insight into the trade-offs between rapid growth and the structural integrity and of root tissues in relation to the belowground resource acquisition strategy of plants.

Root symbionts are another important functional trait that represent an evolutionary adaptation for plants to acquire essential soil macronutrients for growth (Cornelissen et al. 2003). Mycorrhizal fungi and N_2-fixing bacterial symbioses are two of the most common trade-off mechanisms that provide improved resource capture at a C cost to the plant (Schlesinger 1997). The interaction between mycorrhizal fungi and their host occurs within cells (Arbuscular mycorrhizae) and/or in the intercellular space (Ecto-mycorrhizae) of the root cortex (Marschner 1986). In this interaction, the fungus obtains C from their plant host in exchange for providing nutrients from the soil, particularly P (Marschner 1986, Brundrett 1991). These fungi enhance nutrient uptake by extending hyphae into the soil environment surrounding the root (Marschner 1986, Brundrett 1991, Schlesinger 1997) and release extracellular enzymes to breakdown nutrients into plant available forms (Eissenstat and Yanai 1997), although the ability of mycorrhizal types to do this varies (Read and Perez-Moreno 2003). In addition to increased nutrient uptake, mycorrhizal fungi can increase root longevity by improving tolerance to soil desiccation, root pathogens and herbivory (Gange et al. 1994, Gange and West 1994, Newsham et al. 1995, Eissenstat and Yanai 1997, Eissenstat et al. 2000). Arbuscular mycorrhizal fungi (AMF) (order Glomales) are the most ancient of plant-fungal symbioses and are the dominant mycorrhizal association in plants, particularly in tropical biomes (Alexander 1989). Ecto-mycorrhizal fungi (EMF) are the second most common form of mycorrhizae and are more dominant in temperate biomes (Schlesinger 1997). A small percentage of plants are dually colonized by AMF and EMF as dual mycorrhizal colonization can provide wider access to soil nutrients (McGee 1988). N_2-fixing bacteria (Rhizobia) are most commonly found in root nodules of plants in the family Fabaceae and are supplied with C from the plant host in exchange for fixed N (Marschner 1986, Schlesinger 1997). Plants who support this symbiosis may be at an advantage in N-limited environments as other plants are required to scavenge inorganic N mineralized by free living bacteria from the soil environment (Marschner 1986). Plant roots may also be dually colonized by N_2-fixing bacteria and mycorrhizal fungi as P acquired by mycorrhizae can be turned into energy used for N fixation (Rose and Youngberg 1981). However studies have shown decreased AM colonization in roots harboring N_2-fixing bacteria suggesting a potential antagonism between these two symbioses (Bethlenfalvay et al. 1985, Bethlenfalvay et al. 1997). In addition, symbiont strategies are energetically costly, and do not always result in a net benefit for the plant (Klironomos 2003, Menge et al. 2008). Peng et al. (1993) reported that belowground C costs for mycorrhizal plants can be 10-20% higher than for non-mycorrhizal plants. Therefore, plants employing rapid resource acquisition strategies may simply utilize direct nutrient uptake by creating new roots (Eissenstat and Yanai 1997) or increasing SRL and branching (Brundrett 2002) which are also associated with lower mycorrhizal colonization (Brundrett 1991, Hetrick et al. 1991, Eissenstat 1992, Newsham et al. 1995, Cornelissen et al. 2003). The C cost of N-fixation can be 2-4x higher than the cost of acquiring inorganic N from the soil (Chapin et al. 2002). For this reason, plants may also select against N_2-fixing bacteria when the cost of maintaining this symbiosis becomes higher than the benefit, for example, when plant available soil N or nitrogen use efficiency (NUE) is high (Menge et al. 2008). Considering the type and magnitude of a plant's root symbiont(s) can help to elucidate the underlying mechanisms of the plant's resource acquisition strategy.

In the context of these morphological, chemical, and symbiont traits, we examined the hypothesis **that the roots of lianas would have higher SRL, higher branching intensity, lower tissue density, lower C, higher N and P, and lower root symbiont colonization than those of co-occurring trees (H2).** This particular suite of functional traits (Figure 2) parallels our first hypothesis **that the root functional traits of lianas would be more strongly characterized by strategies for rapid resource acquisition than those of co-occurring trees (H1)**. Determining the validity of these hypotheses is a critical factor in understanding the mechanisms driving the current increase in liana abundance in tropical forests.

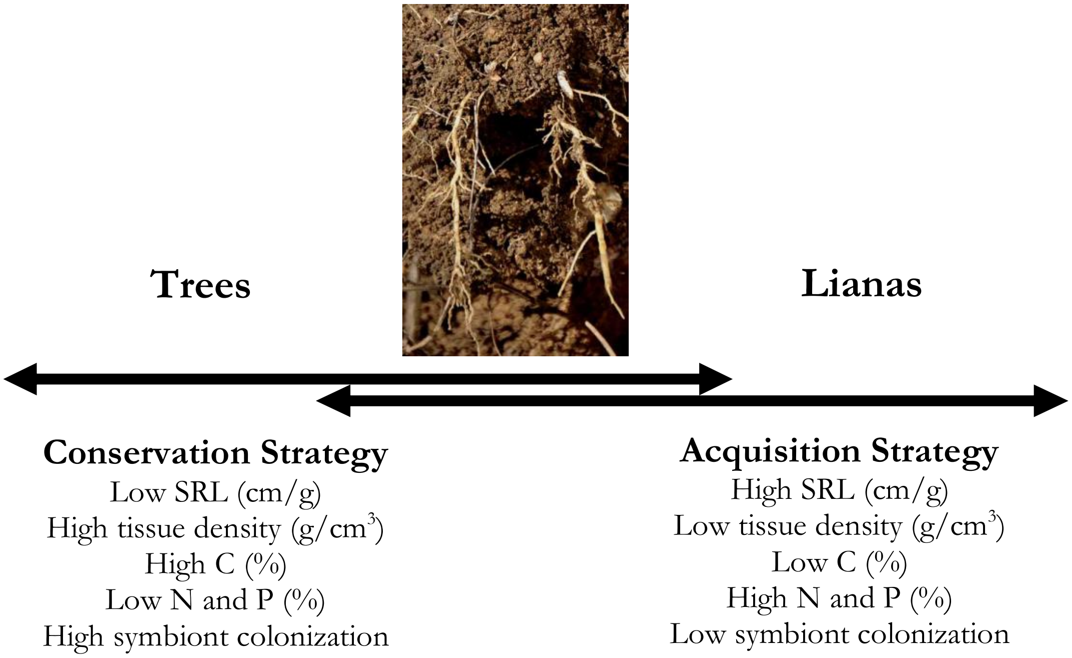

Figure 2

CHAPTER 2

METHODS

SITE DESCRIPTION

Barro Colorado Island (BCI), (9009'N, 7905 1'W) is a 15-km^2 island in Gatun Lake, at the northwestern (Caribbean) end of the Panama Canal, in the central part of the Republic of Panama, Central America. The climate is predominately warm and wet, with an annual mean temperature of 27°C, and an annual mean precipitation of 267 cm. It has distinct annual wet (May to December) and dry (January to April) seasons, with the dry season receiving on average less than 13 cm of rainfall monthly (Yavitt and Wieder 1988, Baillie et al. 2006). The vegetation is considered tropical moist forest (Holdridge and Budowski 1956) and trees are the dominant growth form with approximately 365 species comprising about 27.7% of the total vegetation on the island, and approximately 171 lianas species comprising about 13% of the total vegetation (Croat 1978) although the percentage of lianas may have since increased (see introduction). One-half of the island supports old-growth forest (>300 yr old); while the other half is secondary forest developed on previous agricultural land that was abandoned prior to BCI receiving preserve status in the 1930's (Yavitt and Wieder 1988). Andesitic-basaltic bedrock, derived from an early Miocene lava flow (Woodring 1958, Baillie et al. 2006), forms a thick cap at high elevations near the center of the island. Sedimentary bedrock, composed of two different Oligocene formations (Woodring 1958) occurs at low elevations along the outer parts of the island. The basalt-derived soils are relatively nutrient-poor oxisols, while the sediment-derived soils are less weathered, higher nutrient Alfisols (Yavitt and Wieder 1988).

SPECIES SELECTION

Six intra-familial tree-liana pairs (Table 1) were selected to control for extraneous phylogenetic variation that may interfere with the detection of functional trait differences between growth forms. Species pairs were selected at the family level using the Maximum-parsimony tree of 281 species of woody plants on BCI (Kress et al. 2009). The plant families selected were evenly distributed across this cladogram to control for phylogenetic deviation between families. Species within families were chosen based on prevalence within the 25 hectare (ha) plot and the feasibility of root sampling (roots were abundant and shallow enough to be excavated without causing significant destruction to the forest or the fine root architecture of the sample).

Table 1

Family	**Liana species**	**Tree species**
Polygonaceae	*Coccoloba parimensis* Benth.	*Coccoloba manzinellensis* Beurl.
Rubiaceae	*Chomelia psilocarpa* Dwyer & M.V. Hayden	*Alseis blackiana* Hemsl.
Fabaceae(caes.)	*Clitoria javitensis* Benth.	*Platypodium elegans* Vogel
Combretaceae	*Combretum decandrum* Jacq.	*Terminalia amazonia* (J.F. Gmel.) Exell
Bignoniaceae	*Paragonia pyramidata* (Rich.) Bureau	*Tabebuia guayacan* (Seem.) Hemsl.
Cestralaceae	*Prinostemma aspera* Miers	*Maytenus schippii* Lundell

ROOT COLLECTION AND PROCESSING

From May to July 2012, fine (<2mm diameter) roots were sampled with an n=10 individuals of each tree and liana species (Table 1) for a total n=120. Sampling took place within the 25 ha and 6 ha AVA plot on BCI. These adjacent forest dynamics plots are comprised of mature secondary successional forest (on previous agricultural lands) on the upper andesitic-basaltic plateau cap at the center of the island (Yavitt and Wieder 1988, Baillie et al. 2006). These plots contain Lake, AVA, and Marron soils which are classified as Pale-swelling clay, Red-light clay, and Brown-fine loam respectively and are all derived from the same parent material (andesitic-basaltic lava flow) (Yavitt and Wieder 1988, Baillie et al. 2006). Ranges for total N and P and net mineralization potentials for nitrate, ammonium and phosphate in these soils are listed in Table 2 (Yavitt and Wieder 1988).

Table 2

Total (mg/g dry soil)		CaCl2-extractable (µg/g dry soil)		
N	P	NO_3^-–N	NH_4^+-N	PO_4^{3-}–P
4.9-5.1	1.15-1.3	14.4-17.3	0.42-0.7	0.28-0.31

Individuals of target species were chosen based on accessibility of root systems. Direct access to full sunlight of canopy leaves was visually assessed (using binoculars) for each individual. Individuals were all sampled during the wet season (May-July) to ensure for similar soil moisture conditions. Disturbance and basic species composition was also consistent across the entire sampling area (Knight 1975).

Following the methodology of Cornilessen et al. (2003) and Holdaway et al. (2011) ~5g of fine (<2mm diameter) roots were carefully excavated from the top 20 cm of soil from n=120 individual trees and lianas. Roots were directly traced from the main plant stem to ensure correct species identification. After excavation, roots were stored on ice and transported back to the laboratory for immediate processing.

Root functional traits (Table 3) were selected based upon consensus in the literature (see introduction) and practicality of sampling. Roots were rinsed with de-ionized (DI) water and cleaned with paintbrushes to remove soil particles. Roots were measured with digital calipers and samples were divided into two diameter size classes: 0-1mm to encompass lower branching order lateral roots and 1-2 mm to encompass higher branching order lateral roots (Fitter 1982, Pregitzer et al. 2002, Guo et al. 2008). Root order is an important consideration for root function, however for the purposes of this study, we used a diameter size class sorting system similar to Trumbore et al. (2006). Our rationale is that the smaller diameter size class is a generally representative of roots involved in nutrient and resource acquisition and the higher size class of roots are generally involved in root structure and transport.

Table 3

Root functional traits	**Trait category (see introduction)**
Total C, N, P (%)	Chemical
C:N, C:P, and N:P (%:%)	Chemical
Branching intensity (forks/cm)	Morphological
Tissue density (g/cm^3)	Morphological
Specific root length (SRL) (cm/g)	Morphological
Mycorrhizal colonization (% root length)	Symbiont
Nodulation biomass (g/cm)	Symbiont

After splitting into respective size classes, a small portion of the 0-1 mm size class of each sample was removed and stored in 95% ethanol (ETOH) at 4º C for subsequent mycorrhizal assessment. All samples were then scanned at 300 DPI (CanoScan LiDE210, Canon, U.S.A) into WINRHIZO (Regent Instruments Inc., Quebec, Canada, 2000) to quantify root length (cm), volume (cm^3) and forks. Samples were then dried at 60º C for 72 hours and weighed for dry mass (g). Dry mass data were combined with WINRHIZO data to calculate the SRL (cm/g) and tissue density (g/cm^3) for each sample. Dried roots were then ground completely to a fine powder using a ball-mill grinder for tissue chemistry analyses. Total C and N were determined using a Carlo Erba NA1500 CHN combustion analyzer (Milan, Italy) via the micro-Dumas combustion analysis method. Total P was determined using an Alpkem 300 Series Colorimetric auto-analyzer (Clackamas, Oregon, USA) via the Plant Dry Ash/Acid Extraction method and a Continuous Flow Colorimetric Assay. Some individual samples lacked a sufficient amount of root tissue for both analyses (C/N and P), and occasionally two to three individuals' root tissue were pooled into one sample for a minimum of 7 replicates per species.

Roots stored in ETOH were subsequently rinsed with DI water. Using the methodology of Cornilessen et al.(2003), roots were cleared in a 5% potassium hydroxide (KOH) solution at 60°C in a water bath for 4-6 hours. Next, roots were soaked in a 2% Hydrogen Chloride (HCL) solution briefly to acidify the roots and then stained at 60°C for 15 minutes using a 0.05% trypan blue solution (trypan blue in 2:1:1 lactic acid: water: glycerol). Stained roots were rinsed repeatedly and stored in a de-stain solution (2:1:1 lactic acid: water: glycerol) prior to microscopic analysis. AMF colonization for each sample was quantified at 40x magnification using the magnified intersections method of McGonigle et al. (1990). This method involves randomly selecting a root fragment from each sample and marking the presence or absence of arbuscules, hyphae, and/or vesicles at 10 intersections along the fragment. 10 root fragments were analyzed for each sample for a total of 100 intersections per individual sampled. Arbuscular, vesicular, and hyphal percent colonizations were calculated by dividing the count for each structure by 100 and total percent colonization was calculated by subtracting 1-the count of intersections completely absent of fungal structures and multiplying by 100. Species of the genus *Coccoloba* (family Polygonaceae), however, were dually colonized by AMF and EMF with a significantly higher proportion of EMF colonization in their roots. Due to the higher percentage of EMF and difficulty in distinguishing AMF arbuscules below EMF mantle, I quantified the presence of an EMF mantle and/or AMF hyphae and vesicles at each intersection, and used these values to calculate total, mantle, hyphal, and vesicular colonization percentages as described above. The EMF mantle count replaced the AMF arbuscular count in all subsequent statistical analyses for this tree-liana pair.

Finally for roots of the family Fabaceae, N_2-fixing nodules were removed prior to scanning and placed into a separate container. They were then dried at 60º C for 72 hours and weighed for dry mass (g). Dry mass data was combined with root length data from WINRHIZO to calculate nodulation biomass per unit root length (g/cm).

STATISTICAL ANALYSES

We tested if different growth forms (lianas versus trees) differed in functional traits. We ran Two-way Multivariate Analysis of Variance (MANOVA) tests to determine if different suites of functional traits (all, morphological, chemical, morphological & chemical, and symbiont-Table 3) were different between growth forms at each root size class with family included as a blocking factor. Nodulation biomass was not included in MANOVAs since this trait was only present in one family (Fabaceae), thus for the symbiont category, only mycorrhizal colonization data were used.

We then ran Mixed Effects linear models with growth form as the fixed effect and family as the random effect on each functional trait to determine which traits were significantly different between growth forms at each root size class. We used these models to estimate the direction and magnitude of the differences when present.

A Two-Tailed t-test was run for nodulation biomass as this trait was only present in one family. Additionally, Mycorrhizal analyses (MANOVA and ANOVAs) were run with and without the family Fabaceae due to the potential of the N_2-fixing symbiosis to alter patterns in mycorrhizal colonization (see introduction). All other species associate with only mycorrhizae as their sole root symbiont (although the genus *Coccoloba* associates with both ecto- and arbuscular mycorrhizae-see above).

CHAPTER 3

RESULTS

Liana root functional traits were significantly different from those of trees for most traits examined in at least one root size class, with the exception of nodulation biomass and total N. Root functional traits of lianas were more indicative of a rapid resource acquisition strategy than those of co-occurring trees, in support of H1. In addition, liana roots had higher SRL, higher branching intensity (forks/cm), lower tissue density, lower total C, higher total P, lower C:N, C:P, and N:P and lower mycorrhizal colonization than those of co-occurring trees, in support of H2.

For the MANOVAs, we tested for significant differences between growth forms using all traits and multiple combinations of trait categories (morphological, chemical, morphological & chemical, and mycorrhizal-Table 4) to determine the categories, if any, that might deviate from the overall Multivariate trend. The results of the MANOVAs indicate that lianas have significantly different traits to those of trees for nearly all trait combinations in both root size classes (Table 4). One exception was that overall, mycorrhizal traits were not significantly different between trees and lianas. This was potentially due to the confounding effect of the N_2 fixation symbiosis, in the family Fabaceae, and after removing this family from the analysis, we observed significantly lower mycorrhizal colonization on liana versus tree roots. Mycorrhizal colonization was only quantified for the 0-1mm size class because it represents the lowest roots orders (~1-5) which are more likely to associate with mycorrhizal fungi ((Guo et al. 2008)-see Materials and methods).

For the Mixed-Effects linear models we tested for significant differences between growth forms for each individual functional trait using family as a random effect. For the 0-1mm size class lianas had a significantly higher SRL, significantly higher forks/cm, significantly higher percent total P, and a significantly lower percent C:N and C:P (Table 5, Figures 3-6). For the 1-2 mm size class, lianas had a significantly lower tissue density, a significantly lower percent total C, a significantly lower percent C:N and C:P, and a significantly lower percent N:P. (Table 5, Figures 7-14). For C:P (Fig. 12), the tree *Maytenus schippii* (Celastraceae) was a significant outlier, however 5 out of the 6 families showed a similar trend of trees>lianas in C:P, therefore this species was unlikely to skew the overall growth form mean. For mycorrhizal traits, lianas had a significantly lower percent root length colonized by arbuscules-mantle (mantle for Polygonaceae and arbuscules for remaining plant families; see materials and methods) when the family Fabaceae was removed from the analysis (Table 6, Figures 15, 16).

For the 2-tailed T-Test, the Satterthwaite method was used due to inequality of variances ($F_{5,9}$ =14.74; p=0.0008). Nodulation biomass was not significantly different between trees and lianas in the family Fabaceae, however this may be due to an extremely small sample size (n=16) and lack of normal distribution of the data (Table 7).

Table 4					
Multivariate analyses		0-1mm			
Results of two-way MANOVAs for growth form (liana v. tree) with multiple trait category combinations Results are listed by root diameter size class excluding mycorrhizae which is only 0-1 mm. Bold p values indicate growth form was significant		growth form			
	Response variables	F	num df	den df	P
	(a-m) all	4.16	13	65	**<0.0001**
	(a-i) morph chem.	6.84	9	105	**<0.0001**
	(a-c) morph	14.28	3	111	**<0.0001**
	(d-i) chem.	3.15	6	108	**0.007**
	(j-m) mycorr	0.52	4	74	0.7184
	(j-m) mycorr*	2.19	4	61	**0.0812**
	*=without Fabaceae				
		1-2mm			
		growth form			
	Response variables	F	num df	den df	P
	(a-m) all	3.38	13	63	**0.0006**
	(a-i) morph chem.	5.7	9	103	**<0.0001**
	(a-c) morph	2.7	3	111	**0.0493**
	(d-i) chem.	7.94	6	106	**<0.0001**

Table 5					
Chemical and Morphological traits		0-1mm		1-2mm	
Results of Mixed Effects Models comparing root functional traits between growth forms (liana v. tree) using family as the random effect and growth form as the fixed effect. Results are listed by root diameter size class Bold p values indicate growth form was significant		growth form		growth form	
	Response variable	F (1,113)	p	F (1,111)	P
	a) SRL	42.0992	**<0.0001**	0.0002	0.9890
	b) Tissue density	3.6761	0.0577	5.7785	**0.0178**
	c) Forks/cm	5.9860	**0.0160**	0.0663	0.7973
	d) Total N	0.4281	0.5143	0.7802	0.3789
	e) Total C	1.1598	0.2838	39.7266	**<0.0001**
	f) Total P	5.2286	**0.0241**	8.3882	**0.0046**
	g) C:N	4.6122	**0.0339**	7.4316	**0.0074**
	h) C:P	9.4710	**0.0026**	17.7873	**<0.0001**
	i)N:P	3.5810	0.0610	11.7484	**0.0009**

Table 6

Mycorrhizal traits		all families		without Fabaceae	
Results of two-way ANOVA with randomized block design comparing mycorrhizal colonization between growth forms (liana v. tree) using family as the blocking factor. Bold p values indicate growth form was significant		growth form		growth form	
	Response variable	F (1,77)	p	F (1,64)	P
	j) Total mcoln	0.1061	0.7455	2.6117	0.1110
	k)Arbs-mantle	0.3690	0.5454	8.0616	**0.0061**
	l) Vesicles	0.0012	0.9723	0.0179	0.8940
	m) Hyphae	0.9617	0.3298	0.2652	0.6084

Table 7

Nitrogen Fixation		Satterthwaite	
Two-tailed t-test comparing Nodulation biomass (g/cm) between growth forms (liana v. tree) in the family Fabaceae		growth form	
	Response variable	T (5.4102, 0.05)	P
	n)Nodulation biomass	-1.47	0.1982

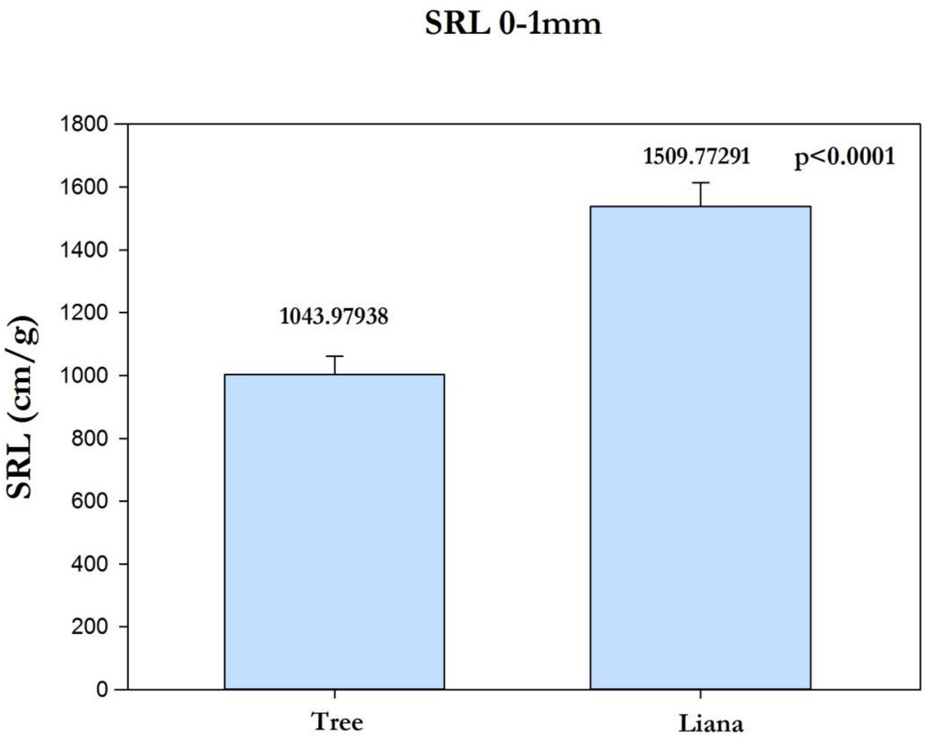

Fig. 3. Specific Root Length of trees and lianas in the 0-1mm root size class. Bars are growth form means (+SE)

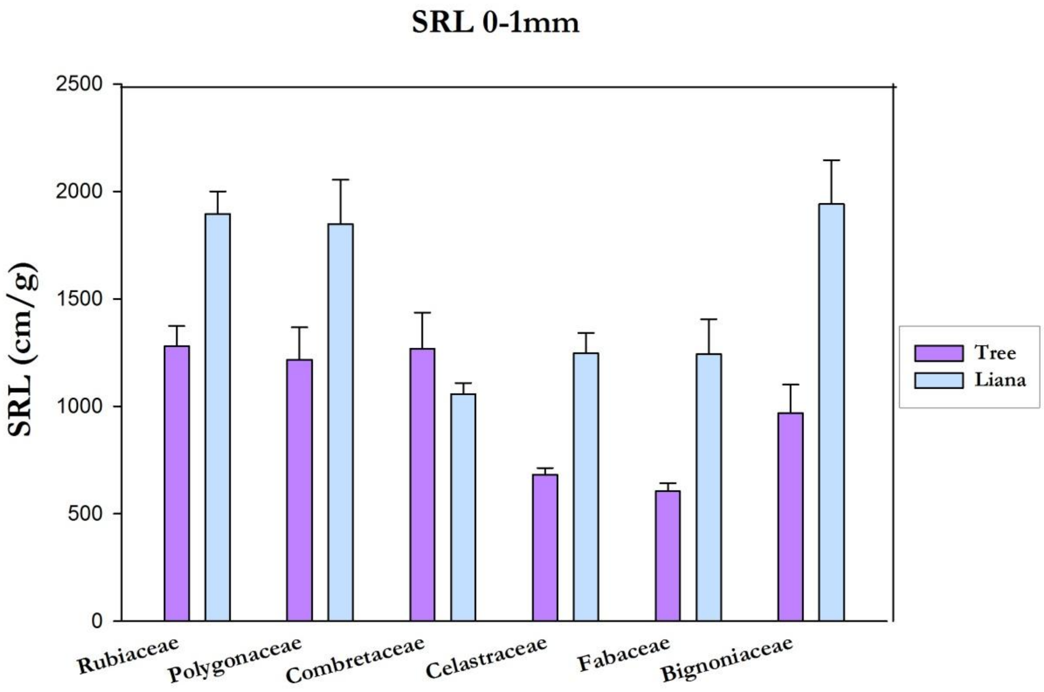

Fig. 4 Specific Root Length of trees and lianas in the 0-1mm root size class Bars are species means (+SE)

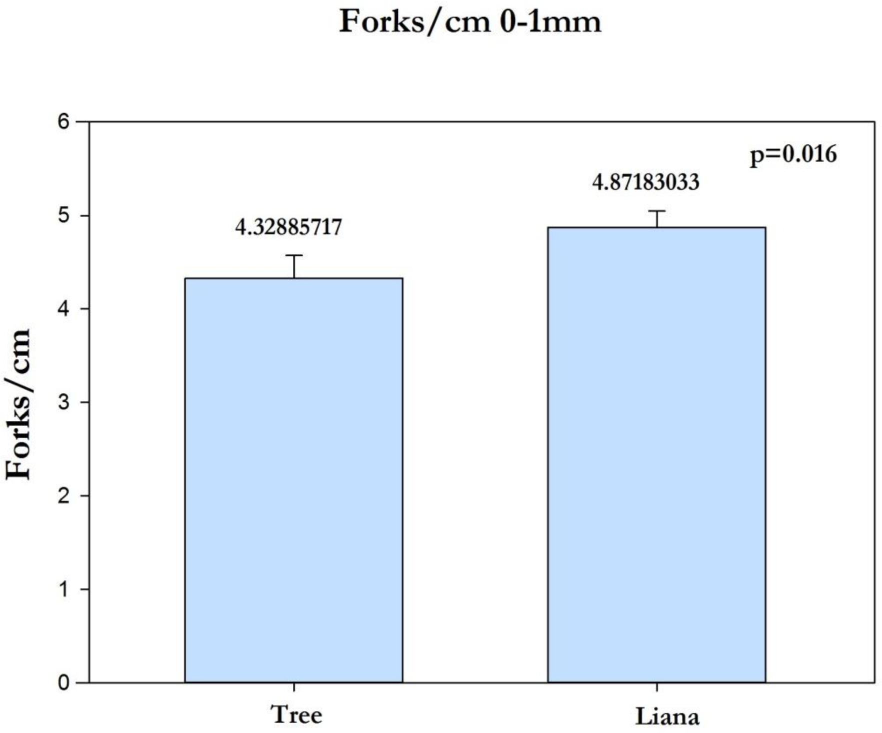

Fig. 5 Branching intensity (forks/cm) of trees and lianas in the 0-1mm root size class Bars are growth form means (+SE)

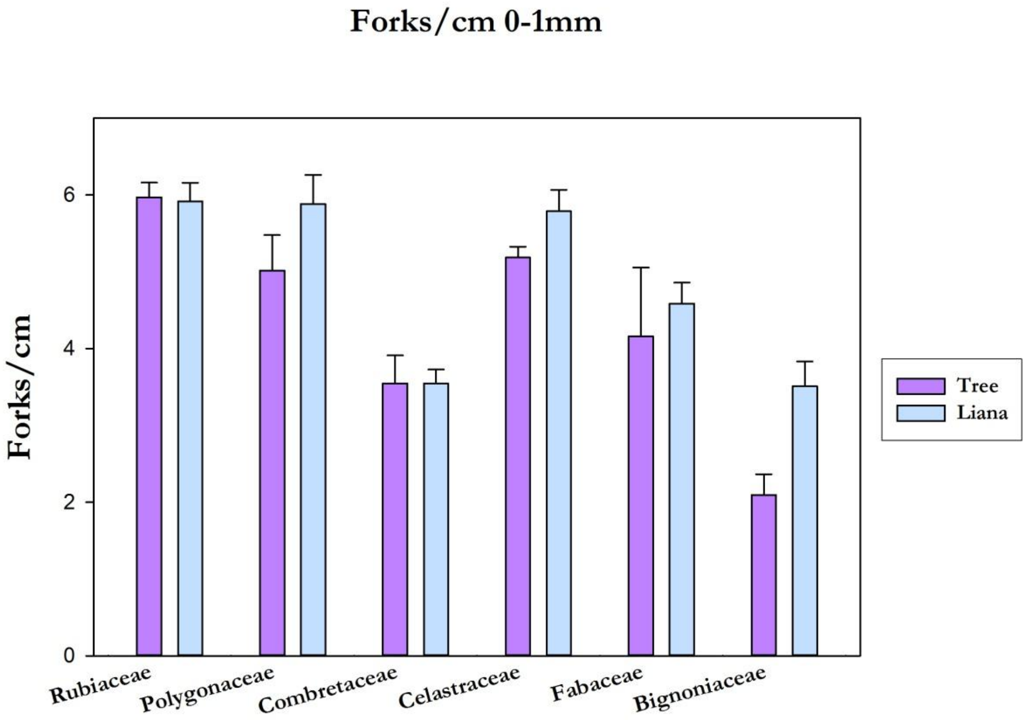

Fig. 6 Branching intensity (forks/cm) of trees and lianas in the 0-1mm root size class Bars are species means (+SE)

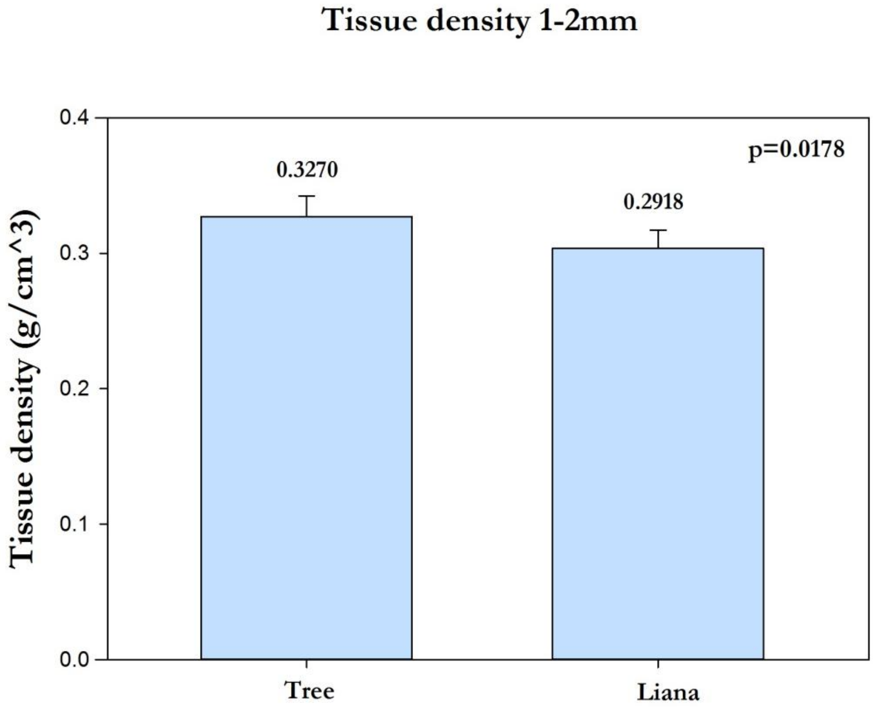

Fig. 7 Tissue density of trees and lianas in the 1-2mm root size class
Bars are growth form means (+/- SE)

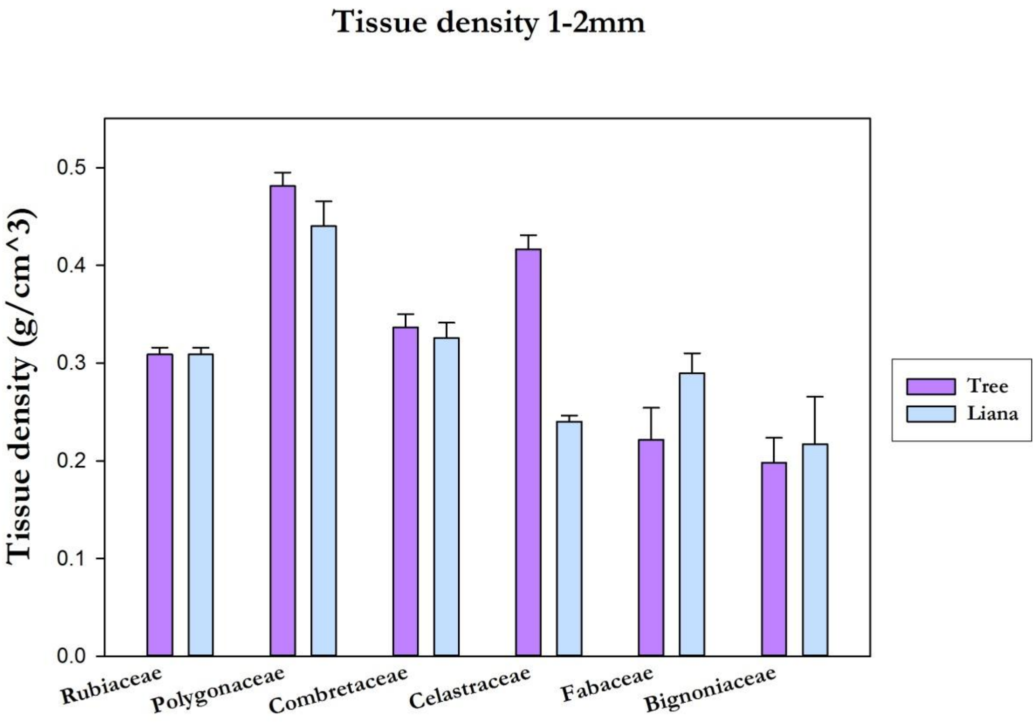

Fig. 8 Tissue densityof trees and lianas in the 1-2mm root size class
Bars are species means (+SE)

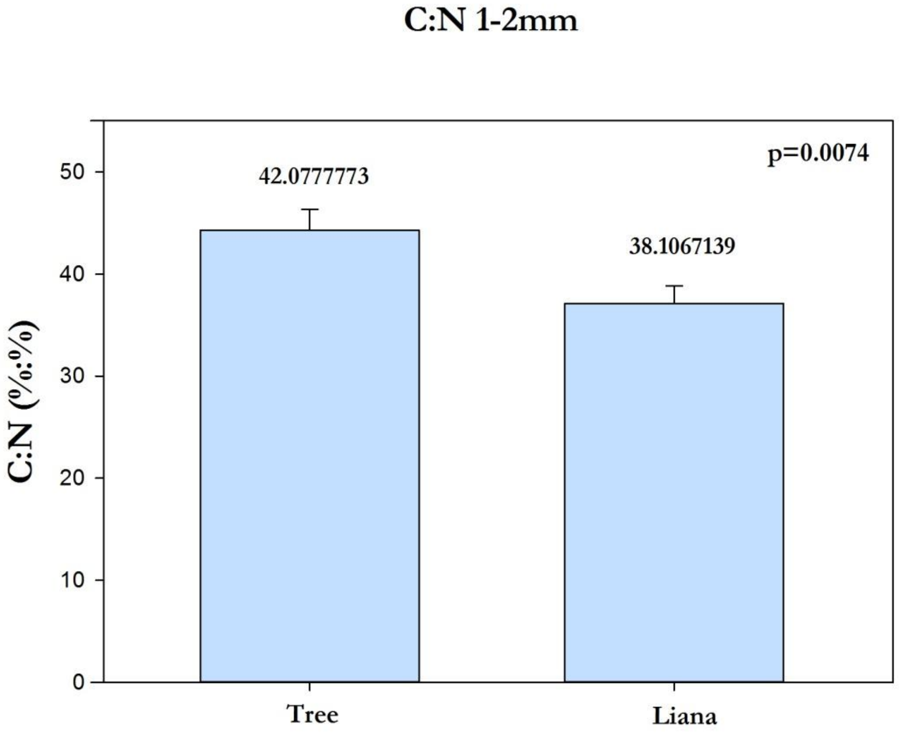

Fig. 9 C:N tissue chemistry of trees and lianas in the 1-2m root size class
Bars are growth form means (+/-SE)

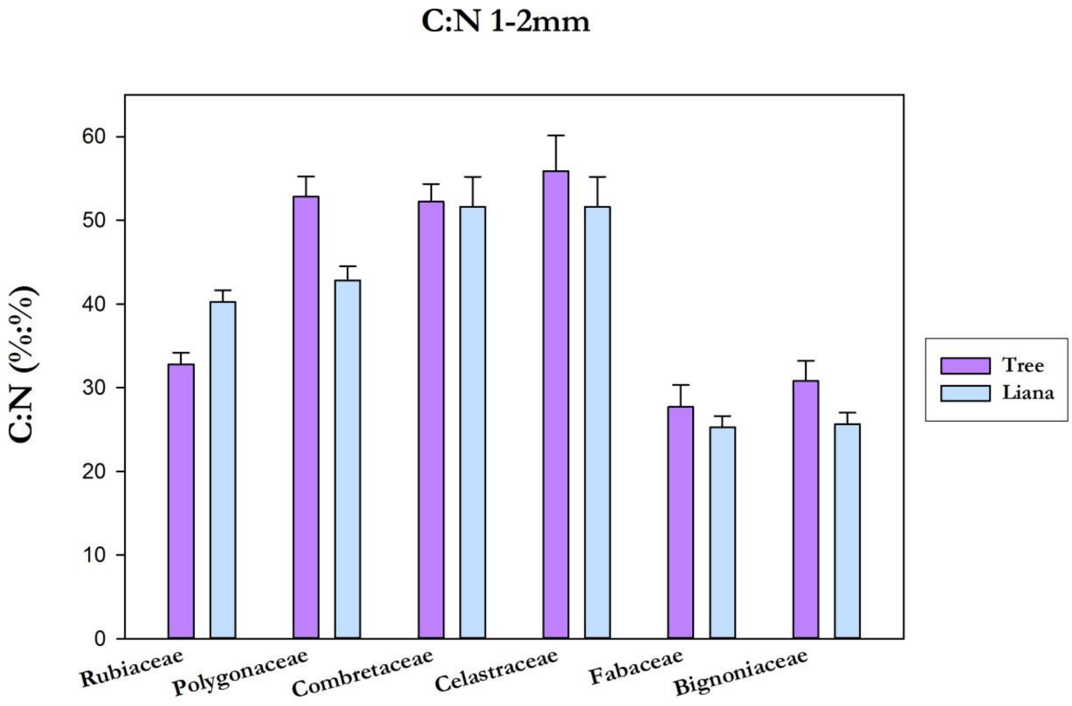

Fig. 10 C:N tissue chemistry of tress and lianas in the 1-2mm root size class
Bars are species means (+SE)

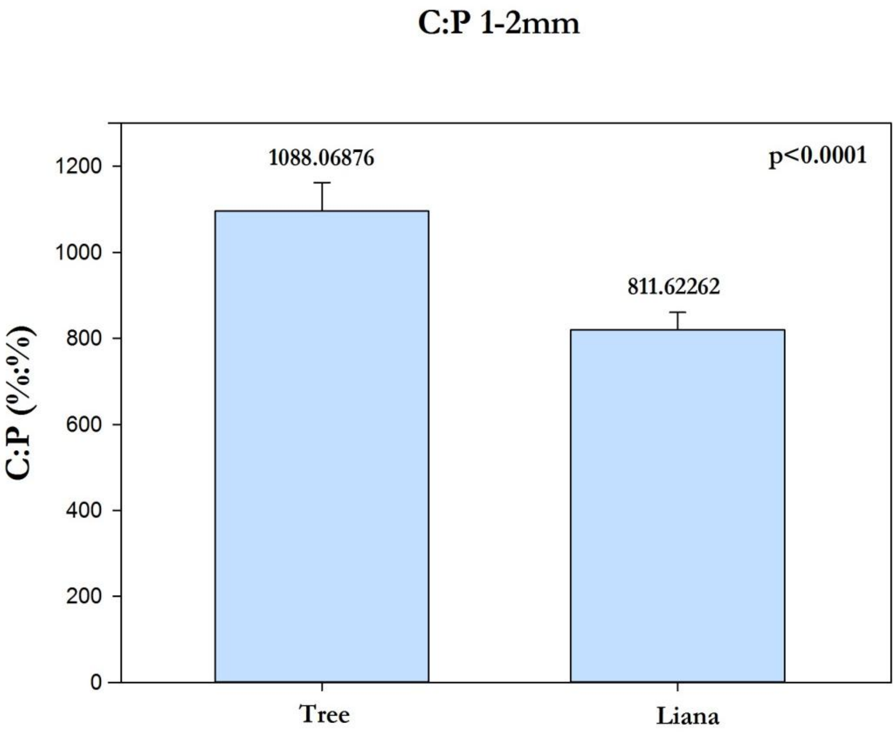

Fig. 11 C:P tissue chemistry of trees and lianas in the 1-2mm root size class
Bars are growth form means (+SE)

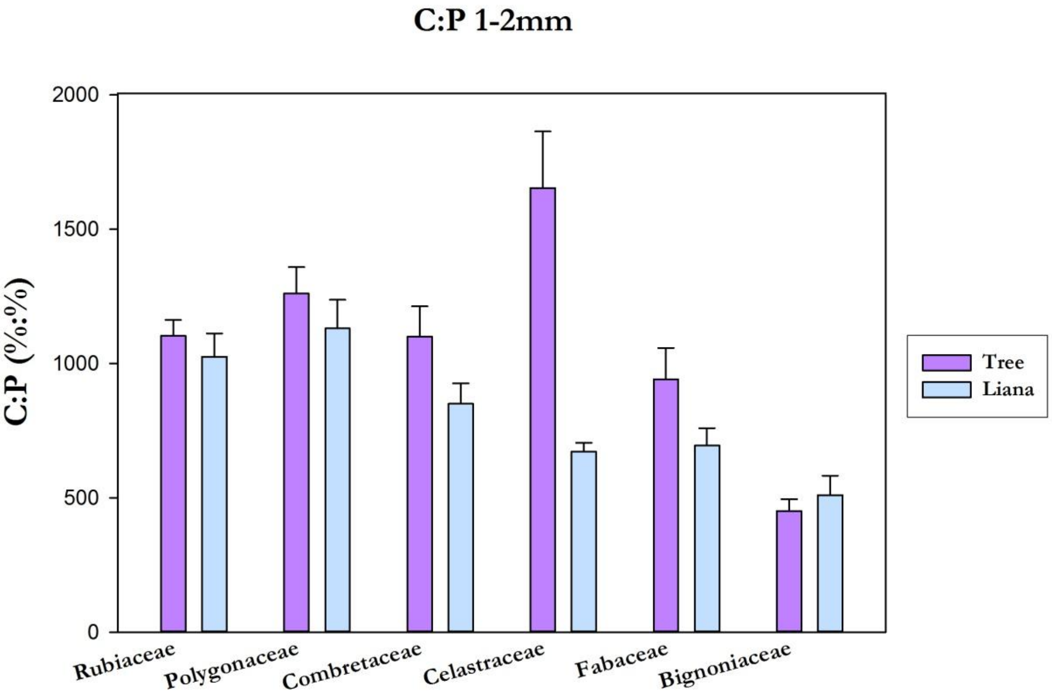

Fig. 12 C:P tissue chemistry for trees and lianas in the 1-2mm root size class
Bars are species means (+ SE)

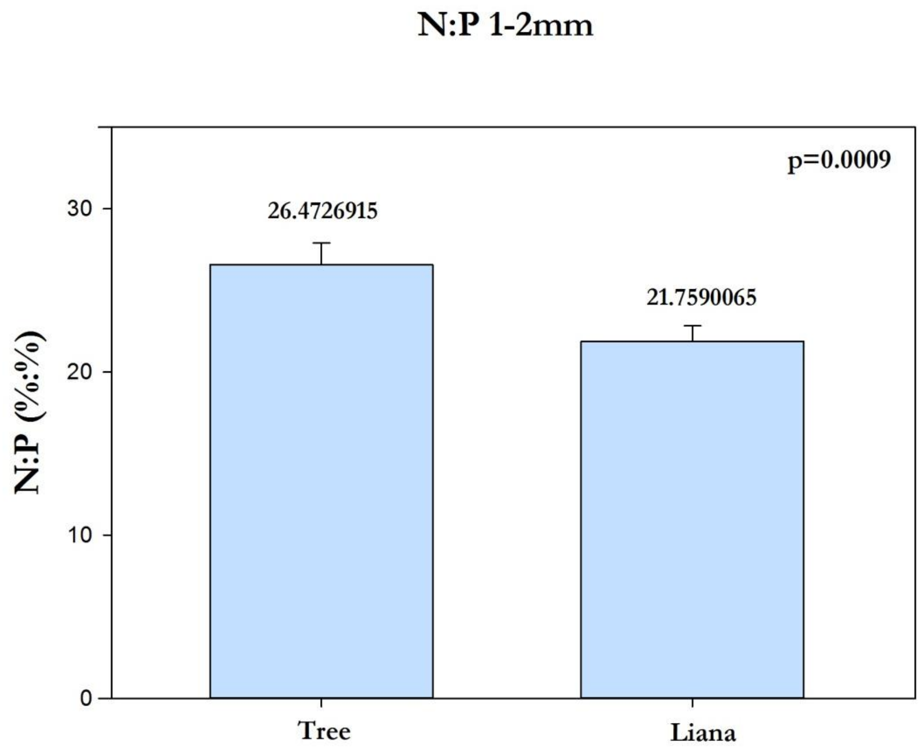

Fig. 13 N:P tissue chemistry of trees and lianas in the 1-2mm root size class
Bars are growth form means (+/-SE)

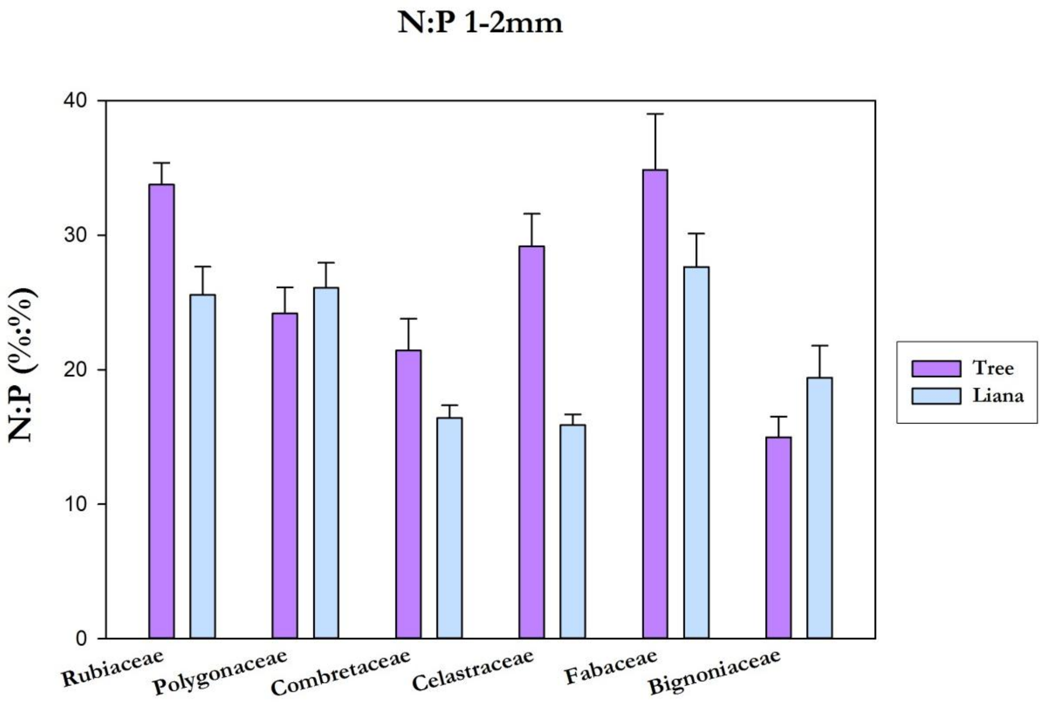

Fig. 14 N:P tissue chemistry of trees and lianas in the 1-2mm root size class
Bars are species means (+SE)

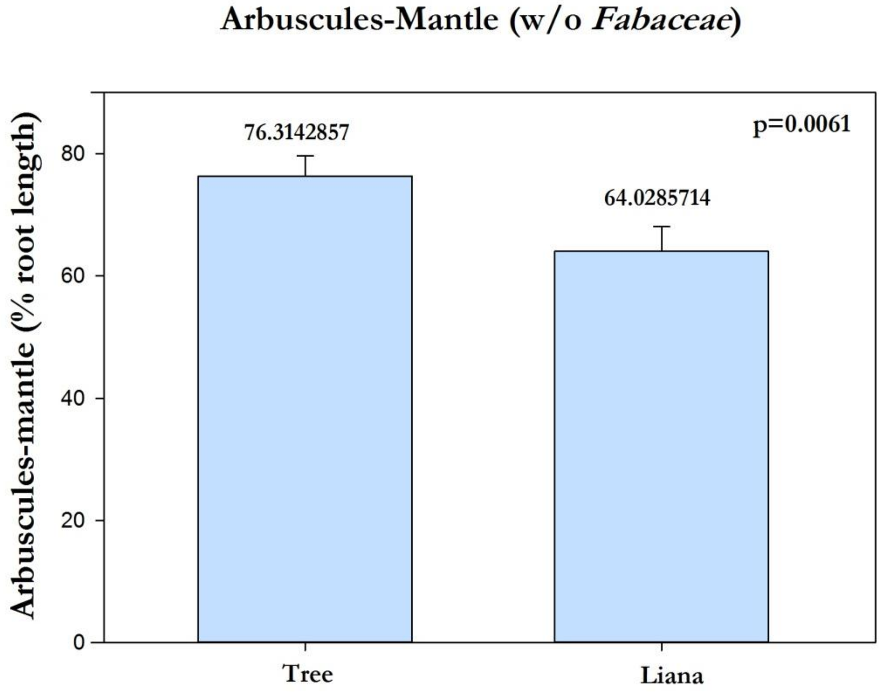

Fig. 15 Arbuscules-Mantle colonization percentage of trees and lianas excluding Fabaceae
Bars are growth form means (+SE)

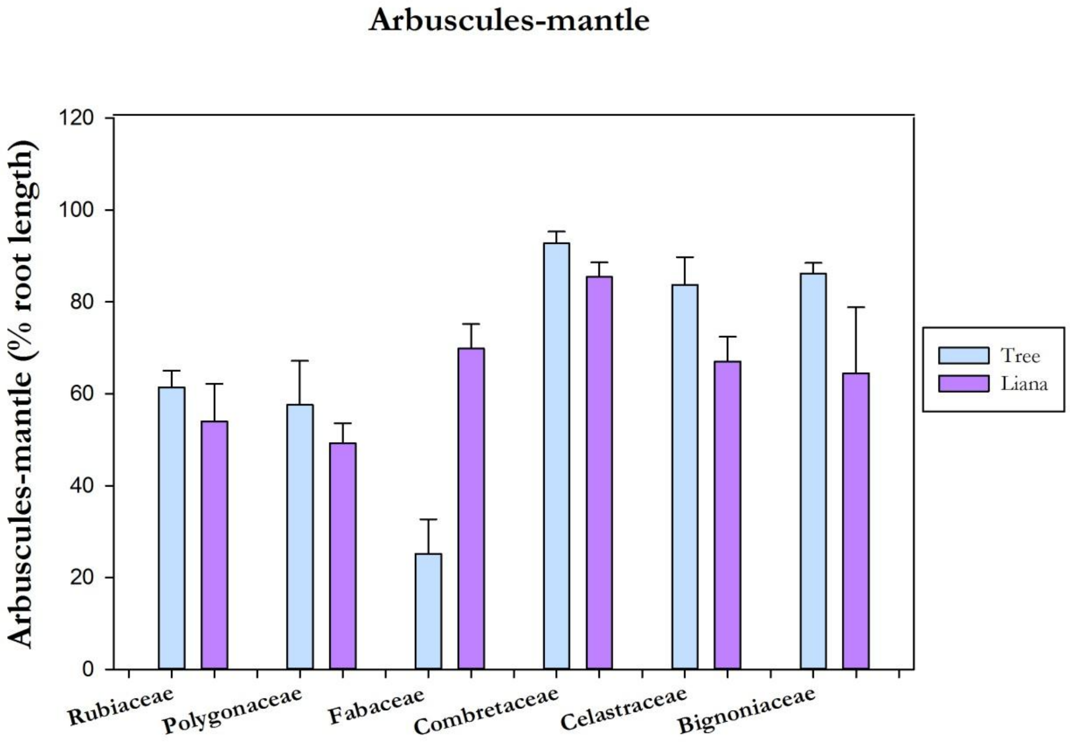

Fig. 16 Arbuscules-mantle colonization perecentage of trees and lianas.
Bars are species means (+/-SE)

CHAPTER 4

DISCUSSION

In a lowland tropical forest of Panama, lianas display a significantly different suite of root functional traits in comparison to co-occurring trees. These traits can be applied to the concepts of the leaf and plant economic spectrum (Wright et al. 2004a, Freschet et al. 2010), and suggest that lianas are more characterized by a strategy of rapid resource (*e.g.*, water and nutrients) acquisition belowground relative to related species of trees. A similar pattern has been observed among aboveground functional traits of lianas and trees (Andrade et al. 2005, Selaya et al. 2008, Cai et al. 2009, Zhu and Cao 2010), however, to our knowledge, this is the first study to compare an extensive set of root functional traits between lianas and trees.

Liana roots exhibited traits that are indicative of a rapid resource acquisition strategy, which has been characterized by a quick return of water and nutrients per unit C invested at the cost of lowered resistance to physical and biological stressors and shorter tissue lifespan. In this study, liana roots displayed higher SRL, lower tissue density, higher branching intensity, lower C:N, C:P, and N:P ratios and lower percent mycorrhizal colonization than the roots of related trees in similar habitat conditions. These traits depict a trade-off between resource acquisition and root resilience and lifespan as a part of the plant's overall growth strategy.

Among morphological traits, liana roots had higher SRL, lower tissue density, and higher branching intensity (forks/cm) than did co-occurring trees, supporting our hypothesis that liana traits would be more indicative of a rapid resource acquisition strategy. SRL captures the potential for resource acquisition relative to a given C investment to root biomass. This is based on the principle that root length is a better predictor of nutrient and water uptake than is root mass (Eissenstat 1992, Chapin et al. 2002). High values of SRL are indicative of rapid root growth, high water and nutrient absorption capacity, and an overall lower C cost to the plant (Eissenstat 1992, Tjoelker et al. 2005). In support of this, Reich et al. (1998) saw a strong positive correlation between N uptake values and SRL in nine boreal tree species. Similarly, Eissenstat (1991) found a positive correlation between rapid root proliferation, water uptake and SRL in citrus roots . However, high SRL comes at the cost of decreased lifespan and increased vulnerability to stressors (Eissenstat 1992, Eissenstat and Yanai 1997, Ryser 1998). McCormack et al. (2012) identified a negative correlation between SRL and root lifespan in 12 temperate tree species. Similar to SRL, root tissue density reflects C investment in root tissue per unit volume and is related to root longevity and "toughness" (Eissenstat and Yanai 1997, Ryser 1998). Typically, low tissue densities coincide with rapid root growth rates, but also reflect a lower tolerance of desiccation, herbivory, and turnover (Chapin et al. 2002). Ryser (1996) compared five ecologically contrasting species of grasses and found that species with lower root tissue densities had shorter root lifespans (*i.e.*, faster root turnover). Finally, root branching intensity (forks/cm) depicts the abundance of lateral fine roots per unit root length. Greater root branching intensity increases the length and surface area of fine lateral roots (*i.e.,* the roots involved in nutrient uptake), in a given soil volume (Robinson et al. 2003). Highly branched roots may offset the need for symbiotic nutrient acquisition as mycorrhizal dependent roots of warm season grasses were less branched than cool season grasses with lower dependencies on mycorrhizal fungi (Hetrick et al. 1991). However, high branching intensity also increases the proportion of the lowest root orders and therefore tends to reduce the lifespan of the root system (Eissenstat and Yanai 1997). In our study system, liana morphological root traits are suggestive of rapid resource acquisition at the cost of limited stress tolerance and rapid tissue turnover relative to co-occurring trees.

Among chemical traits, we observed that lianas had lower C:N, C:P, and N:P in root tissues than did co-occurring trees, supporting our hypothesis that liana traits would be more indicative of rapid growth and a rapid resource acquisition strategy. Root elemental ratios (C, N and P) are useful for determining strategies of resource acquisition versus resource conservation (Tjoelker et al. 2005) and may provide insight into the biochemical traits impacting resource acquisition in lianas and trees. Carbon to nutrient ratios in root tissues reflect the potential for growth and metabolic activity relative to turnover and maintenance costs (Chapin et al. 1986, Chapin et al. 2002). For example, low C:N and C:P are indicative of rapid root growth and respiration rates and lower C construction costs but also increased root turnover (Eissenstat and Yanai 1997, Tjoelker et al. 2005). Tjolker et al. (2005) detected that higher N concentrations in roots was associated with lower root lifespan among 39 grass, forb, legume, and woody plant species of a savanna community. McCormack et al. (2012) also observed that lower C:N ratios were associated with lower root longevity in 12 temperate tree species. Additionally, a higher N content in tissues can be representative of a higher proportion of energy allocated to proteins associated with rapid nutrient uptake and assimilation versus lignin and phenols which are associated with resistance and defense (Eissenstat and Yanai 1997). Lower C can also result in decreased protection from herbivory by root exudates as is evidenced in isotopic studies (McDougal.Bm and Rovira 1970). N:P ratios in plant tissues are positively correlated with tissue thickness and negatively correlated with relative growth rate which are important considerations for tissue turnover (Nielsen et al. 1996, Sterner and Elser 2002). Additionally, lower root N:P creates a higher potential for the construction of biological compounds associated with energy and growth (sugar phosphates and nucleic acids) and lower potential construction of N-rich proteins (Agren 2004). Liana roots had chemical traits significantly different from trees in our study system suggestive of a unique resource acquisition strategy for this growth form.

Among symbiont traits, we observed that lianas support lower mycorrhizal colonization than do co-occurring trees in all families sampled except Fabaceae. This was consistent with our expectations that liana root functional traits would reflect a rapid resource acquisition strategy. Root symbionts such as mycorrhizal fungi and N_2-fixing bacteria reflect the trade-off between improved resource acquisition and increased C cost for the host (Eissenstat and Yanai 1997). Mycorrhizal fungi can enhance plant nutrient uptake by increasing the volume of soil exploited by the production of extramatrical fungal hyphae (Brundrett 1991, Chapin et al. 2002) while N_{2}-fixing bacterial symbioses also enhance nutrient uptake by supplying plant available N to plants through root nodules (Chapin et al. 2002). These symbionts represent a high C cost, where plants typically invest 4-20% of their gross primary production (GPP) to mycorrhizae (Peng et al. 1993, Chapin et al. 2002) and ~25% of their GPP to N_2 fixation (Chapin et al. 2002). Therefore, plants employing rapid resource acquisition strategies may simply utilize direct nutrient uptake by creating new roots which may represent an overall lower C cost than supporting root symbioses (Eissenstat and Yanai 1997). However, beyond the ability to acquire nutrients, these symbioses also provide a number of benefits to plants including enhanced root longevity, resistance to herbivory, pathogens, and desiccation (Eissenstat et al. 2000). For example, Espeleta et al. (1999) demonstrated that association with mycorrhizal fungi increased the tolerance of roots to drought in citrus plants. AM fungal colonization can also reduce root infestation by weevils (Gange et al. 1994) and infestation by pathogenic fungi (Newsham et al. 1995). Finally, Tu (1978) reported an up to 75% decrease of soil pathogen sporulation in leguminous (N_{2}-fixing) soybeans than non-legumes. For this study, in contrast to the pattern with mycorrhizal fungi, lianas and trees did not significantly differ in root nodulation biomass, suggesting that lianas do not differentially invest in rhizobial symbionts for N acquisition relative to trees. The lack of a response could be due to a number of factors. First, nodulation biomass (g nodule/cm root) is an estimate of N_2 fixation rate per unit root length but fails to capture differences in specific nodule activity (*i.e.,* nitrogenase activity) between species. Second, our inferences are limited because we only sampled one species-pair in the Fabaceae for comparison, suggesting that more research is needed to determine how plant investment in symbiotic N_2 fixation differs between lianas and trees. However, among morphological, chemical and symbiont traits, our results suggest that root functional traits of lianas promote the rapid acquisition of water and nutrients, and the highest potential return of these resources at the lowest C cost, relative to those of trees.

The results of our study are consistent with the reasoning that lianas employ a strategy for rapid growth, because unlike trees, they have fewer resource demands for maintaining structural stability (Putz 1983, 1984, Tyree and Ewers 1991, Niklas 1992, Cernusak et al. 2008, Selaya et al. 2008, Cai et al. 2009). To further this point, every unit increase in tree height must be proportionally balanced by an increase in stem basal area, to prevent the stem from buckling (Greenhill 1881). This substantial C investment is not required by lianas, as their stems are tree-supported and need not be resistant to bending (Putz 1983). Lianas may therefore allocate a greater proportion of their resources towards resource acquisition and growth, as evidenced by the fact that lianas support a much higher leaf weight per cross sectional stem area than do trees (Putz 1983). Our results indicate that lianas display a specialized suite of root functional traits that are likely to promote rapid growth, providing further support for the distinctive growth strategies of lianas versus trees. This knowledge is an important piece of the puzzle in understanding the mechanisms driving the current increase in liana abundance in tropical forests.

One of the strengths of this study was the phylogenetic approach in which we sampled across a diverse subset of species, paired by family, within the liana and tree communities. In this way our results are more representative of each growth form, rather than a few functionally similar species. This supports the concept that suites of root functional traits are consistent across the liana and tree communities and may represent a specialized resource acquisition strategy for each growth form. Other studies have also shown consistency in root functional trait syndromes across significant phylogenetic plant diversity. Roumet et al. (2006) found that fast growing herbaceous annuals exhibited high SRL, low root tissue density and high root N concentration as compared to slower growing perennials in central Argentina. Across fast and slow growing tree species, Comas et al. (2002) detected that roots of fast-growing species had greater SRL, smaller diameter, faster respiration and higher N concentration than those of slow-growing species across three major families in Northeastern temperate forests. Comas and Eissenstat (2004) also observed among five taxonomic contrasts of related fast and slow growing species that roots of fast-growing species generally had higher specific root length, smaller diameters, and a greater degree of branching than those of slow-growing species.

This study was based on the core principle that functional traits provide a basis from which to understand how changes in plant community composition will affect ecosystem function (Tilman et al. 1997, Diaz and Cabido 2001). In this study, lianas and trees were found to employ distinct root functional traits as part of their overall growth strategy. As lianas continue to increase, this will likely affect the overall functional composition (presence and relative abundance of certain functional traits) of the ecosystem (Diaz and Cabido 2001). An increase in the relative abundance of lianas could modify the biotic and abiotic environment for co-occurring species, especially trees, through their root functional traits. This may have significant implications for ecosystem function.

Root morphology may have significant effects on ecosystem function, especially in relation to root turnover rates (Eissenstat and Yanai 1997, Gill and Jackson 2000). SRL, tissue density, branching intensity are all factors affecting the rate of individual root turnover (Fitter et al. 1991, Ryser 1996, Ryser 1998, Eissenstat et al. 2000, Gill and Jackson 2000). Higher rates of root turnover may lead to increased soil microbial decomposition of root litter and mineralization of soil nutrients

(Swift et al. 1979). We found liana roots to have a higher SRL, lower tissue density, and higher branching intensity relative to trees which are all traits associated with higher rates of root turnover (Eissenstat and Yanai 1997). In this way, the morphological traits of liana roots may promote enhanced soil nutrient availability and microbial function.

Root tissue chemistry may also affect ecosystem functioning by controlling the stoichiometry of root litter for soil microbes (Vitousek 1982). For example, at lower C:N ratios of substrate, microbes may enhance N mineralization and excrete excess N into the soil, thus increasing the N availability to other plants (Gosz 1981, Vitousek 1982, Chapin et al. 2002). Additionally, in ecosystems with low P availability, such as tropical forests, the C:P ratio of soil organic matter can affect the balance between microbial mineralization and immobilization, affecting the supply of plant available P (Smeck 1985). We found liana roots to be lower in C:N, C:P and N:P relative to trees which may create higher rates of root turnover and litter with higher nutrient (*i.e.*, N,P) content. Additionally, studies have suggested that C:N ratios in plant litter may largely influence the composition of the local soil microbial community, especially for decomposers(De Deyn et al. 2008, Bardgett 2011). In this way, increased liana root litter with distinct tissue chemistry may have large impacts on the functioning of belowground ecosystems including the composition of soil microbial communities, nutrient dynamics, decomposition, root turnover, and plant available nutrient supply.

Root symbioses have important implications for ecosystem function especially in relation to nutrient cycling. Mycorrhizal fungi are excellent scavengers for soil nutrients and in some cases can excrete extracellular enzymes to breakdown organic nutrients into plant available forms in the soil (Brundrett 1991, Chapin et al. 2002). These fungi can also affect rates of root turnover as mycorrhizae facilitate root protection and have been associated with increased root lifespan (Gange et al. 1994, Gange and West 1994, Newsham et al. 1995). We observed that liana roots have lower mycorrhizal colonization relative to trees in non-leguminous families. Reduced mycorrhizal association in liana roots may decrease the overall dependency on mycorrhizal fungi within the ecosystem. Lowered mycorrhizal colonization may also increase the rates of root turnover which could provide enhanced plant available nutrients as described above. Additionally, while most tropical plant species associate with AM fungi (Alexander 1989), one of our pairs (*Coccoloba manzinellensis* and *Coccoloba panimensis*) associates with both AM and EM fungi. Some EM fungi are highly saprotrophic and have the enzymatic capabilities to break down numerous organic molecules and access limiting nutrients from the soil (Read and Perez-Moreno 2003). AM fungi on the other hand are much less capable of mineralizing nutrients from organic material and rely mostly on simple phosphatases and scavenging previously mineralized nutrients from the soil (Read and Perez-Moreno 2003). We found that *Coccoloba parimensis* (liana) had lower EM colonization than the congeneric *Coccoloba manzinellensis* (tree) which could decrease the overall presence of EM in the soil fungal community as lianas continue to increase. This is especially pertinent considering that *Coccoloba parimensis* was one of the top 10 most abundant liana species in the Barro Colorado Nature Monument (BCI and adjacent protected mainland peninsulas) and the single most abundant species at several sites on BCI including the 50 hectare forest dynamics plot. (Dewalt et al. 2000, Schnitzer et al. 2012). Finally, DeDeyn et al.(2008) suggested that a belowground environment that is less dominated by mycorrhizal fungi may decrease the overall long-term stability of Soil Organic Carbon (SOC) pools belowground as many of these fungi incorporate highly stable C compounds into their mycelial networks comprising a large terrestrial soil C sink. An increase in lianas and a likely decrease of the presence of mycorrhizae in soil microbial communities may therefore decrease overall SOC stability and shift tropical soils from C sinks to sources. Overall, an increase in liana abundance is likely to have major implications for ecosystem functioning, especially nutrient and C cycling.

Plant traits offer a valuable tool for predicting how changes in plant species composition associated with global change will affect the Earth (Bardgett 2011) . In support of this, changes in the relative abundance of the dominant plant life form have shown to alter hydrology, belowground C pools, and nutrient cycling (Connin et al. 1997, Gill and Burke 1999) and it is possible that the shift of tropical forests to a more liana dominated system will have similar consequences. The functional traits discussed in this study could potentially alter resource dynamics and produce plant-soil feedbacks promoting further competitive advantages for lianas over trees, particularly in the context of global change. Powers et al. (2004) found that in a tropical forest, tree species did not modify the chemistry of the soil environment beneath their crowns, as has been shown in temperate forests (Zinke 1962, Rhoades 1996). They hypothesized that this was likely due to the effect of liana litter (with distinct chemical composition) homogenizing any localized effects of individual tree litter. Additionally, the shift in the relative abundances of certain functional traits as a result of liana increase may also cause a more evenly distributed functional composition of the ecosystem. This may create overlap or redundancy of important ecosystem functions and therefore insurance against global change impacts (Yachi and Loreau 1999). However, if these traits become disproportionately distributed within the ecosystem, it is possible that tropical forests may become increasingly vulnerable to perturbations caused by global change. Nonetheless, an increase in liana functional traits is likely to have significant impacts on vital processes in these ecosystems.

Many of the factors of global change (elevated CO_2, temperature rise, and changes in precipitation) are projected to modify the belowground environment of tropical forests, and may also interact in a number of ways with the effects of a disproportionate increase in liana traits. Elevated CO_2 may increase microbial immobilization of limiting nutrients in nutrient-poor environments and N mineralization has been shown to rapidly increase under higher temperatures (Rustad et al. 2001) and pulses of precipitation (Davidson et al. 1993). Plant available P may also increase due to more frequent anaerobic events under higher temperatures and/or rainfall (Silver et al. 1999) while elevated atmospheric CO_2 and precipitation can raise the C:N and C:P ratios of plant litter (Kanowski 2001, Santiago et al. 2005). Finally, heightened rainfall intensity and anthropogenic N deposition may amplify N-leaching from tropical soils (Matson et al. 1999) and changes in temperature and precipitation may alter natural cycles of fine root growth, architecture, and nutrient uptake in seasonal tropical forests (Pregitzer et al. 2000, Yavitt and Wright 2001). Changes to the belowground environment as a result of global change may have significant interactions with the root functional traits of the dominant vegetation in tropical forests and may mitigate or exacerbate some of the potential effects of the increased liana functional type.

There are still many unknowns, however, in how global change will continue to affect the growth of lianas in tropical forests. While many studies have shown an increase in lianas with elevated atmospheric CO_2, this response may level off or even reverse at certain concentrations. Granados and Korner (2002) tested the growth response of tropical liana species at three different levels of CO_2 enrichment and reported that growth was most pronounced at the lowest CO_2 level (280-420 ppm) and was much smaller, and for some species even negative, at the highest level (560-700 ppm). This suggests that current atmospheric conditions are having a positive effect on liana growth but this trend may change if CO_2 concentrations continue to increase. In considering changes in precipitation, while lianas have shown a growth advantage during seasonal drought, studies have also shown that lianas decrease in density and basal area with increasing mean annual precipitation (Schnitzer 2005, DeWalt et al. 2010). In this way, if tropical forests continue to get wetter overall as a result of global change, this may reverse some of the net increase in liana growth. Finally, Wang (2011) saw that although the liana *Ipomoea cairica* increased in total biomass under elevated temperatures, this growth was not evenly distributed above and belowground. *I. cairica* increased its biomass allocated to stems and leaves while it simultaneously decreased its allocation to root biomass and its total root to shoot ratio. These discrepancies in above and belowground growth could modify or potentially amend some of the effects of liana root functional traits on belowground processes.

In conclusion, this was the first systematic survey of belowground functional traits in tropical lianas and the first comparison study of liana and tree root functional traits within family. We observed that similarly to leaf traits (Cai et al. 2009), the root traits of lianas and trees reflect unique resource acquisition strategies employed by each growth form. In this way, we can extend the concepts of the leaf economic spectrum to belowground organs in this ecosystem and thus have the knowledge to consider many of the potential consequence of our results from a whole plant perspective. In short, lianas employ a rapid resource acquisition growth strategy by way of a unique suite of root functional traits. This strategy emphasizes a quick return of water and nutrients per unit C invested to roots at the cost of lowered resistance to physical and biological stressors and shorter tissue lifespan. In contrast, co-occurring trees utilize a strategy of resource conservation and long term stability through traits that promote physical protection and slower turnover at a higher C cost. These discrepancies in trait strategies may have significant impacts on the long term stability and function of tropical forests, especially if lianas continue to increase disproportionately to trees. An increase in the relative proportion of liana root traits may alter the overall functioning and composition of the soil microbial community and belowground nutrient dynamics by increasing decomposition, root turnover, and plant available nutrient supply. Additionally, liana increase may create a more favorable belowground environment for decomposers, through root traits of fast turnover, high nutrient content, and more easily decomposable organic matter. This has the potential to cause a disproportionate increase in soil CO_2 efflux through the priming of soil microbes (Sayer et al. 2011), and thereby further exacerbate the conditions of global change. However there are still many unknowns in how global change will interact with the soil environment on its own and how lianas will continue to respond to global change factors over time. How lianas will continue to alter tropical forests through their functional traits and the potential interactions of these outcomes with the impacts of global change requires further study. In particular, linking liana functional traits to population changes will help to determine which mechanisms in particular are driving increases in liana abundance (Schnitzer and Bongers 2011). This study provides empirical evidence and important information for future research in this field.

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