Title
Disentangling Physiological Factors Contributing to Liana Success Over Trees in Tropical Forests: Nutrient Limitation of Photosynthetic Processes and the Role of Phylogeny

Author
Pasquini, Sarah Cecilia

Publication Date
2017

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Disentangling Physiological Factors Contributing to Liana Success Over Trees in Tropical Forests: Nutrient Limitation of Photosynthetic Processes and the Role of Phylogeny

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Plant Biology

by

Sarah Cecilia Pasquini

September 2017

Dissertation Committee:
Dr. Louis S. Santiago, Chairperson
Dr. Michael F. Allen
Dr. G. Darrel Jenerette

The Dissertation of Sarah Cecilia Pasquini is approved:

Committee Chairperson

University of California, Riverside

Acknowledgements

The text of this dissertation, in part or in full, is a reprint of the material as it appears in Pasquini, S.C., and L.S. Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 168:311-319; and Pasquini, S.C., S.J. Wright, and L.S. Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. Ecology 96:1866-1876. The co-author Louis S. Santiago listed in those publications directed and supervised the research which forms the basis for this dissertation. The co-author S. Joseph Wright was the Principal Investigator of the Gigante Fertilization Project at the STRI. I would like to thank my dissertation committee members Louis Santiago, Michael Allen, Darrel Jenerette. I also thank Jim Sickman and Dee Lucero for help with stable isotope measurements. I would also like to thank Ted Garland for assistance with the phylogenetic analyses. Many people provided field help and commented on manuscripts, including Caroline DeVan, Katia Silvera, Hailey Buckingham, Mark De Guzman, Alex Pivovaroff, Juan Carrion, Eric Griffin, Walter Carson, George Vourlitis, and John Wenzel. Steve Hovick and Jonathan Pruitt provided statistical advice. I also thank Omar Hernández, Rufino González, and David Brassfield at STRI for field help. This research was funded by the Dept. of Botany and Plant Sciences, a STRI Short-Term Fellowship, a UC Regent's Faculty Fellowship (Santiago), NSF (DEB- 07706813 to Santiago), and the Smithsonian Scholarly Studies program (Wright).

Dedication

This dissertation is dedicated to my parents Richard and Margaret, my brother Vincent, and Walter Carson.

ABSTRACT OF THE DISSERTATION

Disentangling Physiological Factors Contributing to Liana Success Over Trees in Tropical Forests: Nutrient Limitation of Photosynthetic Processes and the Role of Phylogeny

by

Sarah Cecilia Pasquini

Doctor of Philosophy, Graduate Program in Plant Biology
University of California, Riverside, September 2017
Dr. Louis S. Santiago, Chairperson

Trees and lianas are growth forms that account for the vast majority of the plant biomass in tropical forests. There is now compelling evidence that lianas are increasing in abundance relative to trees, particularly throughout Neotropical forests. The mechanisms that underlie this increase in lianas remain poorly understood. To address this knowledge gap, I asked: 1) To what degree is the physiological performance of tree seedlings limited by soil macronutrients (nitrogen, phosphorus, and potassium) within the deeply shaded habitats that characterizes tropical forest understories; 2) Are seedlings of lianas more limited by these macronutrients than seedlings of trees; and 3) Are photosynthetic and leaf trait differences that exist in trees versus lianas caused by inherent growth-

form differences or are they due to phylogenetic relatedness? This research demonstrated that the addition of two key soil resources, nitrogen and potassium, increased the photosynthetic performance of seedlings of an abundant tree species, *Alseis blackiana*, even in deep shade. Surprisingly, while seedlings of lianas and trees were limited to a similar degree by soil nutrients, lianas always out-performed trees in terms of their photosynthetic performance, regardless of nutrient addition. Moreover, my analyses demonstrated that lianas, as a distinct growth-form, had increased rates of photosynthesis and respiration versus trees. Nonetheless, a suite of other traits that were thought to clearly distinguish the liana growth-form from trees (low LMA and high foliar nitrogen), were determined to be due to phylogeny. Together, these findings provide a potential mechanistic basis for increases in liana abundance in the Neotropics.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1: Light and nutrient limitation of trees and lianas

Background

It is generally assumed that woody plant species growing in the understories of tropical forests are limited by light and not soil resources (Pearcy 1988, Hättenschwiler 2002). Evidence for this assumption is largely based on pot studies where there is no belowground competition and pots may have affected roots (Yavitt and Wright 2008). Oddly, this assumption has been tested in the field only a few times, and any such generalization requires a rigorous experimental evaluation. Whereas there is no doubt that light in the understory is limiting to most of these plant species, the degree to which soil resources are also limiting or co-limiting remains unknown. To date, the studies that have evaluated the degree to which soil resources are limiting have focused on resource limitation by entire communities, and in particular, those tree species that are in the canopy. This focus on the canopy ignores the critical dynamics that occur in the understory that ultimately determine which species make it to the canopy. Currently, it remains unclear if the soil resources that limit growth for trees in the canopy are the same soil resources that limit growth in the shaded understory. To my knowledge there are only eight studies that have evaluated soil resource limitation of photosynthesis or growth under low-light conditions (<5% daylight photosynthetically active radiation; PAR) *in situ* within the understory of tropical forests (Denslow et al. 1990, Denslow et al. 1991, Coomes and Grubb 1998, Lewis and Tanner 2000, Hättenschwiler 2002, Newbery et al. 2002, Barberis and Tanner 2005, Yavitt and Wright 2008), and only two of these considered resource limitation separately among the macronutrients (nitrogen: Coomes and Grubb 1998, phosphorus: Newbery et al. 2002). Essentially this means we do not know if macronutrients (i.e., nitrogen: N, phosphorus: P, potassium: K) typically limit growth in the understory, more less which ones or which combinations. Additionally, there are two major and contrasting life forms in tropical forests that make up the bulk of community biomass: lianas and trees. While it is well known that trees dominate tropical forests, it is less appreciated that lianas can constitute 10% of total plant biomass and 10-45% of woody individuals and species (Rollet 1969, Putz 1984, Schnitzer 2005, Gentry 2009). Overall, we have little knowledge of whether soil resource limitation differs between these two dominant groups. The goal of my research is to fill these knowledge gaps by experimentally evaluating which soil resource or resource combination limits plant growth in the understory. Furthermore, I will evaluate whether resource limitation differs between the two plant growth forms that dominate tropical forests.

Studies from around the world are demonstrating that lianas are increasing in abundance in tropical forests worldwide (Phillips et al. 2002, Wright et al. 2004, Wright and Calderón 2006, Swaine and Grace 2007, Chave et al. 2008). This may be occurring at the expense of tree species. Understanding why any species or group of species is increasing in abundance requires an understanding of the resources that limit their growth. For example, the increase in the abundance of lianas may be linked to the atmospheric deposition of N in tropical regions, but this is likely to be true only if N limits plant growth.

Lianas parasitize trees and reduce their performance, and thus, any increase in abundance of lianas is likely to reduce the abundance and potentially the diversity of tree species. Indeed, in a tropical forest in Panama, Schnitzer and Carson (2010) provided the first-ever experimental evidence *in situ* that lianas reduce tree growth, density, and diversity. Their findings were consistent with many previous correlative studies that provided evidence that lianas could out-compete trees at least in some habitats and among the species studied. While there is now compelling evidence that lianas are better competitors than trees, our understanding of the physiological basis for this remains rudimentary. Thus, there are a number of critical gaps in our understanding of the performance of trees and lianas in the understories of tropical forests. These gaps in our understanding lead to the following questions about the performance of woody species in tropical forest understories:

1. Do resources other than light limit the growth of woody species, and if so, which resources or resource combinations (e.g., N vs. P vs. K)?
2. Are lianas limited more, in terms of photosynthetic processes, by soil resources than trees?

3. Is there a phylogenetic signal to physiological trait differences between trees and lianas?

These questions address fundamental issues in tropical forest ecology because it remains unknown whether resources other than light are limiting in tropical forest understories, whether this limitation contrasts between key life-forms (trees versus lianas), and whether we can identify physiological trade-offs that promote liana growth over tree growth.

I address the first question (*Do resources other than light limit the growth of woody species, and if so which resources or resource combinations in very low light?*) in Chapter 2 where I present findings from a long-term, full-factorial NPK fertilization experiment in lowland tropical forest in Panama. This study was published in 2012 (Pasquini and Santiago 2012) in *Oecologia* and found that even in low light, seedlings of the tree *Alseis blackiana* increased rates of various photosynthetic processes in response to N, P, K, and a combination of P and K.

I address the second question (*Are lianas limited more, in terms of photosynthetic processes, by soil resources than trees?)* in Chapter 3 where I show that in the same NPK fertilization experiment in Panama, that liana seedlings outperformed tree seedlings in terms of photosynthetic performance regardless of nutrient addition. This study was published in 2015 (Pasquini et al. 2015) in *Ecology*.

The third question (*Is there a phylogenetic signal to physiological trait differences between trees and lianas?)* is addressed in Chapter 4 where I show that while lianas and trees differ in key photosynthetic and leaf traits, that when phylogeny is incorporated into analyses, some differences between lianas and trees are attributed to evolutionary history (i.e., plant families that lianas and trees are found in) rather than inherent differences between the growth forms. A subset of these data were published as a non-phylogenetic comparison between trees and lianas in a 2015 book chapter (Santiago et al. 2015).

Literature Cited

Barberis, I.M., and E.V.J. Tanner. 2005. Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. Ecology 86:667-674.

Chave, J., J. Olivier, F. Bongers, P. Châtelet, P.-M. Forget, P. van der Meer, N. Norden, B. Riéra, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. Journal of Tropical Ecology 24:355-366.

Coomes, D.A., and P.J. Grubb. 1998. Responses of juvenile trees to above- and belowground competition in nutrient-starved Amazonian rain forest. Ecology 79:768-782.

Denslow, J.S., E. Newell, and A.M. Ellison. 1991. The effect of understorey palm and cyclanths on the growth and survival of *Inga* seedlings. Biotropica 23:225-234.

Denslow, J.S., J.C. Schultz, P.M. Vitousek, and B.R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology 71:165-179.

Gentry, A.H. 2009. The distribution and evolution of climbing plants. Pages 3-51 *in* F.E. Putz and H.A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Hättenschwiler, S. 2002. Liana seedling growth in response to fertilisation in a neotropical forest understorey. Basic and Applied Ecology 3:135-143.

Lewis, S.L., and E.V.J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rain forest seedlings. Ecology 81:2525-2538.

Newbery, D.M., G.B. Chuyong, J.J. Green, N.C. Songwe, F. Tchuenteu, and L. Zimmermann. 2002. Does low phosphorus supply limit seedling establishment and tree growth in groves of ectomycorrhizal trees in a central African rainforest? New Phytologist 156:297-311.

Pasquini, S.C., and L.S. Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 168:311-319.

Pasquini, S.C., S.J. Wright, and L.S. Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. Ecology 96:1866-1876.

Pearcy, R.W. 1988. Photosynthetic utilisation of lightflecks by understory plants. Australian Journal of Plant Physiology 15:223-238.

Phillips, O.L., R.V. Martínez, L. Arroyo, T.R. Baker, T. Killeen, S.L. Lewis, Y. Malhi, A.M. Mendoza, D. Neill, P.N. Vargas, M. Alexiades, C. Cerón, A. di Fiore, T. Erwin, A. Jardim, M.S. Palacios, and B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418.

Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713-1724.

Rollet, B. 1969. Le regénération naturelle en forêt dense humide sempervirente de Plaine de la Guyane Vénézuélienne. Bois et Forets des Tropiques 14:19-38.

Santiago, L.S., S.C. Pasquini, and M.E. De Guzman. 2015. Physiological implications of the liana growth form. Pages 288-298 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford, UK.

Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166:262-276.

Schnitzer, S.A., and W.P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849-857.

Swaine, M.D., and J. Grace. 2007. Lianas may be favoured by low rainfall: evidence from Ghana. Plant Ecology 192:271-276.

Wright, S.J., O. Calderdón, A. Hernandéz, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484-489.

Wright, S.J., and O. Calderón. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. Ecology Letters 9:35-44.

Yavitt, J.B., and S.J. Wright. 2008. Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. Journal of Tropical Ecology 24:19-26.

Chapter 2: Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species

Published as: Pasquini, SC and LS Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 163:311-319.

Abstract

We investigated how photosynthesis by understory seedlings of the lowland tropical tree species *Alseis blackiana* responded to 10 years of soil nutrient fertilization with nitrogen (N), phosphorus (P), and potassium (K). We ask whether nutrients are limiting to light and CO_2 acquisition in a low light understory environment. We measured foliar nutrient concentrations of N, P, and K, isotopic composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), and light response curves of photosynthesis and chlorophyll fluorescence. Canopy openness was measured above each study seedling and included in statistical analyses to account for variation in light availability. Foliar N concentration increased by 20% with N addition. Foliar P concentration increased by 78% with P addition and decreased by 14% with N addition. Foliar K increased by 8% with K addition. Foliar $\delta^{13}C$ showed no significant responses, and foliar $\delta^{15}N$ decreased strongly with N addition, matching the low $\delta^{15}N$ values of applied fertilizer. Canopy openness ranged from 0.01 to 6.71% with a mean of 1.76 ± 0.14 (±1SE). Maximum photosynthetic CO_2 assimilation rate increased by 9% with N addition. Stomatal conductance increased with P addition and with P and K in combination. Chlorophyll fluorescence measurements revealed that quantum yield of photosystem II increased with K addition, maximum electron transport rate trended 9% greater with N addition ($p = 0.07$), and saturating photosynthetically active radiation increased with N addition. The results demonstrate that nutrient addition can enhance photosynthetic processes, even under low light availability.

Introduction

The understory environment in forests with tall trees and a thick canopy are among the darkest habitats occupied by vascular plants. Within these habitats, light availability is limited to low levels of diffuse light most of the time, interspersed by short-duration, high-intensity lightflecks (Chazdon 1988, Pearcy 1988). Because the energy provided by lightflecks is one to two orders of magnitude greater than the predominant diffuse light conditions, up to 65% of the total photosynthetic carbon gain of understory plants can be achieved during lightflecks (Pfitsch and Pearcy 1989). As a result, photosynthesis in forest understory environments is considered to be primarily limited by light (Pearcy 1988). However, plant allocation to carbon gain capacity reflects total resource availability (Field 1991), so belowground resources could co-limit photosynthesis, even in low light. If nutrients were limiting to plant growth, and limitation were alleviated by frequent fertilization, investment in plant organs to acquire limiting resources could change, favoring allocation to enhance the light and CO_2 acquisition capacity of leaves (Bloom et al. 1985, Giardina et al. 2003, Bucci et al. 2006). This study addresses photosynthetic responses of seedlings of the shade-tolerant pioneer tropical tree species, *Alseis blackiana*, to long-term factorial fertilization with nitrogen (N), phosphorus (P), and potassium (K) in a lowland tropical forest.

Leaf N is a strong determinant of photosynthesis (Field and Mooney 1986, Wright et al. 2004), primarily because the proteins of the Calvin cycle and thylakoids make up the majority of N in leaves. N addition in shade plants is expected to increase N allocation toward proteins of the thylakoid membrane of the chloroplast, including the pigment–protein complexes and components of the electron transport chain (Evans 1989). N addition could also increase the maximum rate of CO_2 assimilation (A_{max}), because carboxylation capacity and electron transport are tightly coupled (Wullschleger 1993). Leaf P is a component of polyphosphates and phospholipids and is necessary for activity of the Calvin cycle and rubisco regeneration (Marschner 1995), and thus P addition has been shown to stimulate A_{max}, but reduce A_{max} per unit leaf P (Cordell et al. 2001), because of the ability of leaves to sequester large amounts of P in vacuoles (Sinclair and Vadez 2002, Ostertag 2009). K^+ is the most abundant ion in plant cells and is critical for numerous biochemical functions including osmoregulation, photosynthesis, cell extension, oxidative phosphorylation and protein activation (Evans and Sorger 1966, Morgan 1984, Marschner 1995, Santiago and Wright 2007). Therefore, K addition has the potential to increase photosynthesis through efficient biochemistry and stomatal control. In addition, enhanced N, P and K supply have all been linked to increased water use efficiency of plant productivity (Raven et al. 2004). Therefore, nutrient addition has the potential to increase the carbon gain capacity of understory plants by increasing efficient use of limited light resources.

Limitation of plant growth by N and P is widespread, and has most often been demonstrated experimentally as a positive growth response to nutrient addition (Vitousek 2004). Relative to N and P, less is known regarding K-limitation, but recent explorations suggest that the role of K in forest ecosystems is unique, and has closer similarity to N than other base cations (Tripler et al. 2006). At the site of the study reported in this paper, seedlings primarily increase height growth in response to K addition, and secondarily with N and P added in combination (Santiago et al. 2012). Saplings (10–25 mm diameter) increase diameter growth with N and K added in combination (Wright et al. 2011). The growth response of seedlings and saplings to added nutrients suggests two possibilities. The first possibility is that these plants grow more in response to added nutrients by allocating less photosynthate to root growth, which causes an increase in above-ground growth. Consistent with this hypothesis, at the site of this study, seedling root-to-shoot biomass ratio decreases with K addition (Santiago et al. 2012), and K addition decreases stand-level fine root biomass (Yavitt et al. 2010, Wright et al. 2011). The second possibility is that increased nutrient supply provides a resource that may be used to increase the uptake of another limiting resource such as light (Fahey et al. 1998).

In this paper, we investigate the second possibility. We present photosynthesis data in response to long-term N, P, and K factorial fertilization in lowland Panama to test the question of whether nutrient addition increases acquisition of light and CO_2, which are also limiting in the low light environment of the tropical forest understory. We hypothesized that N, P, and K fertilization all had the potential to limit aspects of photosynthetic carbon gain. The alternative hypothesis is that plants would be unresponsive to nutrient addition in the understory because there is not enough light energy to physiologically take advantage of the increase in nutrient availability.

Materials and Methods

Study site and species

The study was conducted in mature (~200 years) lowland tropical forest on the Gigante Peninsula (9°06’31’’ N, 79°50’ 37’’ W), within the Barro Colorado Nature Monument (BCNM) in central Panamanian moist tropical forest (Appendix A: Fig. A1). Annual precipitation averages 2,600 mm, less than 10% of which falls during the 4-month dry season. The soils consist of Endogleyic Cambisols and Acric Nitisols (Koehler et al. 2009), and are relatively fertile for lowland tropical forest soils (Fyllas et al. 2009, Dieter et al. 2010, Wright et al. 2011).

The study species was *A. blackiana* Hemsl. (Rubiaceae), one of the most common tree species at the site. *Alseis* is a medium-sized forest tree growing just into the canopy and is one of the most common canopy species in seasonally moist tropical forest in central Panama (Croat 1978). *Alseis* recruits from tiny, wind-dispersed seeds exclusively in canopy gaps, but unlike other pioneer tree species, it is able to persist in the shaded understory (Dalling et al. 2001).

Experimental design

The eight treatments of a 2 × 2 × 2 factorial NPK experiment were replicated four times. The four replicates were arranged perpendicular to the 36-m topographic gradient. Within each replicate, we blocked the N, P, K and NPK treatments versus the NP, NK, PK and control treatments. This balanced, incomplete-block design minimizes uncontrolled error associated with spatial variation, enables evaluation of main effects and two-way interactions, but limits power to evaluate the three-way interaction (Winer et al. 1991). The 32 experimental plots were 40 × 40 m and the minimum distance between plots was 40 m, with the exception of two plots separated by 20 m and located on opposite sides of a stream.

Stand-level fertilization was initiated in 1998, with fertilizer added by hand in four equal doses each wet season with 6–8 weeks between applications (May 15–30, July 1–15, September 1–15 and October 15–30). Fertilizers are applied at annual dosages of 125 kg N ha^{-1} year^{-1} (as urea), 50 kg P ha^{-1} year^{-1} (as triple super-phosphate) and 50 kg K ha^{-1} year^{-1} (as KCl).

Photosynthetic traits

During the wet season of 2008 (July–August), photosynthetic gas exchange and chlorophyll fluorescence were measured on 1–9 (median = 5) individuals in each plot for a total of 146 plants. A total of 16–20 seedlings <0.5 m height in each of the eight treatment combinations were measured. We characterized photosynthesis with fluorescence-light curves (White and Critchley 1999, Rascher et al. 2000) simultaneously measured with CO_2 assimilation using a portable infrared gas analyzer (Model LI-6400; Li-Cor Biosciences, Lincoln, NE, USA) equipped with a leaf chamber chlorophyll fluorescence meter and red/blue light source (Model LI-6400-40; Li-Cor Biosciences). Leaves were dark adapted for 30 s before an initial measurement was taken at 0 μmol m^{-2} s^{-1} photon flux density (PFD). Irradiance was then increased in a stepwise fashion (10, 50, 70, 100, 250, 500, 750, 1,000 μmol m^{-2} s^{-1} PFD). At each PFD, photosynthetic CO_2 assimilation (A), stomatal conductance to water vapor (g_s), leaf transpiration (E), and chlorophyll fluorescence were recorded once leaves reached steady-state values, defined as coefficients of variation of CO_2 and water vapor within the chamber of <0.25% (Caruso et al. 2005).

Electron transport rate (ETR) was calculated based on chlorophyll fluorescence data using the equation:

$$\mathrm{ETR} = \Phi_{\mathrm{PSII}} \cdot \mathrm{PFD} \cdot f \cdot \alpha$$

where ETR is electron transport rate, Φ_{PSII} is the effective quantum yield of PSII measured during a 0.8-s saturating flash (2,000–3,000 μmol m^{-2} s^{-1}), f is a factor that accounts for the partitioning of energy between PSII and PSI and is assumed to be 0.5, indicating that excitation energy is distributed equally between the two photosystems (Maxwell and Johnson 2000), and α is the proportion of light absorptance by photosynthetic tissue in decimal format and was assumed to be 0.84 as a mean value for a wide variety of leaves (Björkman and Demmig 1987, Stemke and Santiago 2011).

Following photosynthetic measurements, leaves were harvested, sealed in plastic bags, and returned to the laboratory on Barro Colorado Island where their area was recorded with an area meter (Model LI-3100; Li-Cor Biosciences). Leaves were then dried for 48 h at 60°C and weighed to determine specific leaf area (SLA; cm^2/g).

Leaf and fertilizer chemistry

Dried leaf samples were ground in a ball mill (8000D; Spex Sample Prep, Stanmore, UK) to a fine powder. Samples of each of the four applications of urea nitrogen fertilizer per year from 2004 to 2008 were pooled and ground with a mortar and pestle. N concentration, as well as stable isotopic composition of N ($\delta^{15}N$) and C ($\delta^{13}C$) were determined with an elemental analyzer (ECS 4010; Costech, Valencia, CA, USA) interfaced with an isotope ratio mass spectrometer (Delta V Advantage; Thermo Scientific, Bremen, Germany) at the University of California Facility for Isotope Ratio Mass Spectrometry (FIRMS), Riverside, CA, USA. Leaf P and K were determined on pooled samples from each plot using inductively coupled plasma atomic emission spectroscopy after nitric acid digestion at the University of California Analytical Laboratory, Davis, CA, USA.

Light availability

Hemispherical photographs were used to quantify the light environment for each plant measured for fluorescence-light response curves. Photographs were taken using a digital camera (Coolpix 4500; Nikon, Japan) and a fisheye converter lens (FC-E8; Nikon) with an exposure time of 1/125 s and aperture of 2.8 (Engelbrecht and Herz 2001). The camera was positioned at each measurement plant at approximately the height of the measured leaf and oriented toward magnetic north using a compass. All photographs were taken with overcast skies, common during the wet season in Panama, to maximize contrast between foliage and sky. Determination of percent direct and diffuse light transmittance from hemispherical photographs was accomplished with the Gap Light Analyzer program (Frazer et al. 1999) and used to calculate total light transmittance (T_{total}).

Data analyses

The maximum A for each curve (A_{max}), the g_s and E at A_{max}, the maximum observed ETR (ETR_{max}), and Φ_{PSII} at 1,000 μmol m^{-2} s^{-1} PFD were used to evaluate the effects of nutrient fertilization on photosynthesis. Saturating photosynthetically active radiation (PFD_{sat}) was calculated by evaluating ETR as a function of PFD in Photosynthesis Assistant (ver. 1.1; Dundee Scientific, Dundee, UK). Multiple regression analysis of photosynthetic parameters for individual leaves was used to analyze responses to nutrient addition. Total transmittance of each measurement leaf was included in the multiple regression model to account for variation in canopy openness above each leaf because allocation to photosynthetic capacity responds strongly to light availability (Montgomery and Givnish 2008) and because light is extremely heterogeneous in tropical forest understory environments (Montgomery and Chazdon 2001). Responses of foliar chemistry to nutrient addition were analyzed using ANOVA on mean values for plots with nutrient main effects, two-way interactions, and blocking effects.

Results

Photosynthetic traits

The multiple regression analysis revealed that all photosynthetic traits except for g_s and c_i were significantly affected by T_{total} (Table 2.1). Mean SLA decreased with N addition and increased with addition of N and P in combination (Tables 2.1 and 2.2). Values of A_{max} increased significantly by 9% with N addition (Fig. 2.1A; Table 2.1). Values of g_s increased significantly by 14% with P addition (Fig. 2.1B) and trended 9% greater with K addition (Table 2.1). There was also a significant P × K interaction for g_s (Table 2.1), indicating an increase in g_s when P and K were added in combination. There was a significant increase in c_i with K addition, and with P and K in combination (Table 2.1). P addition caused a significant increase in E, but there was also an N × P interaction, indicating that N and P in combination caused a decrease in E (Fig. 2.1C). The mean PFD at which A_{max} was observed was 832 μmol m^{-2} s^{-1}, but there was no effect of nutrient addition (P = 0.14).

ETR_{max} trended 9% greater with N addition ($P = 0.07$) (Fig. 2.2A; Table 2.1). The mean PFD at which ETR_{max} was observed was 436 μmol m^{-2} s^{-1}, but there was no effect of nutrient addition ($P = 0.24$). PFD_{sat} showed a significant increase with N addition (Fig. 2.2B; Table 2.1). There was a significant increase in Φ_{PSII} with K addition (Table 2.1), and a significant N × K interaction on Φ_{PSII} because N and K added in combination caused a decrease in Φ_{PSII} (Fig. 2.2C). There was significant correlation between A_{max} and ETR_{max} across all seedlings demonstrating the functional interdependence of these two independently measured variables (Fig. 2.3).

Leaf structure and chemistry

Foliar nutrient concentration responded strongly to nutrient addition. Foliar N concentration increased by 20% with N addition (Fig. 2.4A) and was not affected by other elements (Table 2.3). Foliar P concentration increased by 78% with P addition and decreased by 14% with N addition (Table 2.3; Fig. 2.4B). There was also a significant N × K interaction on foliar P concentration (Table 2.3), indicating that N and K in combination decreased foliar P concentration by 11% below control values (Fig. 2.4B). Foliar K increased 8% with K addition (Table 2.3; Fig. 2.4C). Foliar $\delta^{13}C$ showed no significant responses to nutrient addition (Fig. 2.4D). Foliar $\delta^{15}N$ decreased strongly with N fertilizer addition (Table 2.3; Fig. 2.4E), consistent with the low urea fertilizer $\delta^{15}N$ values of -1.86% ± 0.10 (±1 SE), relative to soil $\delta^{15}N$ values of +4.86% ± 0.52 at 0–5 cm depth in control plots (Koehler et al. 2009).

Discussion

The results of this long-term factorial nutrient fertilization experiment indicate that multiple elements limit photosynthetic processes in seedlings of a tropical tree species. There is a clear effect of added N on photosynthesis that includes increased A_{max} and $\mathrm{PFD}_{\mathrm{sat}}$, and a parallel trend in $\mathrm{ETR}_{\mathrm{max}}$. These results suggest that increased N supply is allocated to enzymes of the light harvesting complex and carboxylation reactions. Other significant responses of photosynthetic processes to nutrient addition include a strong effect of P, and to a lesser extent K, on g_s indicating that stomatal function may be limited by nutrient availability and important for maximizing carbon gain in light-limited environments with rapidly changing light conditions (Chazdon and Pearcy 1986, Valladares et al. 1997). Our results also indicate that enhanced photosynthesis may play a role in the increased growth of tree seedlings, saplings and poles in response to fertilization measured at this study site (Wright et al. 2011, Santiago et al. 2012). The increase in height growth of seedlings in response to K addition, and to N and P added in combination is consistent with limitation of photosynthesis by multiple elements measured in this study. In addition to decreased root biomass with K addition, the increased A_{max} with N addition and increased g_s with P addition may contribute to positive effects of N and P on seedling height growth.

The larger increase in foliar P compared to foliar N with fertilization is consistent with other fertilization experiments in tropical (Cordell et al. 2001, Campo and Dirzo 2003). In addition to increases in foliar nutrients that are allocated to metabolic function, Chapin et al. (1990) recognize three types of storage: accumulation, in which compounds do not directly promote growth, reserve formation, which involves synthesis of storage compounds from resources that might otherwise promote growth, and recycling, in which compounds are broken down and may be mobilized for later growth. A greater degree of accumulation is expected for elements stored primarily as inorganic compounds such as P and K (Chapin et al. 1990). In contrast, reserve formation is likely for elements stored primarily as organic compounds such as N, which is not commonly stored as inorganic N in leaves but rather stored in forms such as amino acids or proteins, thus incurring a metabolic cost for storage (Chapin et al. 1990, Ostertag 2010). Inorganic P on the other hand can be stored in vacuoles and can make up substantial fractions of total plant P (Sinclair and Vadez 2002, Ostertag 2009). Our results are consistent with these predictions for N and P; increases in foliar P were much greater than increases in foliar N with addition of the same element (Fig. 2.4A-B). Foliar P also decreased with N addition. N addition in the same long-term fertilization experiment reduced soil pH by 0.5 pH units (Yavitt et al. 2010), which may have affected the solubility of P or other elements. Foliar K increased by 8%, which was more modest than expected for an element that can be stored inorganically. Yet the significant effect of K on Φ_{PSII} (Fig. 1.2C) and the combined effect with P on g_s (Table 2.1), suggest that increased foliar K was allocated to metabolic function. Our results indicate that substantial physiological changes accompany increases in foliar nutrient concentration and that altered physiological function may be related to previously reported growth responses of seedlings, saplings and poles, as well as changes in litterfall productivity at this study site (Kaspari et al. 2008, Wright et al. 2011, Santiago et al. 2012).

The response of A_{max} to nutrient addition is consistent with other studies investigating fertilization effects on tropical tree seedlings in low light. For example, seedlings of *Flindersia brayleyana*, an Australian tropical rainforest tree species with broad tolerance to sun and shade, increase A_{max} and $\mathrm{PFD}_{\mathrm{sat}}$ in response to nutrient addition (Thompson et al. 1988). In addition, nutrient addition causes an increase in A_{max} in seedlings of two out of three shade-tolerant tree species and one shade-intolerant tree species (Thompson et al. 1992). Furthermore, nutrient addition causes an increase in A_{max} in West African tree seedlings (Riddoch et al. 1991). Although the studies by Thompson et al. (1988, 1992) and Riddoch et al. (1991) showed similar results to our data, their low light treatments (25–35 μmol m^{-2} s^{-1} PFD) likely had greater light availability than our study plants, whose ambient irradiance during our measurements, as recorded by the external PFD sensor on our infrared gas analyzer, was 6.7 μmol m^{-2} s^{-1} ± 0.5 (±1SE). Another difference between the studies by Thompson et al. (1988, 1992) and Riddoch et al. (1991) and the current study is that they added all elements together in nutrient treatments, limiting the potential to determine which elements affected photosynthetic processes. Our factorial design allowed us to distinguish elemental effects and interactions.

We expected allocation of increased N supply to thylakoids to increase ETR in N addition treatments (Evans 1989). Indeed, ETR_{max} trended 9% greater with N addition (Fig. 2.2A; Table 2.1), but the most noteworthy response of photosynthesis to N addition was the increase in A_{max} (Fig. 2.1A). The positive linear relationship between A_{max} and foliar N concentration has been well studied (Field and Mooney 1986, Wright et al. 2004), and our measured response of A_{max} to N addition demonstrates that even in a tropical forest with relatively high N availability (Yavitt et al. 2009), plants can use more N to enhance photosynthetic rates. The strong increase in g_s in response to P addition and interaction with K addition was also striking (Fig. 2.1B; Table 2.1), and suggests that the efficiency of stomatal responses to changing light conditions are co-limited by P and K. The role of K in guard cell control and osmoregulation is well documented (Morgan 1984, Marschner 1995), and consistent with increased g_s and increased carbon gain during short-duration high-intensity lightflecks. Detailed molecular physiology studies are needed to sort out the precise mechanisms for the observed photosynthetic responses to nutrient addition.

The responses of photosynthetic processes to N, P, and K are consistent with the multiple limiting nutrients hypothesis (Bloom et al. 1985), which postulates that the addition of any resource should increase plant growth because plants adjust allocation of resources until growth is equally limiting by all resources. Interestingly, we observed relatively small effects of the +NPK treatment, suggesting that although multiple resources limit photosynthetic processes in this study system, individual processes often respond to specific elements. Numerous studies have investigated the effects of nutrient addition on ecosystem net primary productivity (Vitousek 2004 and references therein). Incorporating a physiologically based view into these processes will improve our ability to predict the effects of environmental change on ecosystem function. Nutrient limitation of photosynthetic processes could be important for mediating plant responses to global change and may represent an important constraint for plant responses to increasing CO_2 concentration and alterations of temperature and precipitation regimes.

Literature Cited

Björkman, O., and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489-504.

Bloom, A.J., F.S. Chapin, III, and H.A. Mooney. 1985. Resource limitation in plants – An economic analogy. Annual Review of Ecology and Systematics 16:363-392.

Bucci, S.J., F.G. Scholz, G. Goldstein, F.C. Meinzer, A.C. Franco, P.I. Campanello, R. Villalobos-Vega, M. Bustamante, and F. Miralles-Wilhelm. 2006. Nutrient availability constrains the hydraulic architecture and water relations of savannah trees. Plant Cell and Environment 29:2153-2167.

Campo, J., and R. Dirzo. 2003. Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatan, Mexico. Journal of Tropical Ecology 19:525-530.

Caruso, C.M., H. Maherali, A. Mikulyuk, K. Carlson, and R.B. Jackson. 2005. Genetic variance and covariance for physiological traits in *Lobelia*: Are there constraints on adaptive evolution? Evolution 59:826-837.

Chapin, F.S., III, E.D. Schulze, and H.A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecology and Systematics 21:423-447.

Chazdon, R.L. 1988. Sunflecks and their importance to forest understory plants. Advances in Ecological Research 18:1-63.

Chazdon, R.L., and R.W. Pearcy. 1986. Photosynthetic responses to light variation in rain-forest species. 2. Carbon gain and photosynthetic efficiency during lightflecks. Oecologia 69:524-531.

Cordell, S., G. Goldstein, F.C. Meinzer, and P.M. Vitousek. 2001. Regulation of leaf life-span and nutrient-use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. Oecologia 127:198-206.

Croat, T.B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA.

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

Dieter, D., H. Elsenbeer, and B.L. Turner. 2010. Phosphorus fractionation in lowland tropical rainforest soils in central Panama. Catena 82:118-125.

Engelbrecht, B.M.J., and H.M. Herz. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. Journal of Tropical Ecology 17:207-224.

Evans, H.J., and G.J. Sorger. 1966. Role of mineral elements with emphasis on univalent cations. Annual Review of Plant Physiology 17:47-76.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78:9-19.

Fahey, T.J., J.J. Battles, and G.F. Wilson. 1998. Responses of early successional northern hardwood forests to changes in nutrient availability. Ecological Monographs 68:183-212.

Field, C., and H.A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25-55 *in* T.J. Givnish, editor. On the economy of plant form and function. Cambridge University Press, Cambridge, UK.

Field, C.B. 1991. Ecological scaling of carbon gain to stress and resource availability. Pages 35-65 *in* H.A. Mooney, W.E. Winner, and E.J. Pell, editors. Response of plants to multiple stresses. Academic Press, New York, NY, USA.

Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light indices from true-colour fisheye photographs. Simon Fraser University, Burnaby, Canada, and the Institute of Ecosystem Studies, Millbrook, NY, USA.

Fyllas, N.M., S. Patino, T.R. Baker, G.B. Nardoto, L.A. Martinelli, C.A. Quesada, R. Paiva, M. Schwarz, V. Horna, L.M. Mercado, A. Santos, L. Arroyo, E.M. Jimenez, F.J. Luizao, D.A. Neill, N. Silva, A. Prieto, A. Rudas, M. Silviera, I.C.G. Vieira, G. Lopez-Gonzalez, Y. Malhi, O.L. Phillips, and J. Lloyd. 2009. Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate. Biogeosciences 6:2677-2708.

Giardina, C.P., M.G. Ryan, D. Binkley, and J.H. Fownes. 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. Global Change Biology 9:1438-1450.

Kaspari, M., M.N. Garcia, K.E. Harms, M. Santana, S.J. Wright, and J.B. Yavitt. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology Letters 11:35-43.

Koehler, B., M.D. Corre, E. Veldkamp, H. Wullaert, and S.J. Wright. 2009. Immediate and long-term nitrogen oxide emissions from tropical forest soils exposed to elevated nitrogen input. Global Change Biology 15:2049-2066.

Marschner, H. 1995. Mineral nutrition in higher plants. 2nd edition. Academic Press, London, UK.

Maxwell, K., and G.N. Johnson. 2000. Chlorophyll fluorescence – A practical guide. Journal of Experimental Botany 51:659-668.

Montgomery, R.A., and R.L. Chazdon. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82:2707-2718.

Montgomery, R.A., and T.J. Givnish. 2008. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: Dynamic photosynthetic responses. Oecologia 155:455-467.

Morgan, J.M. 1984. Osmoregulation and water-stress in higher-plants. Annual Review of Plant Physiology and Plant Molecular Biology 35:299-319.

Ostertag, R. 2009. Foliar phosphorus accumulation in relation to leaf traits: An example in a tropical wet forest in Hawaii. South African Journal of Botany 75:415-415.

Ostertag, R. 2010. Foliar nitrogen and phosphorus accumulation responses after fertilization: An example from nutrient-limited Hawaiian forests. Plant Soil 334:85-98.

Pearcy, R.W. 1988. Photosynthetic utilisation of lightflecks by understory plants. Australian Journal of Plant Physiology 15:223-238.

Pfitsch, W.A., and R.W. Pearcy. 1989. Daily carbon gain by *Adenocaulon bicolor* (Asteraceae), a redwood forest understory herb, in relation to its light environment. Oecologia 80:465-470.

Rascher, U., M. Liebig, and U. Luttge. 2000. Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. Plant Cell and Environment 23:1397-1405.

Raven, J.A., L.L. Handley, and B. Wollenseber. 2004. Plant nutrition and water use efficiency. Pages 171-197 *in* M.A. Bacon, editor. Water use efficiency in plant biology. CRC Press, Boca Raton, FL, USA.

Riddoch, I., T. Lehto, and J. Grace. 1991. Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. New Phytologist 119:137-147.

Santiago, L.S., and S.J. Wright. 2007. Leaf functional traits of tropical forest plants in relation to growth form. Functional Ecology 21:19-27.

Santiago, L.S., S.J. Wright, K.E. Harms, J.B. Yavitt, C. Korine, M.N. Garcia, and B.L. Turner. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. Journal of Ecology 100:309-316.

Sinclair, T.R., and V. Vadez. 2002. Physiological traits for crop yield improvement in low N and P environments. Plant and Soil 245:1-15.

Stemke, J.A., and L.S. Santiago. 2011. Consequences of light absorptance in calculating electron transport rate of desert and succulent plants. Photosynthetica 49:195-200.

Thompson, W.A., L.K. Huang, and P.E. Kriedemann. 1992. Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rain-forest trees. 2. Leaf gas-exchange and component processes of photosynthesis. Australian Journal of Plant Physiology 19:19-42.

Thompson, W.A., G.C. Stocker, and P.E. Kriedemann. 1988. Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rainforest tree with broad tolerance to sun and shade. Australian Journal of Plant Physiology 15:299-315.

Tripler, C.E., S.S. Kaushal, G.E. Likens, and M.T. Walter. 2006. Patterns in potassium dynamics in forest ecosystems. Ecology Letters 9:451-466.

Valladares, F., M.T. Allen, and R.W. Pearcy. 1997. Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. Oecologia 111:505-514.

Vitousek, P.M. 2004. Nutrient cycling and limitation: Hawai'i as a model system. Princeton University Press, Princeton, NJ, USA.

White, A.J., and C. Critchley. 1999. Rapid light curves: a new fluorescence method to assess the state of the photosynthetic apparatus. Photosynthesis Research 59:63-72.

Winer, B.J., D.R. Brown, and K.M. Michels. 1991. Statistical principles in experimental design. 3rd edition. McGraw-Hill, New York, NY, USA.

Wright, I.J., P.B. Reich, M. Westoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, F.S. Chapin, III, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.

Wright, S.J., J.B. Yavitt, N. Wurzburger, B.L. Turner, E.V.J. Tanner, E.J. Sayer, L.S. Santiago, M. Kaspari, L.O. Hedin, K.E. Harms, M.N. Garcia, and M.D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616-1625.

Wullschleger, S.D. 1993. Biochemical limitations to carbon assimilation in C_3 plants - A retrospective analysis of the A/C_i curves from 109 species. Journal of Experimental Botany 44:907-920.

Yavitt, J.B., K.E. Harms, M.N. Garcia, M.J. Mirabello, and S.J. Wright. 2010. Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. Austral Ecology 36.

Yavitt, J.B., K.E. Harms, M.N. Garcia, S.J. Wright, F. He, and M.J. Mirabello. 2009. Spatial heterogeneity of soil chemical properties in a lowland tropical moist forest, Panama. Australian Journal of Soil Research 47:674-687.

Table 2.1. Multiple regression results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on leaf physiological parameters for *Alseis blackiana* in lowland tropical forest in Panama.

Factor	SLA	A_{max}	g_s	c_i	E	ETR_{max}	PFD_{sat}	Φ_{PSII}
Overall model	**≤0.001**	**0.022**	**≤0.005**	**≤0.001**	**≤0.001**	**≤0.001**	**≤0.001**	**≤0.001**
T_{total}	**0.021**	**0.042**	0.217	0.419	**0.040**	**≤0.001**	**≤0.001**	**≤0.001**
N	**0.039**	**0.054**	0.512	0.242	0.916	0.070	**0.054**	0.706
P	0.920	0.091	**≤0.001**	0.077	**0.018**	0.852	0.741	0.961
K	0.364	0.241	0.075	**≤0.005**	0.696	0.951	0.946	**0.038**
N × P	**0.043**	0.511	0.121	0.879	**0.014**	0.375	0.225	0.088
N × K	0.645	0.193	0.615	0.150	0.553	0.482	0.606	**0.053**
P × K	0.810	0.214	**≤0.005**	**0.022**	0.293	0.768	0.619	0.848

P-values are presented for the overall model, as well as main effects and interactions. Total canopy light transmission above seedling specific leaf area (SLA), maximum photosynthetic CO_2 assimilation rate per area (A_{max}), stomatal conductance at maximum photosynthesis (g_s), internal CO_2 concentration (c_i), transpiration at maximum photosynthesis (E), maximum electron transport rate (ETR_{max}), saturating photon flux density (PFD_{sat}), and quantum yield of photosystem II (Φ_{PSII}). Bold values are significant at $P \leq 0.05$.

Table 2.2. Summary of significant effects of fertilization with nitrogen (N), phosphorus (P), and potassium (K) on specific leaf area (SLA) for seedlings of *Alseis blackiana* in lowland tropical forest in Panama.

Treatment	SLA
+N	431.5 ± 6.8
-N	451.5 ± 6.8
+N and P	459.5 ± 16.1
-N and P	438.3 ± 9.4

Treatments include all plots receiving N addition (+N), no N (-N), N and P in combination (+N and P), and plots that did not receive N and P in combination (-N and P). See Table 2.1 for complete statistical results.

Table 2.3. Results of analysis of variance for foliar nitrogen (N), phosphorus (P), and potassium (K), carbon stable isotopic composition ($\delta^{13}C$), and nitrogen stable isotopic composition ($\delta^{15}N$) for seedlings of *Alseis blackiana* in response to fertilization with N, P, and K.

		Foliar N		Foliar P		Foliar K		Foliar $\delta^{13}C$		Foliar $\delta^{15}N$	
Factor	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between blocks											
Rep	3	2.28	0.114	0.79	0.513	0.89	0.465	**8.45**	**0.001**	2.48	0.094
Block (Rep)	4	1.43	0.266	1.76	0.182	2.34	0.094	0.70	0.601	1.07	0.402
Within blocks		**16.26**	**0.0008**	**17.04**	**0.0006**	3.41	0.081	0.68	0.420	**22.95**	**<0.0001**
N	1	1.52	0.233	**246.24**	**<0.0001**	0.04	0.852	0.00	0.958	1.48	0.240
P	1	0.26	0.616	1.30	0.270	**5.21**	**0.035**	0.25	0.623	1.82	0.195
K	1	0.40	0.536	1.79	0.198	0.14	0.714	2.09	0.165	0.95	0.344
N × P	1	0.25	0.623	**7.31**	**0.015**	0.50	0.487	0.00	0.962	0.93	0.348
N × K	1	0.37	0.552	2.29	0.147	0.85	0.370	0.10	0.756	0.06	0.808
P × K	1	**16.26**	**0.0008**	**17.04**	**0.0006**	3.41	0.081	0.68	0.420	**22.95**	**<0.0001**
Error	18										

Bold type indicates statistical significance of $P \leq 0.05$.

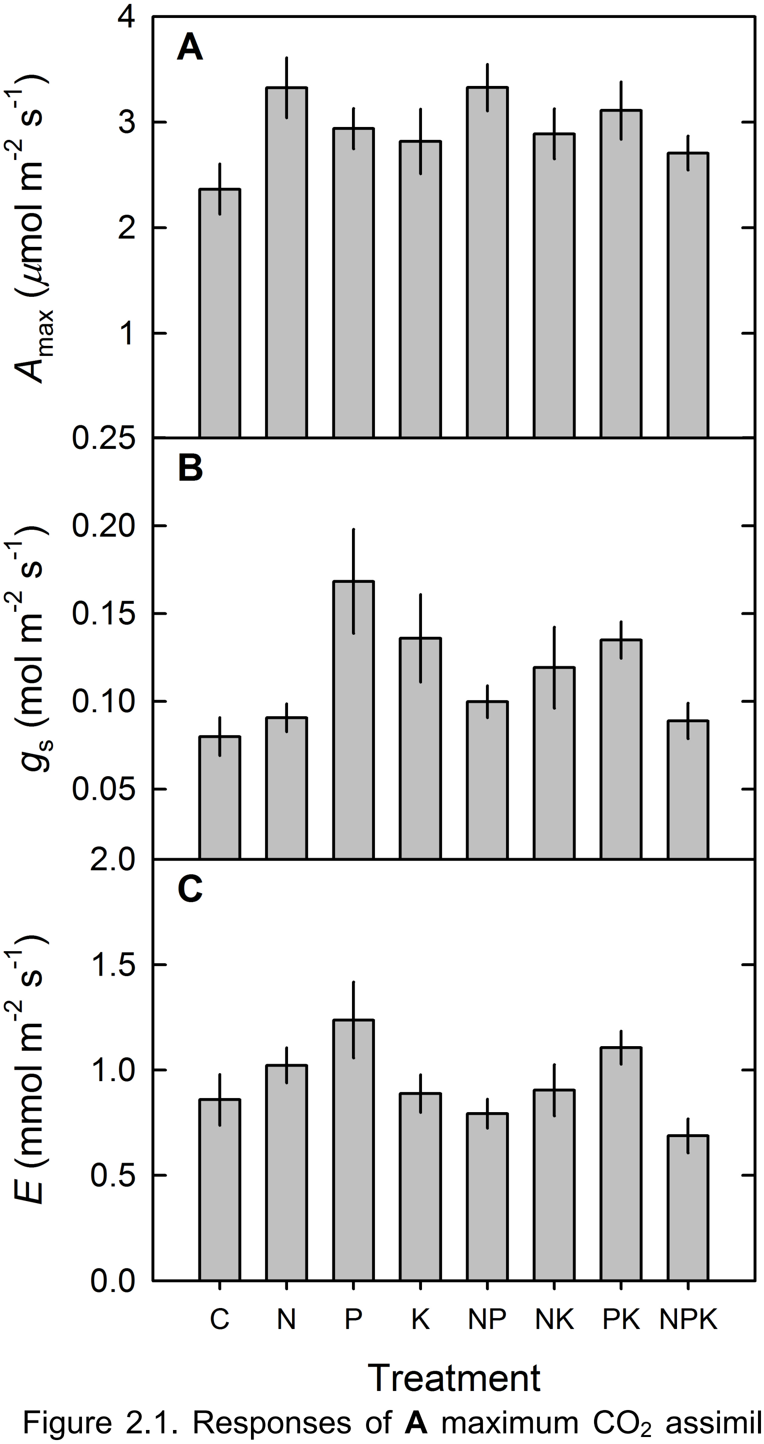

Figure 2.1. Responses of **A** maximum CO_2 assimilation per leaf area (A_{max}), **B** stomatal conductance (g_s) to water vapor at A_{max}, and **C** leaf transpiration (E) at A_{max} of seedlings of the tree species *Alseis blackiana* to factorial addition of nitrogen (N), phosphorus (P), potassium (K), and control (C) treatments in the understory of lowland tropical forest in Panama.

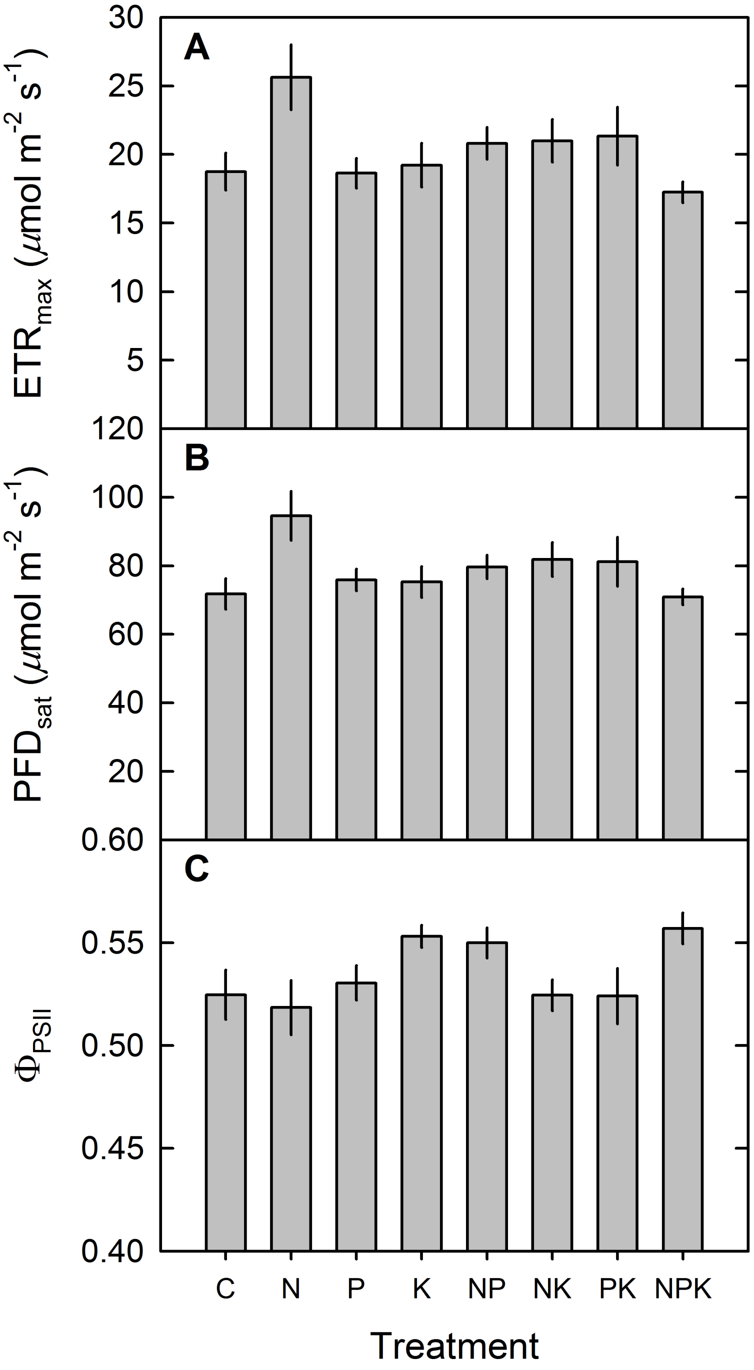

Figure 2.2. Responses of **A** maximum electron transport rate (ETR$_{max}$), **B** saturating photosynthetic photon flux density (PFD$_{sat}$), and **C** effective quantum yield of photosystem II (Φ_{PSII}) at 1,000 μmol m^{-2} s^{-1} PFD of seedlings of the tree species *Alseis blackiana* to factorial addition of nitrogen (N), phosphorus (P), potassium (K), and control (C) treatments in the understory of lowland tropical forest in Panama.

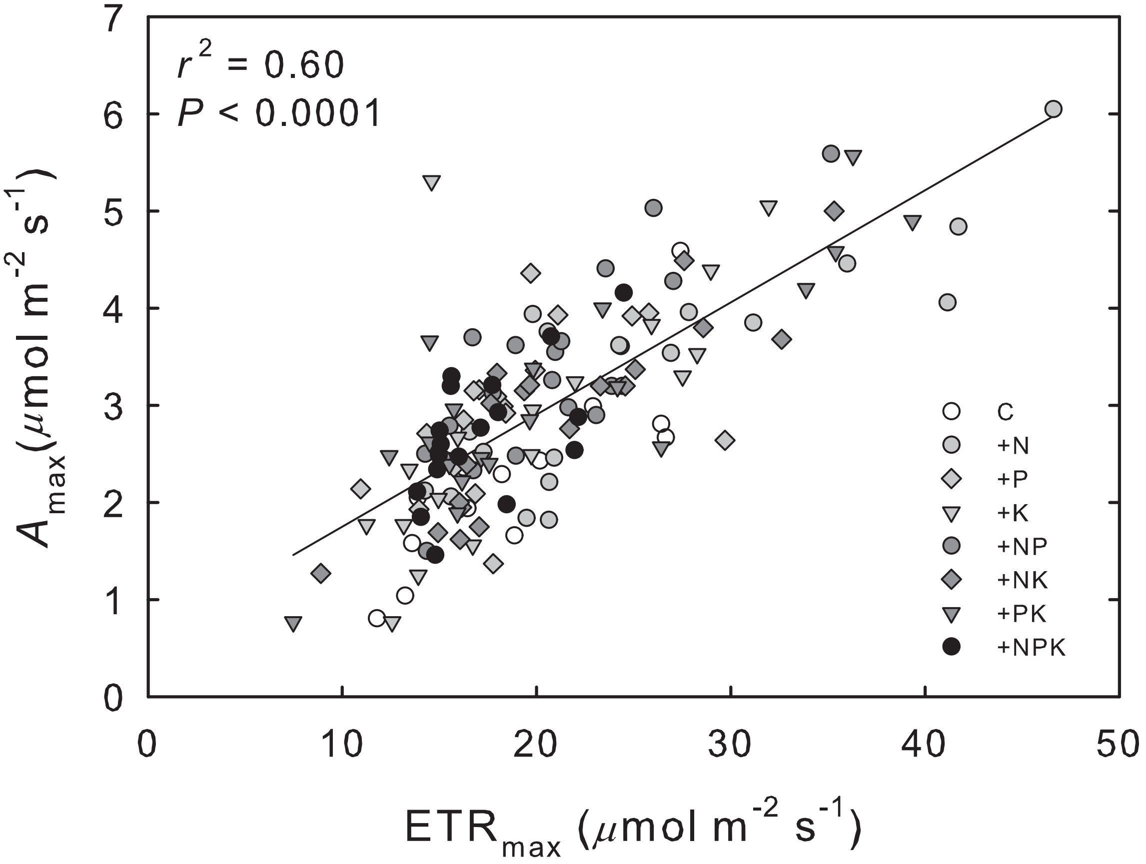

Figure 2.3. Maximum photosynthetic CO_2 assimilation per leaf area (A_{max}) as a function of maximum electron transport rate (ETR_{max}) for 146 seedlings of the tree species *Alseis blackiana* in a factorial fertilization experiment with nitrogen (N), phosphorus (P), potassium (K), and control (C) treatments in the understory of lowland tropical forest in Panama.

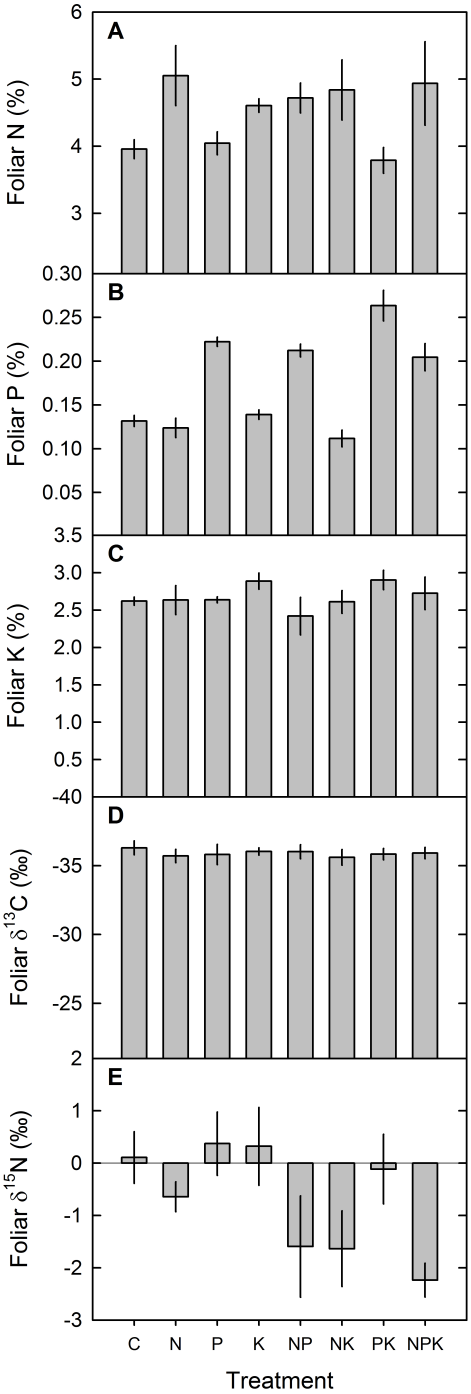

Figure 2.4. Responses of foliar concentrations of **A** nitrogen (N), **B** phosphorus (P), **C** potassium (K), and isotopic concentration of **D** carbon (δ^{13}C) and **E** nitrogen (δ^{15}N) of seedlings of the tree species *Alseis blackiana* to factorial addition of N, P, K, and control (C) treatments in the understory of lowland tropical forest in Panama.

Chapter 3: Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment

Published as: Pasquini, SC, SJ Wright, and LS Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. Ecology 96:1866-1876.

Abstract

Lianas are a prominent growth form in tropical forests, and there is compelling evidence that they are increasing in abundance throughout the Neotropics. While recent evidence shows that soil resources limit tree growth even in deep shade, the degree to which soil resources limit lianas in forest understories, where they coexist with trees for decades, remains unknown. Regardless, the physiological underpinnings of soil resource limitation in deeply shaded tropical habitats remain largely unexplored for either trees or lianas. Theory predicts that lianas should be more limited by soil resources than trees because they occupy the quick-return end of the ‘‘leaf economic spectrum,’’ characterized by high rates of photosynthesis, high specific leaf area, short leaf life span, affinity to high-nutrient sites, and greater foliar nutrient concentrations. To address these issues, we asked whether soil resources (nitrogen: N, phosphorus: P, and potassium: K), alone or in combination, applied experimentally for more than a decade would cause significant changes in the morphology or physiology of tree and liana seedlings in a lowland tropical forest. We found evidence for the first time that P limits the photosynthetic performance of both trees and lianas in deeply shaded understory habitats. More importantly, lianas always showed significantly greater photosynthetic capacity, quenching, and saturating light levels compared to trees across all treatments. We found little evidence for nutrient × growth form interactions, indicating that lianas were not disproportionately favored in nutrient-rich habitats. Tree and liana seedlings differed markedly for six key morphological traits, demonstrating that architectural differences occurred very early in ontogeny prior to lianas finding a trellis (all seedlings were self-supporting). Overall, our results do not support nutrient loading as a mechanism of increasing liana abundance in the Neotropics. Rather, our finding that lianas always outperform trees, in terms of photosynthetic processes and under contrasting rates of resource supply of macronutrients, will allow lianas to increase in abundance if disturbance and tree turnover rates are increasing in Neotropical forests as has been suggested.

Introduction

Lianas and trees are the two dominant plant growth forms in tropical forests, and there is a growing body of evidence suggesting that lianas are increasing relative to trees in Neotropical forests (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright, S.J. et al. 2004, Chave et al. 2008, Foster et al. 2008, Schnitzer and Bongers 2011, Yorke et al. 2013, Schnitzer 2015). We are not sure why. Regardless, these increases in liana abundance will almost certainly have important consequences for forest biodiversity and global carbon budgets (Bunker et al. 2005, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Schnitzer et al. 2014). Indeed, Schnitzer and Carson (2010) and Schnitzer et al. (2014) demonstrated unequivocally that when lianas increase in abundance and displace trees, forest-wide aboveground carbon storage can be reduced by as much as 18%. While exceptions exist, lianas are typically a fast-growing, light-limited growth form associated with high light, nutrient-rich, and disturbed habitats, including forest edges, canopy gaps, and logged forests (Putz 1984, Schnitzer et al. 2000, Schnitzer and Carson 2010). Moreover, they can represent more than a third of all woody species in tropical forests (Pérez-Salicrup et al. 2001, Gentry 2009, Schnitzer et al. 2012).

Lianas differ from trees in critical patterns of biomass allocation and other key life-history traits. For example, in their climbing form, lianas rely on other vegetation as trellises to gain access to the canopy, and thus they typically invest proportionally less resources into woody stem tissue than trees, and proportionally more resources toward leaves and roots (Putz 1983, Suzuki 1987, Castellanos et al. 1989, Niklas 1994, Gerwing and Farias 2000, Hättenschwiler 2002, Santiago and Wright 2007). This biomass allocation pattern of canopy-level lianas (lianas with at least partial foliage in the forest canopy) results in lianas having greater specific leaf area (SLA) and photosynthetic rates (A_{max}) than trees (Zhu and Cao 2009, Han et al. 2010, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015). The abundance of canopy-level lianas often increases with soil fertility (e.g., Proctor et al. 1983, Putz 1983, 1985, Putz and Chai 1987, Balfour and Bond 1993, Bruijnzeel and Proctor 1995) and lianas show higher foliar nutrient concentrations compared to trees (Cai and Bongers 2007, Kusumoto and Enoki 2008, Zhu and Cao 2010, Asner and Martin 2012). This suggests that canopy-level lianas are far more nutrient-limited than trees, yet the few *in situ* experimental nutrient enrichment studies available have found either modest support for this (Hättenschwiler 2002) or no differences at all between the life forms (Cai et al. 2008).

While canopy-level trees and lianas differ strongly in terms of leaf traits, morphology, and physiology, the degree to which seedlings differ is unclear. In early ontogenetic stages, lianas typically exist without a trellis and both trees and lianas have to survive for years within deeply shaded understory habitats; under these conditions they appear strikingly similar in terms of morphology and architecture (Putz 1983). Thus, there appears to be broad overlap in the patterns of growth, survival, and habitat preferences of the seedlings of both lianas and trees (Gilbert et al. 2006). Consequently, contrasting resource uptake and allocation may not occur in early developmental stages where light remains the primary limiting resource, and most differences between trees and lianas may only develop late in ontogeny.

While light may be the most limiting resource in tropical forest understory habitats, it has recently become clear that seedlings of some woody species are also co-limited by soil nutrients. Limitation varies among species (Denslow et al.

1987) and among soil resources including nitrogen (N), phosphorus (P), or potassium (K), and in some cases limitation is caused simultaneously by multiple soil resources (Bloom et al. 1985, Ceccon et al. 2004, Holste et al. 2011, Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Indeed, recent work on the tree seedling *Alseis blackiana* (Helms.; Rubiaceae) demonstrated that photosynthesis, stomatal conductance, and photosynthetic yield were limited by N, P, and K, respectively, even in deep shade (Pasquini and Santiago 2012). In a separate study at the same site, K limited tree seedling growth (Santiago et al. 2012). For liana seedlings, however, both the degree of nutrient limitation, as well as whether liana seedlings are more or less limited by soil resources than tree seedlings, remains unknown.

Here, we test *in situ* the hypothesis that nutrients limit photosynthetic physiology of liana seedlings to a greater degree than tree seedlings. If lianas and trees differ, we would demonstrate that, in spite of their apparent similarities in seedling morphology, physiological divergence happens early in ontogeny, and if not, then physiological differences must develop after they find a trellis and begin ascending into the canopy. Furthermore, testing our hypothesis may provide insight into the underlying mechanism for the increase in lianas in many Neotropical forests. Nutrient deposition, particularly of nitrogen, is increasing throughout the tropics (reviewed by Hedin et al. 2009, Hietz et al. 2011), and tree turnover rates also appear to be increasing (Phillips et al. 2004), as are rates of human disturbances and deforestation (e.g., reviewed by Laurance 2008, Wright

2010). All of these are likely to favor lianas, particularly if they gain an advantage early in ontogeny.

To test our hypothesis, we are using a fully factorial experiment where N, P, and K have been added to large replicated forest plots for more than a decade. We compare how soil resources impact the physiology and morphology of seedlings of a phylogenetically diverse group of lianas and trees from 13 plant families. We hypothesize that (1) lianas will show greater responses to soil nutrients than trees because of their ability to allocate more to growth vs. structural support, (2) lianas will be limited by different soil resources than trees, and (3) lianas in very early developmental stages prior to acquiring a trellis will have contrasting patterns of plant architecture (e.g., internode length and leaf angle) compared to trees. Our goal is to determine whether liana and tree seedlings are constrained by the same or different resources or combinations of resources and link this to key aspects of photosynthetic physiology and seedling architecture. Ultimately, we link our findings back to recent evidence that strongly suggests lianas are not only increasing in abundance throughout the Neotropics, but also altering patterns of carbon storage and sequestration (e.g., Schnitzer et al. 2014, Schnitzer 2015).

Materials and Methods

Study site

We performed this research in seasonally moist, semi-deciduous, tropical forest located on the Gigante Peninsula (9°06'3" N, 79°50'37" W.) within the Barro

Colorado Nature Monument (BCNM) in central Panama (Appendix A: Fig. A1). The dry season occurs between January and April, during which less than 10% of the 2600 mm of average annual rainfall occurs. Our investigation took place from March through April 2010. Soils on the Gigante Peninsula are Oxisols and Inseptisols similar to Typic Eutrudox soils on adjacent Barro Colorado Island (Turner et al. 2012, B. L. Turner personal communication). In terms of N, P, and K availability, soils at this site are relatively fertile for lowland tropical soils (Yavitt et al. 2009, Wright et al. 2011). Tree composition and stature (tree heights up to 45 m) in this forest are characteristic of mature (>200 years) tropical secondary forest in central Panama (Wright et al. 2011).

Experimental design

We used a long-term nutrient addition experiment where N, P, and K have been added in a full 2 × 2 × 2 factorial design with four replicates of each of eight treatments (control, N, P, K, NP, NK, PK, and NPK). The four replicates were placed perpendicular to a slight topographical gradient (36 m in elevation from south-west to northeast corner of site), because tree distributions and soil properties parallel this gradient (Yavitt et al. 2009, Wright et al. 2011). We used a balanced, incomplete-block design, where N, P, K, and NPK treatments were blocked vs. NP, NK, PK, and control treatments within each replicate (Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). This design minimizes uncontrolled error due to heterogeneity and allows evaluation of main and two-way interactions, but limits power to evaluate the three-way interaction

(Winer et al. 1991). Nutrients were added four times annually during the wet season for a total of 125 kg N ha^{-1} yr^{-1} as coated urea [$(NH_2)_2CO$], 50 kg P ha^{-1} yr^{-1} as triple super phosphate [$Ca(H_2PO_4)_2$ H_2O], and 50 kg K ha^{-1} yr^{-1} as potassium chloride (KCl) starting in 1998 (12 years of nutrient addition). The 32 experimental plots were each 40 × 40 m in area and were separated by at least 40 m to minimize nutrient leaching into neighboring plots, with the exception of two plots separated by 20 m and located on opposite sides of a 3-m deep stream. In this same study site, long-term N fertilization led to increased soil acidity (0.8 unit decrease in soil pH; Corre et al. 2010), which may affect availability of P and other soil nutrients.

Species

We selected seven liana and six tree species from 13 plant families because they were common in the study plots. The lianas were *Bauhinia guianenses* Aubl. (Fabaceae: Caesalpinioideae), *Coccoloba parimensis* Benth. (Polygonaceae), *Doliocarpus dentatus* (Aubl.) Standl. (Dilleniaceae), *Maripa panamensis* Hemsl. (Convolvulaceae), *Paullinia fibrigera* Radlk. (Sapindaceae), *Phryganocydia corymbosa* (Vent.) Bureau ex. K. Schum (Bignoniaceae), and *Prionostemma aspera* (Lam.) Miers. (Celastraceae). The trees were *Alseis blackiana* Hemsl. (Rubiaceae), *Desmopsis panamensis* (B. L. Rob.) Saff. (Annonaceae), *Heisteria concinna* Standl. (Olacaceae), *Oenocarpus mapora* H. Karst. (Arecaceae), *Sorocea affinis* Hemls. (Moraceae), and *Tetragastris panamensis* (Engler) Kuntze (Burseraceae). Nomenclature follows Garwood

(2009). Individual seedlings were chosen haphazardly based on the first sightings of the study species within each plot. All liana seedlings were self-supporting (free-standing) and did not exhibit searcher shoots (*sensu* Putz and Holbrook 2009).

Physiological measurements

Chlorophyll fluorescence measurements were used because they are highly correlated with carbon assimilation rates (especially maximum electron transport, Maxwell and Johnson 2000), and we confirmed this relationship for one of our focal species (*A. blackiana*; Pasquini and Santiago 2012). We measured chlorophyll fluorescence of mature, fully expanded leaves using a photosynthesis yield analyzer (Mini-PAM, Heinz Walz GmbH, Effeltrich, Germany). We sampled one leaf from one individual of the 13 species in each of the 32 plots (mean leaves sampled per plot = 12.4, total leaves sampled = 397). We constructed chlorophyll fluorescence-light response curves using photon flux density (PFD) values of 0, 34, 97, 202, 324, 499, 700, 1067, and 1471 μmol m^{-2} s^{-1} to slowly bring the light up to the highest level. We measured the electron transport rate (ETR), which is an *in vivo* measure of overall capacity to provide energy to photosynthetic carboxylation reactions. We also measured photochemical quenching (q_p); the proportion of open photosystem II (PSII) reaction centers and a proxy of the efficiency of PSII. We obtained the maximum electron transport rate (ETR_{max}) and q_P at the highest light level (PFD = 1471 μmol m^{-2} s^{-1}). ETR was determined as:

$$\mathrm{ETR} = \frac{F_m^{'} - F_s}{F_m^{'}} \cdot \mathrm{PFD} \cdot f \cdot \alpha$$

where $F_m^{'}$ is maximal fluorescence measured by a saturation pulse at each light level, F_s is steady-state fluorescence, f is a factor that represents the partitioning of photons between photosystems II and I (PSII and PSI) and is assumed to be 0.5, which indicates equal distribution of excitation energy between the two photosystems (Maxwell and Johnson 2000), and α represents the fraction of photons absorbed by a leaf and is assumed to be 0.84 as an average for a variety of C_3 leaves (Björkman and Demmig 1987, Stemke and Santiago 2011). Photochemical quenching was determined as:

$$q_P = \frac{F_m^{'} - F_s}{F_m^{'} - F_0^{'}}$$

where $F_0^{'}$ is minimum fluorescence of each illuminated sample determined during a brief dark interval following a saturation pulse (see Fig. 3.1 for an example of a fluorescence-light response curve).

Morphological measurements

We measured leaf angle, leaf thickness, internode length, and petiole length to characterize seedling morphology. Crown depth, perpendicular crown width, and seedling height were measured and used to calculate crown depth and crown area, relative to height. Leaf angle was measured using a protractor with a weighted thread as the angle of the leaf measured along the midvein from petiole attachment to leaf tip where a 90° leaf angle is parallel to the ground and perpendicular to the main stem (leaf angle > 90° indicates that leaf at an obtuse angle relative to the ground). We measured leaf thickness on an area of the leaf without major veins using a digital micrometer (IP 65; Mitutoyo, Mizonokuchi, Japan). Additionally, one leaf from each seedling was collected and measured for leaf area (leaf petiole was removed) using a leaf area meter (LI-3100; Li-Cor Biosciences, Lincoln, Nebraska, USA). Leaves were then oven dried at 60°C for 48 h and weighed to determine SLA.

Light availability

Light availability in the tropical forest understory is heterogeneous due to a mosaic of canopy gaps and branch falls of differing ages and sizes. Because photosynthetic processes in the understory are primarily light-limited (Pearcy 1988), we estimated light availability directly above each of the 397 seedlings using hemispherical canopy photographs taken with a digital camera (Coolpix 4500; Nikon, Tokyo, Japan) mounted with a fisheye lens (Fisheye Converter FC-E8 0.213; Nikon).

Data analyses

We analyzed ETR-light response curves for saturating photon flux density (PFD_{sat}) using Photosyn Assistant (version 1.1; Dundee Scientific, Dundee, UK), as described by Prioul and Chartier (1977). Hemispheric canopy photographs were analyzed for total transmittance (T_{total}; proportion of above-canopy ambient light transmitted through the canopy) using Gap Light Analyzer (Frazer et al. 1999). We used a general linear model in SAS (proc glm, version 9.2; SAS

Institute, Cary, North Carolina, USA) to determine whether liana and tree seedlings overall were found in differing light environments. Physiological and morphological data were analyzed by mixed linear models in SAS (proc mixed). The mixed linear model procedure was used rather than the general linear model procedure to yield Akaike information criterion (AIC) values for each model. Models were run on individual leaf physiological and morphological measures with fixed main effects of form (liana vs. tree), species nested within form, single nutrient main effects (N, P, K), two-way nutrient interactions (N × P, N × K, P × K), nutrient by growth form interactions (N × form, P × form, K × form), and T_{total} (to control for heterogeneity of the light environment). Random effects were statistical replicate (Rep) and block nested within replicate. For similar analyses, see Pasquini and Santiago (2012) and Wright et al. (2011). Models that included effects of species as well as growth form were compared using AIC values (Appendix B: Tables B1–B6). Standard data transformations (natural log, square root, and arcsine) were performed to meet the assumption of normality as determined by the Shapiro-Wilk *W*-statistic. T_{total} are proportional data and were logit-transformed accordingly (Warton and Hui 2011). To control for Type I error (α-error) in the multiple comparisons, we used False Discovery Rate (FDR) corrections, as described by Pike (2011) to adjust significant *P*-values; FDR-corrected *P*-values are reported in *Results*, Figs. 3.2-3.7, and Tables 3.1 and 3.2.

Results

Model selection

Mixed linear models were performed in two different ways, with and without species included. For all physiological and morphological variables, the model including species was a better fit to the data as determined by comparing AIC values (Appendix B: Tables B1–B6). Therefore, the findings based on the model with species included are presented.

Physiological indices of performance

Lianas performed substantially better than trees for all physiological metrics (14–21% greater; Table 3.1, Fig. 3.2A–C). As expected, seedling photosynthetic performance was affected by light availability (T_{total}; Table 3.1), and thus it is important to note that mean understory light availability did not differ significantly between liana and tree seedlings (lianas, 6.0% ± 0.6% [SE]; trees, 5.8% ± 0.7%; $F_{1,\,395} = 0.08$, $P = 0.78$; Appendix C: Fig. C1). In addition, species within growth forms differed significantly in physiological performance (Table 3.1).

Nutrient additions, especially P alone, enhanced photosynthetic physiology, whereas N or K addition never did. P addition increased $\mathrm{ETR}_{\max}$ by 9.6% (Table 3.1, Fig. 3.3). P addition also caused a marginally significant increase in q_{P} (8.8%, $P = 0.033$; Table 3.1). Surprisingly, when K was added in combination with P, it decreased the benefit to performance caused by adding P alone, as indicated by consistent significant P × K interactions (Table 3.1, Fig.

3.4A–C). Specifically, P and K together decreased the benefit of adding P alone for ETR_{max}, PFD_{sat}, and q_P by 7.6%, 9.2%, and 10.2%, respectively (Table 3.1, Fig. 3.4A–C). Nutrient additions enhanced the physiological performance of both lianas and trees to a similar degree (i.e., no significant interaction between growth form and nutrient addition). For the effects of all nutrient treatment combinations on the physiological responses of trees vs. lianas, see Appendix C: Fig. C2.

Plant architectural traits

Lianas and tree seedlings were significantly ($P < 0.0115$) different from each other for *all but one metric* of plant architecture (Table 3.2, Fig. 3.5A–F). Liana crowns were 32.0% deeper, their leaves were 10.5% thicker, their internodes were 27.3% longer, and their petioles were 111.2% longer than trees (Table 3.2, Fig. 3.5A–D). Tree leaf angles were 3.9% greater, and they had 9.2% greater SLA than lianas (Table 3.2, Fig. 3.5E-F). Tree crowns were only marginally larger than liana crowns (12.9%, $P = 0.024$; Table 3.2). Surprisingly, light availability (T_{total}) had little impact on seedling architecture, except for SLA (Table 3.2). Species within growth forms differed significantly in seedling architecture (Table 3.2). Liana seedlings averaged 28.2 ± 0.9 cm in height and tree seedlings averaged 29.6 ± 1.0 cm in height (overall seedling height was 28.9 ± 0.7 cm).

Adding nutrients alone or in combination caused very few significant changes in seedling morphology (Table 3.2, Fig. 3.6A, B). Specifically, adding K caused a significant but small increase (6.5%) in SLA, and P alone and K alone caused marginally significant but fairly substantial increases in leaf angle (P, 10.6%, $P = 0.046$; K, 10.0%, $P = 0.042$; Table 3.2). If these results were additive for P and K, then adding P and K together should have caused an even greater increase in leaf angle; however this did not occur. Instead, leaf angles were close to control levels when P and K were added together (significant P × K interaction; Table 3.2, Fig. 3.6B). We did detect one case where nutrient additions caused the opposite response between lianas vs. trees; P addition caused petiole length to increase (15.6%) for lianas but decrease (15.7%) for trees (significant growth form × P interaction; Table 3.2, Fig. 3.7). Nonetheless, the strong signal here is that nutrient amendments had little impact on seven different metrics of seedling morphology. For the effects of all nutrient treatment combinations on the architectural traits of trees vs. lianas, see Appendix C: Figs. C3 and C4.

Discussion

To our knowledge, this is the first study to demonstrate that the early seedling stages of common species of lianas substantially outperform (from 14% to 21%) common species of trees for three key photosynthetic metrics regardless of macronutrient availability. Increasing nutrient supply rates for P alone increased the performance of both lianas and tree seedlings to a similar degree, but adding K with P dragged this performance benefit down. Regardless, the take home message here is that long-term nutrient amendments never benefited lianas more than trees for any macronutrient or any macronutrient combination.

Also, and somewhat surprisingly, N addition never caused any significant change in any physiological or morphological metric. In addition, we were surprised that lianas and trees were architecturally quite different from each other even during the free-standing seedling stages when they appear morphologically quite similar (Table 3.2, Fig. 3.5A-F; Putz 1983). Nutrient enrichment did not change this in any way. Thus, these early morphological differences were robust and did not change even under long-term and sharply contrasting soil nutrient supply rates. We suggest that our findings are broadly applicable because we studied a phylogenetically diverse array of 13 species from 13 families. Overall, our findings demonstrate that liana seedlings growing in deep shade are always capable of higher photosynthetic performance than tree seed-lings under ambient light levels and under sharply contrasting levels of macronutrients (e.g., N vs. P vs. K) or under ambient nutrient levels. Thus, the advantage of having a liana growth habit occurs very early ontogenetically prior to any use of a trellis for support. Our results provide strong evidence that P limits photosynthetic performance of seedlings of both trees and lianas in deeply shaded understory habitats.

P limits photosynthetic performance but P and K together do not

Adding P caused a significant increase in one of three measures of photosynthetic performance (ETR_{max}; Table 3.1, Figs. 3.3 and 3.4A) and a marginally significant increase in a second measure (q_p; Table 3.1, Fig. 3.4B). Adding K also increased photosynthetic performance, but this increase was never significant (Table 3.1, Fig. 3.4A– C). Surprisingly adding P and K together decreased photosynthetic performance relative to the addition of P alone (significant P × K interaction) when it should have caused an increase in performance if the effect of each macronutrient alone was additive (Table 3.1, Fig. 3.4A–C). While the mechanistic basis of this is not clear, we suggest that it is likely linked to alterations in stomatal control that occur with additions of K.

Our results build on past studies that demonstrated that soil resources limit plant performance even in deeply shaded habitats (Cai et al. 2008, Kaspari et al. 2008), but here we identify which macronutrients were limiting or co-limiting. P addition enhanced ETR_{max} because P is known to increase biochemical efficiency of the light reactions of photosynthesis and promote enhanced carbon assimilation rates (Kirschbaum and Tompkins 1990, Raaimakers et al. 1995). Previous studies at this site demonstrate unequivocally that multiple soil resources co-limit trees in deep shade and we extend these results to seedlings of lianas. Thus, even a growth form that is quite light demanding and fast growing can still be limited by soil resources when light is at very low levels. We could not detect any impact of N additions on physiological performance. Nonetheless, N, P, K, P × K, N × P, and N × K all have been shown at times to limit physiological performance, growth rate, or both, among woody species (this study, Wright et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012). Still, our results strongly point to P as the key limiting or co-limiting soil resource within the understory. Overall, we demonstrate that light can no longer be considered the only limiting resource in deeply shaded tropical habitats.

Liana and tree seedling architectures are markedly different

Lianas are classified as a separate growth form from trees because they are structural parasites and require trellises to reach the canopy. Nonetheless, it was unknown whether key architectural traits contrast between seedlings of lianas and trees prior to lianas acquiring a trellis and prior to sending up searcher shoots. Here, counter to conventional wisdom, we show that liana seedlings differ for a suite of architectural traits. Nutrient additions rarely caused changes in any of these traits, at least while these seedlings were in deep shade. Thus, differences in liana architecture are expressed before lianas have located a trellis or before they rapidly increase growth rates under conditions of higher light availability (Den Dubbelden and Oosterbeek 1995). The height at which lianas begin to utilize external support is usually between 30 and 40 cm in lowland tropical forests of Southeast Asia and Latin America (Putz and Holbrook 2009). The average height of seedlings used in this study (29.1 cm) was close to this range, but all study individuals were self-supporting.

We found that lianas had significantly *lower* SLA and *thicker* leaves compared to trees (Table 3.2, Fig. 3.5B and F); in contrast, lianas that have reached the canopy typically have significantly higher SLA and thinner leaves than trees (Lambers and Poorter 1992, Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015). Thus, ontogenetic trait shifts appear to be occurring for these important leaf structural traits. Leaves with low SLA are more costly to build and high SLA is a characteristic of fast-growing plants (Lambers and Poorter 1992, Baruch and Goldstein 1999). Low SLA is also associated with both reduced susceptibility to herbivores (Poorter et al. 2009) and increase leaf lifespan (Wright, I.J. et al. 2004). Low SLA and thick leaves of liana seedlings may allow them to persist for long periods in the understory until they can access the canopy.

The physiology of lianas and their increase in Neotropical forests

There is compelling evidence that lianas are increasing in Neotropical forests (e.g., Schnitzer 2015 and citations therein). Here, we demonstrate that a phylogenetically diverse group of lianas had enhanced physiological performance compared to a phylogenetically diverse group of tree species (Table 3.1, Fig. 3.2A– C). Thus, our findings extend previous research that found greater performance ($A_{\max}$) by canopy-level lianas (Zhu and Cao 2009, Han et al. 2010, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015) to very early seedling stages in the understory. We also demonstrated greater q_P in liana seedlings relative to tree seedlings (Table 3.1, Fig. 3.2B), which suggests that lianas are able to maximize the amount of incoming solar radiation utilized for photosynthesis. This would confer an advantage in photosynthetic carbon assimilation to lianas in rapidly changing light conditions seen in the understory due to short, high-intensity sunflecks (Chazdon 1988, Pearcy 1988). Overall our results suggest that any changes in fertility, whether natural or anthropogenic, will not disproportionally favor lianas because lianas already outperform trees regardless of fertility, and lianas and trees responded similarly to nutrient additions (only one significant growth form by nutrient interaction; Tables 3.1 and 3.2). Thus our results do not support nutrient loading as a mechanism of increasing liana abundance in the Neotropics. Rather, our finding that lianas always outperform trees under sharply contrasting rates of resource supply of macronutrients or their combination will allow lianas to increase in abundance if disturbance rates are increasing in Neotropical forests as some have suggested (Phillips et al. 2004). Moreover, an increase in liana abundance will likely lead to lower forest-wide storage of carbon because lianas often displace trees and only replace 24% of the biomass (Schnitzer et al. 2014).

Literature Cited

Asner, G.P., and R.E. Martin. 2012. Contrasting leaf chemical traits in tropical lianas and trees: Implications for future forest composition. Ecology Letters 15:1001-1007.

Balfour, D.A., and W.J. Bond. 1993. Factors limiting climber distribution and abundance in a southern African forest. Journal of Ecology 81:93-100.

Baruch, Z., and G. Goldstein. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia 121:183-192.

Benítez-Malvido, J., and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. Conservation Biology 17:389-400.

Björkman, O., and B. Demmig. 1987. Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. Planta 170:489-504.

Bloom, A.J., F.S. Chapin, III, and H.A. Mooney. 1985. Resource limitation in plants – An economic analogy. Annual Review of Ecology and Systematics 16:363-392.

Bruijnzeel, L.A., and J. Proctor. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? Pages 38-78 *in* L.S. Hamilton, J.O. Juvik, and F.N. Scatena, editors. Tropical montane cloud forests. Springer-Verlag, New York, NY, USA.

Bunker, D.E., F. DeClerck, J.C. Bradford, R.K. Colwell, I. Perfecto, O.L. Phillips, M. Sankaran, and S. Naeem. 2005. Species loss and aboveground carbon storage in a tropical forest. Science 310:1029-1031.

Cai, Z.-Q., and F. Bongers. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. Journal of Tropical Ecology 23:115-118.

Cai, Z.-Q., L. Poorter, Q. Han, and F. Bongers. 2008. Effects of light and nutrients on seedlings of tropical *Bauhinia* lianas and trees. Tree Physiology 28:1277-1285.

Cai, Z.-Q., S.A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. Oecologia 161:25-33.

Castellanos, A.E., H.A. Mooney, S.H. Bullock, C. Jones, and R. Robichaux. 1989. Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. Biotropica 21:41-49.

Ceccon, E., S. Sánchez, and J. Campo. 2004. Tree seedling dynamics in two abandoned tropical dry forests of differing successional status in Yucatán, Mexico: A field experiment with N and P fertilization. Plant Ecology 170:277-285.

Chave, J., J. Olivier, F. Bongers, P. Châtelet, P.-M. Forget, P. van der Meer, N. Norden, B. Riéra, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. Journal of Tropical Ecology 24:355-366.

Chazdon, R.L. 1988. Sunflecks and their importance to forest understory plants. Advances in Ecological Research 18:1-63.

Corre, M.D., E. Veldkamp, J. Arnold, and S.J. Wright. 2010. Impact of elevated N input on soil N cycling and losses in old-growth lowland and montane forests in Panama. Ecology 91:1715-1729.

Den Dubbelden, K.C., and B. Oosterbeek. 1995. The availability of external support affects allocation patterns and morphology of herbaceous climbing plants. Functional Ecology 9:628-634.

Denslow, J.S., P. Vitousek, and J.C. Schultz. 1987. Bioassays of nutrient limitation in a tropical rain forest soil. Oecologia 74:370-376.

Foster, J.R., P.A. Townsend, and C.E. Zganjar. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. Remote Sensing of Environment 112:2104-2117.

Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light indices from true-colour fisheye photographs. Simon Fraser University, Burnaby, Canada, and the Institute of Ecosystem Studies, Millbrook, NY, USA.

Garwood, N.C. 2009. Seedlings of Barro Colorado Island and the Neotropics. Cornell University Press, Ithaca, New York, USA.

Gentry, A.H. 2009. The distribution and evolution of climbing plants. Pages 3-51 *in* F.E. Putz and H.A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Gerwing, J.J., and D.L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. Journal of Tropical Ecology 16:327-335.

Gilbert, B., S.J. Wright, H.C. Muller-Landau, K. Kitajima, and A. Hernandez. 2006. Life history trade-offs in tropical trees and lianas. Ecology 87:1281-1288.

Han, L., L.J. Xie, K.J. Dai, Q. Yang, and Z.Q. Cai. 2010. Contrasting leaf characteristics of trees and lianas in secondary and mature forests in southwestern China. Photosynthetica 48:559-566.

Hättenschwiler, S. 2002. Liana seedling growth in response to fertilisation in a neotropical forest understorey. Basic and Applied Ecology 3:135-143.

Hedin, L.O., E.N.J. Brookshire, D.N.L. Menge, and A. Barron. 2009. The nitrogen paradox in tropical forest ecosystems. Annual Review of Ecology, Evolution and Systematics 40:613-635.

Hietz, P., B.L. Turner, W. Wanek, A. Richter, C.A. Nock, and S.J. Wright. 2011. Long-term change in the nitrogen cycle of tropical forests. Science 334:664-666.

Holste, E.K., R.K. Kobe, and C.F. Vriesendorp. 2011. Seedling growth responses to soil resources in the understory of a wet tropical forest. Ecology 92:1828-1838.

Kaspari, M., M.N. Garcia, K.E. Harms, M. Santana, S.J. Wright, and J.B. Yavitt. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology Letters 11:35-43.

Kirschbaum, M.U.F., and D. Tompkins. 1990. Photosynthetic responses to phosphorus nutrition in *Eucalyptus grandis* seedlings. Australian Journal of Plant Physiology 17:527-535.

Kusumoto, B., and T. Enoki. 2008. Contribution of a liana species, *Mucuna macrocarpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest. Journal of Forest Research 13:35-42.

Lambers, H., and H. Poorter. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. Advances in Ecological Research 23:187-261.

Laurance, W.F. 2008. Environmental promise and peril in the Amazon. Pages 458-473 *in* W.P. Carson and S.A. Schnitzer, editors. Tropical forest community ecology. Wiley-Blackwell, Oxford, UK.

Maxwell, K., and G.N. Johnson. 2000. Chlorophyll fluorescence – A practical guide. Journal of Experimental Botany 51:659-668.

Niklas, K.J. 1994. Comparisons among biomass allocation and spatial distribution patterns of some vine, pteridophyte, and gymnosperm shoots. American Journal of Botany 81:1416-1421.

Pasquini, S.C., and L.S. Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 168:311-319.

Pearcy, R.W. 1988. Photosynthetic utilisation of lightflecks by understory plants. Australian Journal of Plant Physiology 15:223-238.

Pérez-Salicrup, D.R., V.L. Sork, and F.E. Putz. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33:34-47.

Phillips, O.L., T.R. Baker, L. Arroyo, N. Higuchi, T.J. Killeen, W.F. Laurance, S.L. Lewis, J. Lloyd, Y. Malhi, A. Monteagudo, D.A. Neill, P. Núñez Vargas, J.N.M. Silva, J. Terborgh, R. Vásquez Martínez, M. Alexiades, S. Almeida, S. Brown, J. Chave, J.A. Comiskey, C.I. Czimczik, A. Di Fiore, T. Erwin, C. Kuebler, S.G. Laurance, H.E.M. Nascimento, J. Olivier, W. Palacios, S. Patino, N.C.A. Pitman, C.A. Quesada, M. Saldias, A. Torres Lezama, and B. Vinceti. 2004. Pattern and process in Amazon tree turnover, 1976-2001. Philosophical Transactions of the Royal Society B 359:381-407.

Phillips, O.L., R.V. Martínez, L. Arroyo, T.B. Baker, T. Killeen, S.L. Lewis, Y. Malhi, A.M. Mendoza, D. Neill, P.N. Vargas, M. Alexiades, C. Cerón, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418:770-774.

Pike, N. 2011. Using False Discovery Rates for multiple comparisons in ecology and evolution. Methods in Ecology and Evolution 2:278-282.

Poorter, H., Ü. Niinemets, L. Poorter, I.J. Wright, and R. Villar. 2009. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. New Phytologist 182:565-588.

Prioul, J.L., and P. Chartier. 1977. Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: A critical analysis of the methods used. Annals of Botany 41:789-800.

Proctor, J., J.M. Anderson, P. Chai, and H.W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. Journal of Ecology 71:237-260.

Putz, F.E. 1983. Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro Basin, Venezuela. Biotropica 15:185-189.

Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65:1713-1724.

Putz, F.E. 1985. Woody vines and forest management in Malaysia. Commonwealth Forestry Review 64:1713-1724.

Putz, F.E., and P. Chai. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. Journal of Ecology 75:523-531.

Putz, F.E., and N.M. Holbrook. 2009. Biomechanical studies of vines. Pages 73-97 *in* F.E. Putz and H.A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, UK.

Raaimakers, D., R.G.A. Boot, P. Dijkstra, S. Pot, and T. Pons. 1995. Photosynthetic rates in relation to leaf phosphorus content in pioneer versus climax tropical rainforest trees. Oecologia 102:120-125.

Santiago, L.S., S.C. Pasquini, and M.E. De Guzman. 2015. Physiological implications of the liana growth form. Pages 288-298 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford, UK.

Santiago, L.S., and S.J. Wright. 2007. Leaf functional traits of tropical forest plants in relation to growth form. Functional Ecology 21:19-27.

Santiago, L.S., S.J. Wright, K.E. Harms, J.B. Yavitt, C. Korine, M.N. Garcia, and B.L. Turner. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. Journal of Ecology 100:309-316.

Schnitzer, S.A. 2015. Increasing liana abundance in Neotropical forests: Causes and consequences. Pages 451-464 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of lianas. Wiley-Blackwell, Oxford, UK.

Schnitzer, S.A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters 14:397-406.

Schnitzer, S.A., and W.P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849-857.

Schnitzer, S.A., J.W. Dalling, and W.P. Carson. 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 88:655-666.

Schnitzer, S.A., S.A. Mangan, J.W. Dalling, C.A. Baldeck, S.P. Hubbell, A. Ledo, H.C. Muller-Landau, M.F. Tobin, S. Aguilar, D. Brassfield, A. Hernandez, S. Lao, R. Perez, O. Valdes, and S.R. Yorke. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. PLoS One 7:e52114.

Schnitzer, S.A., G. van der Heijden, J. Mascaro, and W.P. Carson. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. Ecology 95:3008-3017.

Stemke, J.A., and L.S. Santiago. 2011. Consequences of light absorptance in calculating electron transport rate of desert and succulent plants. Photosynthetica 49:195-200.

Suzuki, W. 1987. Comparative ecology of *Rubus* species (Roseaceae). I. Ecological distribution and life history characteristics of three species, *R. palmatus* var. *coptophyllus*, *R. microhyllus* and *R. crataegifolius*. Plant Species Biology 2:85-100.

Turner, B.L., J.B. Yavitt, K.E. Harms, M.N. Garcia, T.E. Romero, and S.J. Wright. 2012. Seasonal changes and treatment effects on soil inorganic nutrients following a decade of fertilizer addition in a lowland tropical forest. Soil Science Society of America Journal 77:1357-1369.

Warton, D.I., and F.K.C. Hui. 2011. The arcsine is asinine: The analysis of proportions in ecology. Ecology 92:3-10.

Winer, B.J., D.R. Brown, and K.M. Michels. 1991. Statistical principles in experimental design. 3rd edition. McGraw-Hill, New York, NY, USA.

Wright, I.J., P.B. Reich, M. Westoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, F.S. Chapin, III, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.

Wright, S.J. 2010. The future of tropical forests. Annals of the New York Academy of Sciences 1195:1-27.

Wright, S.J., O. Calderdón, A. Hernandéz, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484-489.

Wright, S.J., J.B. Yavitt, N. Wurzburger, B.L. Turner, E.V.J. Tanner, E.J. Sayer, L.S. Santiago, M. Kaspari, L.O. Hedin, K.E. Harms, M.N. Garcia, and M.D. Corre. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616-1625.

Yavitt, J.B., K.E. Harms, M.N. Garcia, S.J. Wright, F. He, and M.J. Mirabello. 2009. Spatial heterogeneity of soil chemical properties in a lowland tropical moist forest, Panama. Australian Journal of Soil Research 47:674-687.

Yorke, S.R., S.A. Schnitzer, J. Mascaro, S.G. Letcher, and W.P. Carson. 2013. Increasing liana abundance and basal area in a tropical forest: The contribution of long-distance clonal colonization. Biotropica 45:317-324.

Zhu, S.-D., and K.-F. Cao. 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. Plant Ecology 204:295-304.

Zhu, S.-D., and K.-F. Cao. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rainforest in southwestern China. Oecologia 163:591-599.

Table 3.1. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on physiological traits for liana and tree seedlings.

Factor	ETR_{max}	q_P	PFD_{sat}
Form	**0.0003**	**<0.0001**	**0.0006**
Species (Form)	**<0.0001**	**<0.0001**	**<0.0001**
T_{total}	**0.0012**	**<0.0001**	**0.0014**
N	0.8286	0.3554	0.9483
P	**0.0129**	0.0333	0.3415
K	0.5808	0.1896	0.4405
N × P	0.0552	0.2328	0.1382
N × K	0.6880	0.9682	0.6790
P × K	**0.0079**	**0.0112**	**0.0126**
N × Form	0.1400	0.3081	0.4305
P × Form	0.6397	0.1915	0.7753
K × Form	0.9657	0.6398	0.9068
Sample size	394	393	394

Data presented are *P*-values for fixed effects. Bolded values are statistically significant using the False Discovery Rate (FDR) corrected *P*-value ($P < 0.0237$). Total light transmission (T_{total}; proportion of above-canopy ambient), maximum electron transport rate (ETR_{max}; $\mu mol\ m^{-2}\ s^{-1}$), photochemical quenching (q_P; unitless), and saturating photon flux density (PFD_{sat}; $\mu mol\ m^{-2}\ s^{-1}$).

Table 3.2. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on morphological traits for liana and tree seedlings.

Factor	Rel. depth	Rel. area	Thickness	Angle	Internode	Petiole	SLA
Form	**<0.0001**	0.0239	**<0.0001**	**0.0066**	**0.0028**	**<0.0001**	**<0.0001**
Species (Form)	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
T_{total}	0.9091	0.7875	0.6700	0.2957	0.6846	0.3155	**0.0099**
N	0.4538	0.3545	0.5213	0.2738	0.4407	0.2033	0.3867
P	0.0850	0.3086	0.2669	0.0461	0.4054	0.9743	0.6409
K	0.4931	0.5922	0.8357	0.0420	0.4519	0.2500	**0.0007**
N × P	0.6973	0.2865	0.7166	0.2418	0.0295	0.8915	0.1889
N × K	0.9349	0.5107	0.1359	0.3454	0.5180	0.0793	0.1729
P × K	0.8540	0.8786	0.2692	**0.0002**	0.8828	0.4362	0.1663
N × Form	0.1443	0.0673	0.9326	0.7639	0.9454	0.8491	0.4990
P × Form	0.6641	0.0879	0.6836	0.1787	0.5860	**0.0091**	0.0975
K × Form	0.9091	0.1972	0.9299	0.9715	0.2206	0.0901	0.0710
Sample size	388	390	381	382	383	390	393

Data presented are *P*-values for fixed effects. Bolded values are statistically significant using the False Discovery Rate (FDR) corrected *P*-value ($P < 0.0115$). Total light transmission (T_{total}; proportion of above-canopy ambient), relative crown depth (cm), relative crown area (cm^2), leaf thickness (mm), leaf angle (degrees from main stem), internode length (mm), petiole length (mm), and specific leaf area (SLA; m^2/kg).

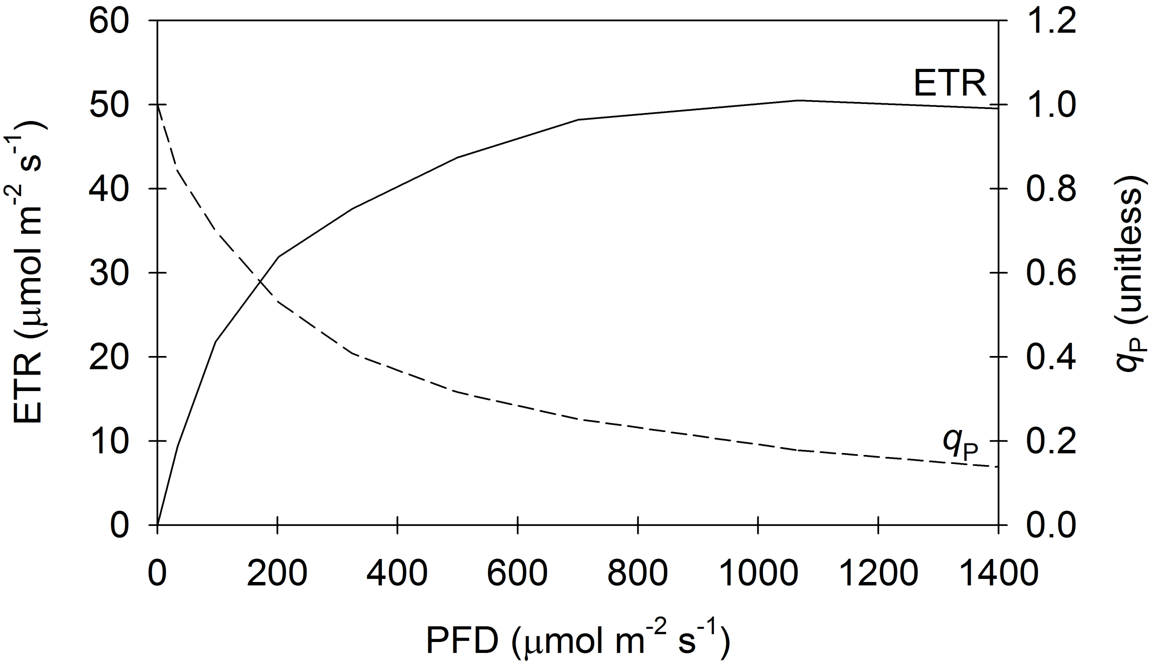

Figure 3.1. Example chlorophyll fluorescence-light response curve generated by the Mini-PAM photosynthesis yield analyzer showing electron transport rate (ETR; solid line) and photochemical quenching (q_P; dashed line), for increasing levels of photon flux density (PFD).

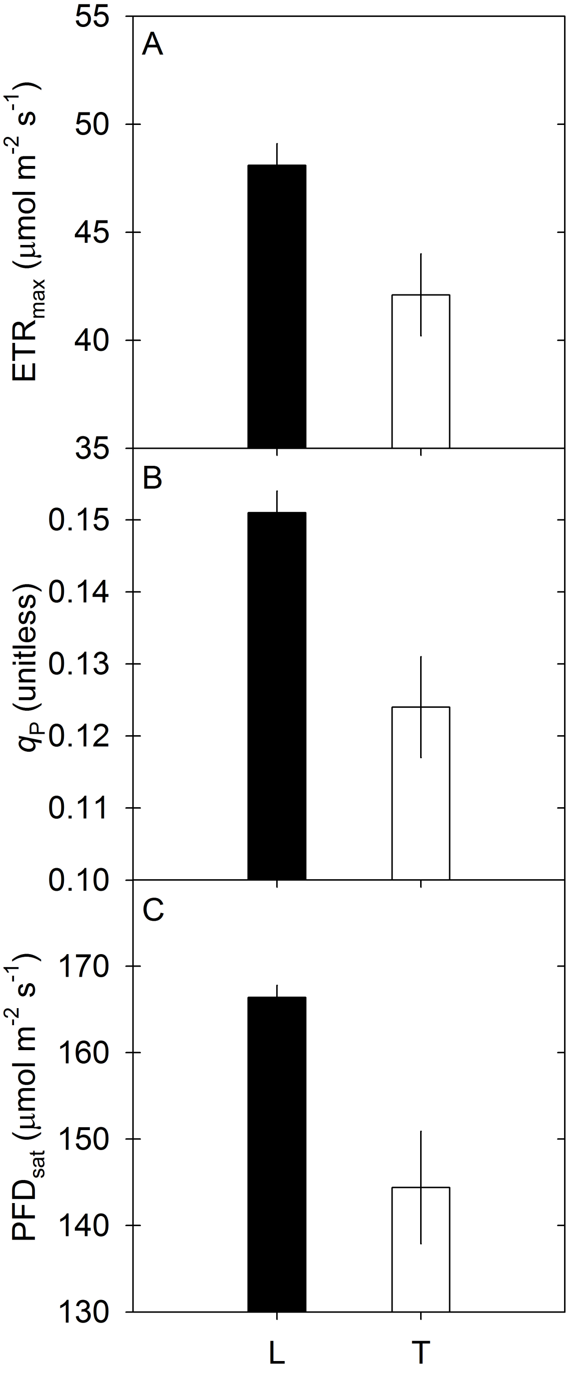

Figure 3.2. Significant main effects of growth form for **A** maximum electron transport rate (ETR$_{max}$), **B** photochemical quenching coefficient (q_P), and **C** saturating photon flux density (PFD$_{sat}$). Lianas and trees are represented by L and black bars, and T and open bars, respectively. All nutrient treatments are pooled. Bars represent means (± 1 SE, N = 32 plots).

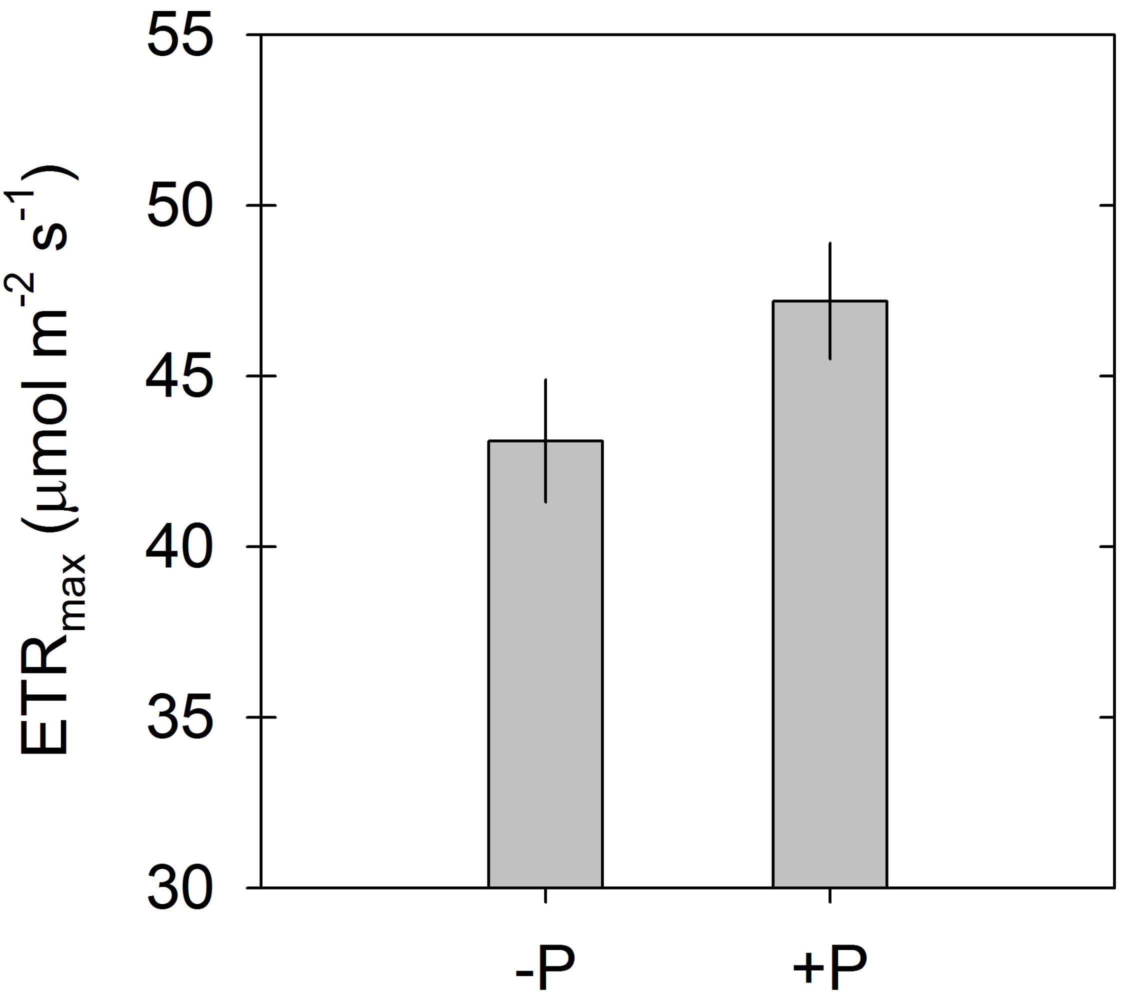

Figure 3.3. Significant main effect of phosphorus (P) addition for maximum electron transport rate (ETR_{max}). Liana and tree seedlings are pooled. Treatments without P (control: C, nitrogen: N, potassium: K, and NK) and treatments with P (P, NP, PK, and NPK) are also pooled. Bars represent means (± 1 SE, *N* = 16 plots).

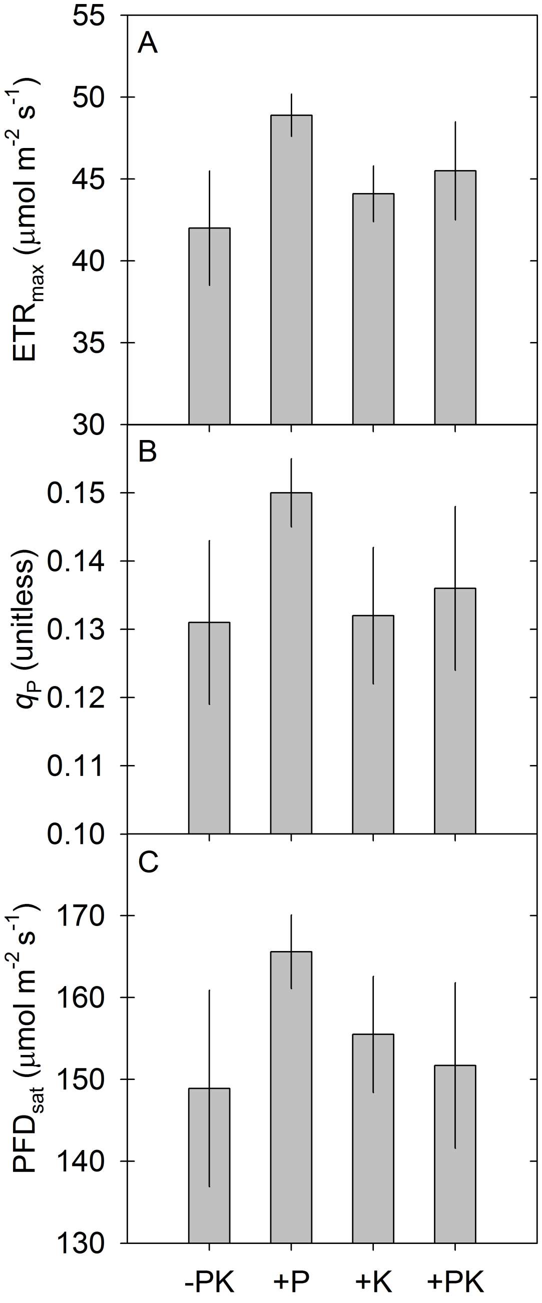

Figure 3.4. Significant phosphorus (P) × potassium (K) interactions for **A** maximum electron transport rate (ETR$_{max}$), **B** photochemical quenching coefficient (q_P), and **C** saturating photon flux density (PFD$_{sat}$). Liana and tree seedlings are pooled. Treatments without P or K (control: C and nitrogen: N), P treatments (P and NP), K treatments (K and NK) and treatments with both P and K (PK and NPK) are also pooled. Bars represent means (± 1 SE, *N* = 8 plots).

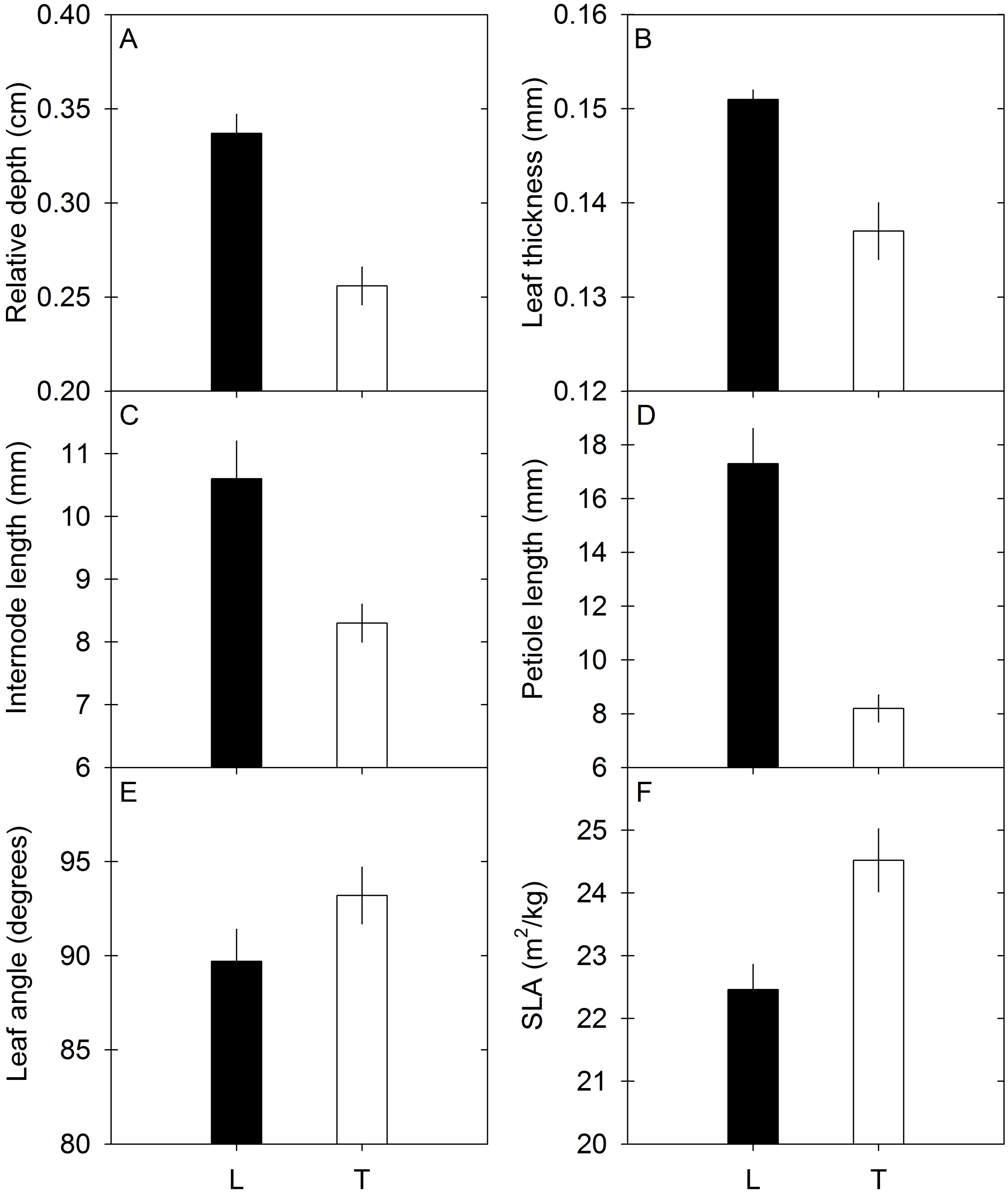

Figure 3.5. Significant main effects of growth form for **A** relative crown depth, **B** leaf thickness, **C** internode length, **D** petiole length, **E** leaf angle, and **F** specific leaf area (SLA). Lianas and trees are represented by L and black bars, and T and open bars, respectively. Bars represent means (± 1 SE, *N* = 32 plots).

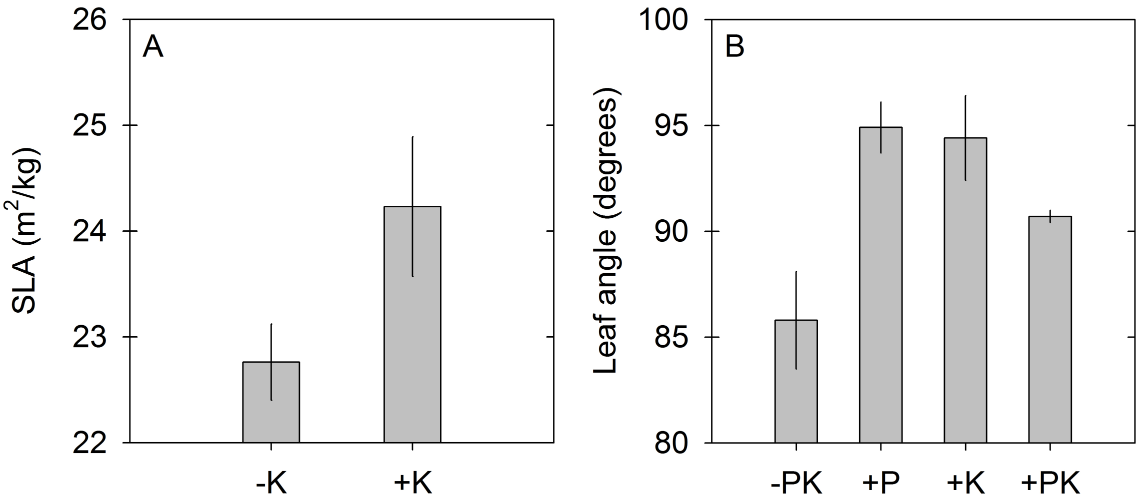

Figure 3.6. Significant main effect of potassium (K) for **A** specific leaf area (SLA) and **B** significant interaction of P × K for leaf angle. Lianas and tree seedlings are pooled and represented by L and T, respectively. Panel A represents a significant main effect of K, where treatments without K (control: C, nitrogen: N, phosphorus: P, and NP) and treatments with K (K, NK, PK, and NPK) are pooled (*N* = 16 plots). Panel B represents a significant P × K interaction where treatments without P or K (C and N), P treatments (P and NP), K treatments (K and NK) and treatments with both P and K (PK and NPK) are pooled (*N* = 8 plots). Bars represent means (± 1 SE).

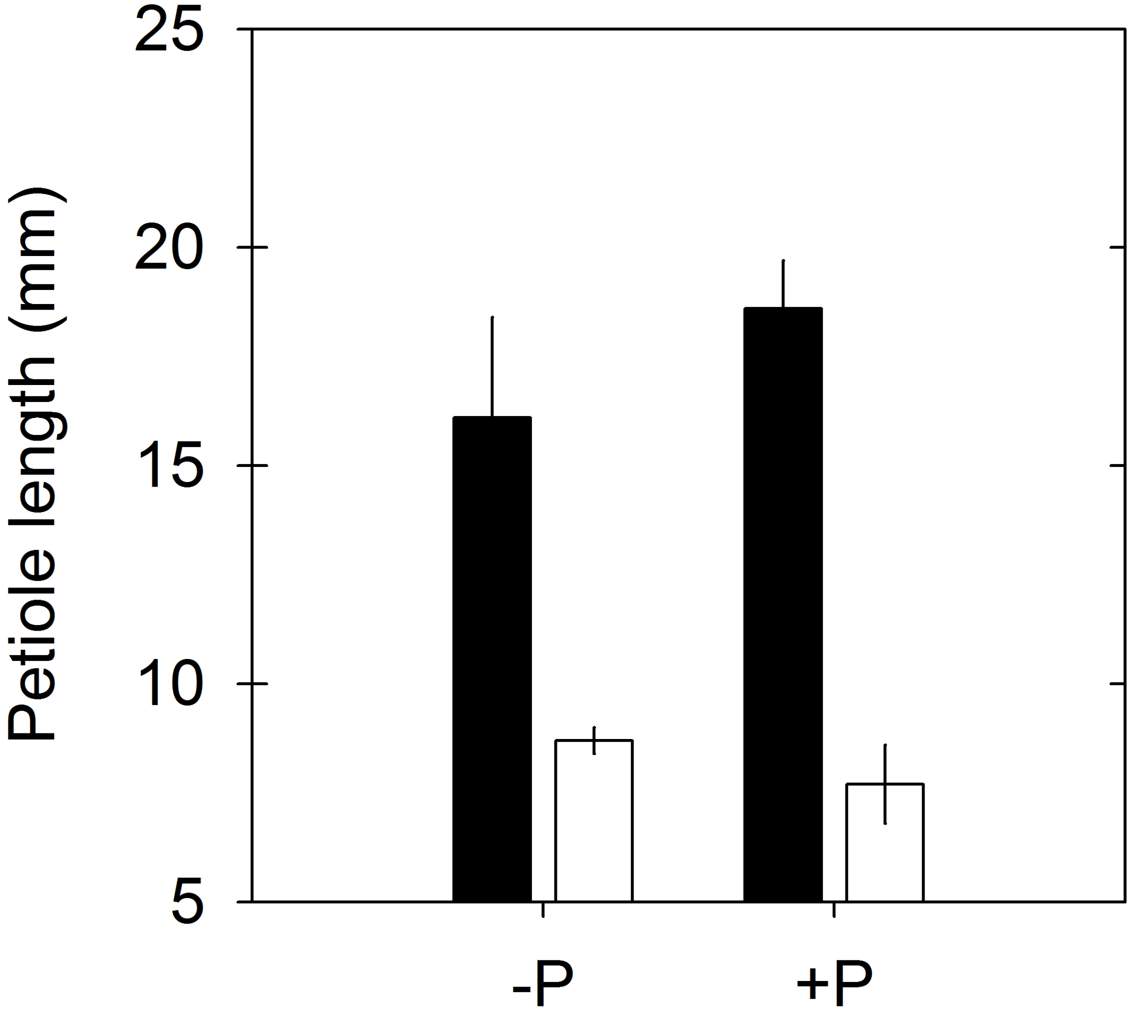

Figure 3.7. Significant interaction of phosphorus (P) × growth form for petiole length. Lianas and trees are represented by L and black bars, and T and open bars, respectively. Treatments without P (control: C, nitrogen: N, potassium: K, and NK) and treatments with P (P and PK, NP and NPK) are pooled by growth form (*N* = 16 plots). Bars represent means (± 1 SE).

Chapter 4: Are lianas fundamentally different from trees in key photosynthetic and leaf traits? A phylogenetic and ecological evaluation

Abstract

Lianas and trees are the two most dominant growth form in tropical forests and there is now compelling evidence that lianas are increasing in abundance throughout the Neotropics, potentially displacing trees. Moreover, recent evidence suggests that climate change may favor lianas over trees because lianas are putatively characterized by highly efficient leaves with low leaf mass area (LMA) and high rates of photosynthesis. What remains unknown is the degree to which lianas are fundamentally different from trees in terms of physiology and leaf traits. Here, we test the hypothesis that differences in leaf and photosynthetic traits between trees versus lianas are due to unique traits associated with their climbing habit rather than due to relatedness. To test this, we compared leaf and photosynthetic traits between trees and lianas using a large, phylogenetically diverse dataset (1115 species from 141 plant families) using multiple statistical approaches. We found that lianas had both substantially higher rates of photosynthesis (A_{mass}) and respiration (R_{area} and R_{mass}), as well as foliar phosphorous (P_{area}) due to inherent differences between the contrasting growth forms. Surprisingly, a suite of traits thought to characterize lianas as distinct from trees did not differ once we accounted for relatedness. These

included leaf lifespan (LL), leaf mass per unit area (LMA), foliar nitrogen (N_{area} and N_{mass}), and partial pressure of CO_2 between atmosphere and intercellular space (c_a-c_i). These results run counter to previous conclusions that traits such as leaf mass per unit area and foliar nitrogen are inherent characteristics that distinguish the liana habit from trees. Nonetheless, lianas as a growth form have much higher rates of photosynthesis, and this key trait alone may partially underlie observed increases in liana abundance throughout the Neotropics. Our findings also predict that lianas will thrive under predicted changes in precipitation (e.g., reduce dry season precipitation) and increases in CO_2.

Introduction

Lianas (woody vines) are a growth form that characterize tropical forests and evidence is accumulating that lianas are increasing in abundance relative to trees in the Neotropics (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright, S.J. et al. 2004, Chave et al. 2008, Foster et al. 2008, Schnitzer and Bongers 2011, Yorke et al. 2013, Schnitzer 2015). An explanation for this increase may be that lianas have superior physiological performance versus trees for key ecophysiological traits that very early in ontogeny (Pasquini et al. 2015). Lianas also differ from trees in patterns of biomass allocation likely because they rely on other vegetation as trellises to reach the canopy whereas trees rely on support from their trunk. These differences allow lianas to invest proportionally more resources into leaves and roots versus trees (Putz 1983, Suzuki 1987, Castellanos et al. 1989, Niklas 1994, Gerwing and Farias 2000, Hättenschwiler 2002, Santiago and Wright 2007). In addition, studies to date provide evidence that lianas and trees contrast in photosynthetic and leaf traits; in particular, adult lianas appear to have greater specific leaf area (SLA), higher photosynthetic rates (A_{mass}), greater mass-based leaf nitrogen and phosphorus (N_{mass} and P_{mass}), while trees have greater area-based leaf nitrogen and phosphorus (N_{area} and P_{area}) (Salzer et al. 2006, Cai et al. 2009, Zhu and Cao 2009, Han et al. 2010, Zhu and Cao 2010, Asner and Martin 2012, Santiago et al. 2015). Pasquini et al. (2015) demonstrated that these ecophysiological differences, as well as morphological differences, occur very early ontogenetically even before lianas reach a trellis.

While there is a growing consensus that lianas contrast both morphologically and physiologically from trees, too few comparisons have been made to draw firm conclusions and most findings are limited to a few major tropical regions (primarily Panama and China). Asner and Martin (2012) compared leaf traits between 778 lianas and 6496 trees and found that lianas showed lower leaf mass area (LMA), higher mass-based nitrogen and phosphorus (N_{mass} and P_{mass}), but lower area-based nitrogen and phosphorus (N_{area} and P_{area}), compared to trees. Their study and others neglected the degree to which phylogenetic relationships account for observed morphological or physiological differences. The most rigorous comparative studies require a phylogenetic approach (Cavender-Bares et al. 2012). The lack of a phylogenetic approach when comparing trees versus lianas is especially significant because lianas have evolved independently many times (Gentry and Dodson 1987). Indeed, they occur in 133 plant families, occur in monocots and dicots, as well as gymnosperms and angiosperms, and climbers occur in most major lineages of Mesangiosperms (Isnard and Feild 2015).

Here, we compare photosynthetic and leaf traits of canopy-level trees and lianas using a large and diverse dataset of 1115 species from 141 plant families from Asia, the Americas, Australia, and Europe. We used standard comparisons as well as two phylogenetically based approaches to determine to what degree differences in leaf and photosynthetic traits between lianas and trees are explained by their climbing habit versus relatedness. The two phylogenetically based approaches have different assumptions; thus when in agreement, they provide a rigorous evaluation of the degree to which lianas fundamentally differ from trees. Overall, if lianas are fundamentally different from trees in critical morphological and physiological traits then this will: (1) Provide a potential mechanistic basis for why lianas are increasing in abundance throughout the Neotropics, (2) Predict that lianas will likely increase pantropically, and (3) Suggest that tropical forests worldwide will store substantially less carbon because lianas competitively displace shade-tolerant tree species (Schnitzer and Carson 2010, Schnitzer et al. 2014).

Materials and Methods

Collection of trait data

We used the Glopnet database to obtain trait data (Wright, I.J. et al. 2004) for 839 species of trees and lianas (823 trees and 16 lianas from 123 plant families). Because Glopnet was heavily weighted towards tree species we conducted an extensive literature search and added an additional 276 taxa (142 trees and 134 lianas, 18 additional plant families; Appendix D: Table D1) resulting in 1115 individual species with 965 trees and 150 lianas. These taxa belonged to 141 different plant families and included 6 gymnosperm families. We used only measures from canopy-level trees and lianas occurring in natural forests or, in a few cases, botanical gardens. We excluded lianas and trees growing in glasshouses, pots, or manipulative field experiments. We evaluated a broad suite of 15 critical plant performance traits (Table 4.1). We calculated photosynthetic nitrogen and phosphorus use efficiencies (PNUE and PPUE) from these data as:

$$\mathrm{PNUE} = \frac{A_{\mathrm{area}}}{\mathrm{N}_{\mathrm{area}}}$$

$$\mathrm{PPUE} = \frac{A_{\mathrm{area}}}{\mathrm{P}_{\mathrm{area}}}$$

Tree construction

We constructed a large phylogenetic tree using Phylomatic (www.phylodiversity.net/phylomatic/phylomatic.html) with the angiosperm consensus tree (Davies et al. 2004) as the base tree and altered it to reflect the most recent consensus tree from the Angiosperm Phylogeny Project (Stevens 2012). Resulting polytomies within the tree were then resolved using published phylogenies, when available for inter-familial relationships (Soltis et al. 2011) and intra-familial relationships (Appendix E: Table E1). We used Mesquite to manipulate the tree (v. 2.75; Maddison and Maddison 2011). For maximally resolved tree see Appendix F, for conservatively resolved tree see Appendix G.

Data analyses

Trait data were compared between trees and lianas using three multiple regression models with the Regressionv2 program for Matlab (Garland et al. 2005, Lavin et al. 2008): ordinary least squares (OLS), phylogenetic generalized least squares (PGLS), and Orstein-Uhlenbeck process (OU). The OLS is a conventional, non-phylogenetic, least squares model where no hierarchical structure is assumed in the phylogenetic tree (star phylogeny). The PGLS is a least squares model using the constructed phylogeny. The OU process model is a regression where the residuals are modeled has having evolved by an OU process (a stochastic process related to Brownian motion). The OU process is used to mimic stabilizing selection on the constructed phylogenetic tree, and can be either an intermediate between a star phylogeny and the constructed phylogeny, or be more hierarchical than the constructed tree (Garland et al. 2005). All phylogenetic comparisons were performed on both the maximally and conservatively resolved phylogenetic trees, and on trees with branch lengths (BL) equal to one or with arbitrary BL (Pagel 1992). Analyses were performed on log and square-root transformed data to meet assumptions of normality.

We used model selection to determine the most parsimonious model from the three methods of regression (OLS, PGLS and OU), two trees (Con and Max), and BL=1 versus arbitrary BL using Akaike Information Criterion (AIC). The model yielding the lowest AIC value for a given trial is considered to be the best match to the data.

To investigate to what extent relatedness is responsible for differences in traits between trees and lianas, the phylogenetic signal of each trait was calculated using the PHYSIG_LL program for Matlab following Blomberg et al. (2003), which calculates the *K*-statistic, randomization tests for phylogenetic signal based on mean squared error (2000 permutations), likelihood of trait evolution based on the phylogenetic tree, and comparison of an assumed model of Brownian motion trait evolution versus the likelihood of a star phylogeny. The *K*-statistics were calculated using the most parsimonious phylogenetic tree, BL, and phylogenetic model based on the AIC values (see above). The PHYSIG_LL program prunes the specified phylogenetic tree to remove taxa showing missing values for a given trait without re-adjusting BL.

To control for type I error (α-error), in multiple comparisons, we used false discovery rate (FDR) corrections to adjust significant *P*-values (Benjamini and Hochberg 1995). These FDR-corrected *P*-values are reported in Figs. 4.1 and 4.2, and Tables 4.1 and 4.2.

Results

Non-phylogenetic comparisons

Non-phylogenetic (OLS) comparisons between trees and lianas showed significant differences in nine of the fourteen traits. For photosynthetic traits, lianas exhibited 39% greater A_{mass}, 320% greater R_{area}, and 42% greater R_{mass} than trees (Table 4.1, Fig. 4.1A-C). Trees showed 241% greater c_a-c_i than lianas (Table 4.1, Fig. 4.1D). There were no significant differences between lianas and trees for A_{area} or g_s (Table 4.1). For leaf traits, lianas exhibited 43% greater $\mathrm{N_{mass}}$ than trees (Table 4.1, Fig. 4.2A). Trees had 100% greater LL, 69% greater LMA, 10% greater $\mathrm{N_{area}}$, and 46% greater $\mathrm{P_{area}}$ than lianas (Table 4.1, Fig. 4.2B-E). Lianas and trees did not differ in $\mathrm{P_{mass}}$ or nutrient use efficiencies (PNUE and PPUE; Table 4.1).

Phylogenetic comparisons

We used AIC values to determine which of the phylogenetic regression models was a best match to our data. The OU model was the best match for all of the traits, except for R_{area} (Table 4.1; Appendix H: Table H1). Additionally, the phylogenetic OU model results yielded identical significant differences in traits between trees and lianas as the non-phylogenetic (OLS) models (Table 4.1). However, traits did differ in which phylogenetic tree was a best fit to the data. The maximally resolved tree with BL=1 was the best fit for A_{mass}, A_{area}, and PNUE, and with arbitrary BL for c_a-c_i and $\mathrm{P_{mass}}$ (Table 4.1). The more conservatively resolved tree with BL=1 was the best fit for g_s, LL, LMA, $\mathrm{N_{area}}$, $\mathrm{N_{mass}}$, and $\mathrm{P_{area}}$, and with arbitrary BL for PPUE and R_{mass} (Table 4.1). R_{area} was best modeled by the non-phylogenetic (OLS) model, but of the phylogenetic models, OU was the best fit with all trees and BLs being equally parsimonious (Table 4.1). Overall, these results mean that our dual approach came to the same conclusion, providing us with confidence in these findings.

Phylogenetic signal

We found significant phylogenetic signal for half (7) of the fourteen traits (*K*-statistic, Table 4.2). For photosynthetic traits, only c_a-c_i and g_s, showed significant phylogenetic signal (Table 4.2). For leaf traits, LL, LMA, N_{area}, N_{mass}, and P_{mass} showed significant phylogenetic signal (Table 4.2). Since, R_{area} was best modeled non-phylogenetically and all of the tree/BL combinations were of equally good fit, *K*-statistics ranged from 0.19-0.25 with *P*-values of 0.0145-0.0690 depending on the tree and BL (Appendix I: Table I1). For R_{area}, averages were reported for *K*, *K*-star, and *P*-value (Table 4.2). We found no significant phylogenetic signal for either of the nutrient use efficiencies (PNUE and PPUE; Table 4.2).

Synthesis of phylogenetic comparisons and phylogenetic signal

When results of phylogenetic comparisons are combined with phylogenetic signal we found that we could categorize the photosynthetic and leaf traits into three categories: (1) Traits that differed significantly between trees and lianas, and showed significant phylogenetic signal. These traits were considered to be due to relatedness; (2) Traits that differed significantly between trees and lianas, but did not have significant phylogenetic signal. These traits were considered to be due to differences between growth forms; and (3) Traits that did not significantly differ between trees and lianas (Table 4.3).

Discussion

We demonstrate unequivocally that key traits are unique to lianas. Specifically, lianas had much higher rates of photosynthesis (A_{mass}), respiration (R_{area} and R_{mass}) and lower P_{area} compared to trees. Our phylogenetic analyses demonstrate that these differences are not due to relatedness and thus are inherent to the liana growth form. Counter to our expectations, differences between lianas and trees for a suite of key traits including c_a-c_i, LL, LMA, N_{area}, and N_{mass} were different between lianas and trees, however these differences were due to relatedness (cf., Asner and Martin 2012). To our knowledge, this is the first study to clearly identify traits that are inherently unique to the liana habit.

Numerous traits were thought to differ between lianas and trees. For example, low LMA (or its inverse, high specific leaf area: SLA) has often been identified as a characteristic trait of lianas (Zhu and Cao 2009, Han et al. 2010, Asner and Martin 2012, Santiago et al. 2015), however, our results do not support this conclusion. Similarly, lianas have been characterized as having high foliar tissue nutrients concentrations. (Cai and Bongers 2007, Kusumoto and Enoki 2008, Zhu and Cao 2009, 2010, Asner and Martin 2012). Nonetheless, we found no support for this for N_{area} and N_{mass} or P_{mass}. We also found no evidence that lianas uniquely had shorter leaf life spans or differences c_a-c_i. Our results suggest that lianas may have a wide range of life-history strategies, just like trees, that reflect their evolutionary histories as much as their climbing habit. This may be due to how many times the liana habit evolved in so many different families. It is important to point out, however, that we did not evaluate any plant defensive traits or belowground traits. There is strong evidence that lianas have deeper roots than trees (Restom and Nepstad 2004, Schnitzer 2005) and future work may well show that lianescence differs in key traits we did not measure.

There is now compelling evidence that lianas are increasing in abundance relative to shade-tolerant trees and are superior competitors and thus can displace trees in forests throughout the world, but especially the Neotropics (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright, S.J. et al. 2004, Chave et al. 2008, Foster et al. 2008, Schnitzer and Carson 2010, Schnitzer and Bongers 2011, Yorke et al. 2013, Schnitzer 2015). Moreover, lianas outperform tress for a suite of physiological traits regardless of soil nutrient supply rates (Pasquini et al. 2015). Our findings here suggest that if physiological traits underlie the increase in lianas that appear to be occurring, then higher rates of photosynthesis and respiration may be partially responsible. Photosynthesis was 39% greater in lianas versus trees and this fundamental difference may underlie increases in liana abundances and explain why lianas compete so well with trees in highly disturbed sites (Laurance et al. 2001, Schnitzer and Carson 2001, Granados and Körner 2002).

CO_2 is likely to continue to increase with climate change, and in the Neotropics novel patterns of precipitation are likely to exacerbate the degree of drought stress region-wide (Holm et al. 2017). Because lianas typically have deeper roots than trees (Restom and Nepstad 2004, Schnitzer 2005) and thus access to water unavailable to trees, lianas are poised to take advantage of lower precipitation and higher CO_2 compared to trees (De Guzman et al. 2016). Thus, lower rainfall combined with higher CO_2 would likely favor lianas over trees (reviewed by Schnitzer 2015). Projected increases in liana abundance will be coupled with decreases in forest-wide carbon storage because lianas that replace trees only replace 24% of the tree biomass (Schnitzer et al. 2014). In addition, and counter to convention, lianas did not have higher tissue nutrient concentration, and for phosphorus, had *lower* tissue concentration. Trees had higher (46%) P_{area} compared to lianas that was attributable to the liana habit. A potential consequence of lower foliar phosphorus may be lower rates of enemy damage. Experiments have demonstrated that higher tissue phosphorus makes woody species more vulnerable to herbivores (Santiago et al. 2012, Cárate-Tandalla et al. 2015, Griffin et al. 2017). Thus, lianas appear to be drought-tolerant, have high rates of photosynthesis, and at least for phosphorus, lower tissue nutrient concentrations; thus a suite of traits that may benefit them as rising atmospheric CO_2 continues to alter global climate.

Literature Cited

Asner, G.P., and R.E. Martin. 2012. Contrasting leaf chemical traits in tropical lianas and trees: Implications for future forest composition. Ecology Letters 15:1001-1007.

Benítez-Malvido, J., and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. Conservation Biology 17:389-400.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B (Methodological) 57:289-300.

Blomberg, S.P., T. Garland, Jr., and A.R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57:717-745.

Cai, Z.-Q., and F. Bongers. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. Journal of Tropical Ecology 23:115-118.

Cai, Z.-Q., S.A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. Oecologia 161:25-33.

Cárate-Tandalla, D., C. Leuschner, and J. Homeier. 2015. Performance of seedlings of a shade-tolerant tropical tree species after moderate addition of N and P. Frontiers in Earth Science 2015:75.

Castellanos, A.E., H.A. Mooney, S.H. Bullock, C. Jones, and R. Robichaux. 1989. Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. Biotropica 21:41-49.

Cavender-Bares, J., D.D. Ackerly, and K.H. Kozak. 2012. Integrating ecology and phylogenetics: The footprint of history in modern-day communities. Ecology 93:S1-S3.

Chave, J., J. Olivier, F. Bongers, P. Châtelet, P.-M. Forget, P. van der Meer, N. Norden, B. Riéra, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. Journal of Tropical Ecology 24:355-366.

Davies, T.J., T.G. Barraclough, M.W. Chase, P.S. Soltis, D.E. Soltis, and V. Savolainen. 2004. Darwin's abominable mystery: Insights from a supertree of the angiosperms. Proceedings of the National Academy of Sciences of the United States of America 101:1904-1909.

De Guzman, M.E., L.S. Santiago, S.A. Schnitzer, and L. Álvarez-Casino. 2016. Trade-offs between water transport capacity and drought resistance in neotropical canopy liana and tree species. Tree Physiology doi: 10.1093/treephys/tpw086.

Foster, J.R., P.A. Townsend, and C.E. Zganjar. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. Remote Sensing of Environment 112:2104-2117.

Garland, T., Jr., A.F. Bennett, and E.L. Rezende. 2005. Phylogenetic approaches in comparative physiology. Journal of Experimental Biology 208:3015-3035.

Gentry, A.H., and C.H. Dodson. 1987. Diversity and biogeography of Neotropical vascular epiphytes. Annals of the Missouri Botanical Garden 74:205-233.

Gerwing, J.J., and D.L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. Journal of Tropical Ecology 16:327-335.

Granados, J., and C. Körner. 2002. In deep shade, elevated CO_2 increases vigor of tropical climbing plants. Global Change Biology 8:1109-1117.

Griffin, E.A., S.J. Wright, P.J. Morin, and W.P. Carson. 2017. Pervasive interactions between foliar microbes and soil nutrients mediate leaf production and herbivore damage in a tropical forest. New Phytologist 216:99-112.

Han, L., L.J. Xie, K.J. Dai, Q. Yang, and Z.Q. Cai. 2010. Contrasting leaf characteristics of trees and lianas in secondary and mature forests in southwestern China. Photosynthetica 48:559-566.

Hättenschwiler, S. 2002. Liana seedling growth in response to fertilisation in a neotropical forest understorey. Basic and Applied Ecology 3:135-143.

Holm, J.A., L.M. Kueppers, and J.Q. Chambers. 2017. Novel tropical forests: Response to Global Change. New Phytologist 213:988-992.

Isnard, S., and T.S. Feild. 2015. The evolution of angiosperm lianescence: A perspective from xylem structure-function. Pages 221-238 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of Lianas. Wiley-Blackwell Publishing, Oxford, UK.

Kusumoto, B., and T. Enoki. 2008. Contribution of a liana species, *Mucuna macrocarpa* Wall., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest. Journal of Forest Research 13:35-42.

Laurance, W.F., D. Pérez-Salicrup, P. Delamônica, P.M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T.E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105-116.

Lavin, S.R., A.R. Karasov, K.M. Middleton, and T. Garland, Jr. 2008. Morphometrics of the avian small intestine, compared with non-flying mammals: A phylogenetic approach. Physiological and Biochemical Zoology 81:526-550.

Maddison, W.P., and D.R. Maddison. 2011. Mesquite: A modular program for evolutionary analysis.

Niklas, K.J. 1994. Comparisons among biomass allocation and spatial distribution patterns of some vine, pteridophyte, and gymnosperm shoots. American Journal of Botany 81:1416-1421.

Pagel, M.D. 1992. A methods for the analysis of comparative data. Journal of Theoretical Biology 156:431-442.

Pasquini, S.C., S.J. Wright, and L.S. Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. Ecology 96:1866-1876.

Phillips, O.L., R.V. Martínez, L. Arroyo, T.B. Baker, T. Killeen, S.L. Lewis, Y. Malhi, A.M. Mendoza, D. Neill, P.N. Vargas, M. Alexiades, C. Cerón, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418:770-774.

Putz, F.E. 1983. Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro Basin, Venezuela. Biotropica 15:185-189.

Restom, T.G., and D.C. Nepstad. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. Forest Ecology and Management 190:109-118.

Salzer, J., S. Matezki, and M. Kazda. 2006. Nutritional differences and leaf acclimation of climbing plants and the associated vegetation in different types of an Andean montane rainforest. Oecologia 147:417-425.

Santiago, L.S., S.C. Pasquini, and M.E. De Guzman. 2015. Physiological implications of the liana growth form. Pages 288-298 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of lianas. Wiley-Blackwell Publishing, Oxford, UK.

Santiago, L.S., and S.J. Wright. 2007. Leaf functional traits of tropical forest plants in relation to growth form. Functional Ecology 21:19-27.

Santiago, L.S., S.J. Wright, K.E. Harms, J.B. Yavitt, C. Korine, M.N. Garcia, and B.L. Turner. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. Journal of Ecology 100:309-316.

Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166:262-276.

Schnitzer, S.A. 2015. Increasing liana abundance in Neotropical forests: Causes and consequences. Pages 451-464 *in* S.A. Schnitzer, F. Bongers, R.J. Burnham, and F.E. Putz, editors. Ecology of lianas. Wiley-Blackwell, Oxford, UK.

Schnitzer, S.A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters 14:397-406.

Schnitzer, S.A., and W.P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913-919.

Schnitzer, S.A., and W.P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849-857.

Schnitzer, S.A., G. van der Heijden, J. Mascaro, and W.P. Carson. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. Ecology 95:3008-3017.

Soltis, D.E., S.A. Smith, N. Cellinese, K.J. Wurdack, D.C. Tank, S.F. Brockington, N.F. Refulio-Rodriguez, J.B. Walker, M.J. Moore, B.S. Carlsward, C.D. Bell, M. Latvis, S. Crawley, C. Black, D. Diouf, Z.X. Xi, C.A. Rushworth, M.A. Gitzendanner, K.J. Sytsma, Y.L. Qiu, K.W. Hilu, C.C. Davis, M.J. Sanderson, R.S. Beaman, R.G. Olmstead, W.S. Judd, M.J. Donoghue, and P.S. Soltis. 2011. Angiosperm phylogeny: 17 genes, 640 taxa. American Journal of Botany 98:704-730.

Stevens, P.F. 2012. Angiosperm phylogeny website, version 12, July 2012. Missouri Botanical Garden, St. Louis, MO, USA.

Suzuki, W. 1987. Comparative ecology of *Rubus* species (Roseaceae). I. Ecological distribution and life history characteristics of three species, *R. palmatus* var. *coptophyllus*, *R. microhyllus* and *R. crataegifolius*. Plant Species Biology 2:85-100.

Wright, I.J., P.B. Reich, M. Westoby, D.D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, F.S. Chapin, III, J.H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P.K. Groom, J. Gulias, K. Hikosaka, B.B. Lamont, T. Lee, W. Lee, C. Lusk, J.J. Midgley, M.-L. Navas, Ü. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. Pyankov, C. Roumet, S.C. Thomas, M.G. Tjoelker, E.J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.

Wright, S.J., O. Calderdón, A. Hernandéz, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484-489.

Yorke, S.R., S.A. Schnitzer, J. Mascaro, S.G. Letcher, and W.P. Carson. 2013. Increasing liana abundance and basal area in a tropical forest: The contribution of long-distance clonal colonization. Biotropica 45:317-324.

Zhu, S.-D., and K.-F. Cao. 2009. Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. Plant Ecology 204:295-304.

Zhu, S.-D., and K.-F. Cao. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rainforest in southwestern China. Oecologia 163:591-599.

Table 4.1. Liana and tree leaf and photosynthetic trait means, results of ordinary least square (OLS) comparisons, phylogenetic comparisons, and phylogenetic models used.

	Lianas		Trees		OLS		Phylogenetic		Model			
Trait	Mean ± 1 SE	*N*	Mean ± 1 SE	*N*	*T*	*P*	*T*	*P*	Tree	Branch	Model	*df*
A_{area}	9.69 ± 0.54	56	9.82 ± 0.21	383	-0.1143	0.9091	0.2411	0.8096	Max	1	OU	437
A_{mass}	132.27 ± 10.56	53	95.04 ± 2.98	355	4.1166	**<0.0001**	4.4993	**<0.0001**	Max	1	OU	406
c_a-c_i	25.93 ± 5.20	11	88.38 ± 4.00	155	-4.9331	**<0.0001**	5.8601	**<0.0001**	Max	Arb	OU	164
g_s	223.44 ± 21.61	24	320.69 ± 21.06	198	-1.3457	0.1798	1.1675	0.2443	Con	1	OU	220
LL	8.64 ± 1.23	15	17.26 ± 0.98	319	-2.3263	**0.0206**	2.4469	**0.0149**	Con	1	OU	332
LMA	71.44 ± 3.82	144	120.49 ± 2.57	854	-10.8958	**<0.0001**	10.3201	**<0.0001**	Con	1	OU	996
N_{area}	1.85 ± 0.10	98	2.03 ± 0.30	740	-2.2768	**0.0231**	2.2501	**0.0247**	Con	1	OU	836
N_{mass}	2.69 ± 0.08	98	1.88 ± 0.30	799	9.5819	**<0.0001**	9.5008	**<0.0001**	Con	1	OU	895
P_{area}	0.10 ± 0.01	57	0.15 ± 0.01	394	-3.6396	**0.0003**	3.2490	**0.0012**	Con	1	OU	449
P_{mass}	0.14 ± 0.01	57	0.14 ± 0.004	391	1.3586	0.1750	1.4111	0.1589	Max	Arb	OU	446
PNUE	78.11 ± 6.39	46	76.31 ± 2.15	321	0.1529	0.8785	0.6649	0.5065	Max	1	OU	365
PPUE	3.15 ± 0.23	37	2.80 ± 0.17	136	1.6347	0.1040	1.4048	0.1619	Con	Arb	OU	171
R_{area}	10.75 ± 1.69	27	2.56 ± 0.34	137	6.3189	**<0.0001**	6.3189	**<0.0001**	*	*	OU	162
R_{mass}	14.06 ± 1.23	26	9.88 ± 0.53	134	3.4038	**0.0008**	2.7975	**0.0058**	Con	Arb	OU	158

Values in boldface are statistically significant *T*-statistics using the false discovery rate (FDR) corrected *P*-value ($P < 0.0321$). Photosynthesis per unit area (A_{area}; μmol m^{-2} s^{-1}) and per unit mass (A_{mass}; μmol g^{-1} s-^{1}), CO_2 difference between atmosphere and intercellular space (c_a-c_i; ppm), stomatal conductance (g_s; mmol m^{-1} s^{-1}), leaf lifespan (LL; mo^{-1}), leaf mass area (LMA; g/m^2), leaf nitrogen and phosphorus per unit area (N_{area} and P_{area}; g/m^2) and per unit mass (N_{mass} and P_{mass}; %), photosynthetic nitrogen and phosphorus use efficiencies (PNUE and PPUE; μmol mol N^{-1} s^{-1}), respiration per unit area (R_{area}; μmol m^{-1} s^{-1}) and per unit mass (R_{mass}; nmol g^{-1} s^{-1}), conservatively resolved tree (Con), maximally resolved tree (Max), branch length (Branch), Pagel's arbitrary branch length (Arb, Pagel 1992), Ornstein-Uhlenbeck model (OU) and degrees of freedom (*df*). *For R_{area}, the OLS model was the best fit. Of the phylogenetic models, all four OU models were equally parsimonious (Appendix H: Table H1).

Table 4.2. Phylogenetic signal (*K*-statistics) of leaf and photosynthetic traits of lianas and trees using Ornstein-Uhlenbeck model (OU).

Trait	*N*	*K*	*K*-star	*P*
A_{area}	439	0.7795	0.8332	0.2890
A_{mass}	408	0.7282	0.8017	0.2535
c_a-c_i	166	0.9581	0.9828	**0.0175**
g_s	222	1.0074	0.9899	**0.0135**
LL	334	0.9212	0.9507	**<0.0001**
LMA	998	0.8920	0.9237	**<0.0001**
$\mathrm{N_{area}}$	838	0.9668	0.9541	**0.0100**
$\mathrm{N_{mass}}$	897	0.8409	0.9133	**<0.0001**
$\mathrm{P_{area}}$	451	0.8758	0.9059	0.1850
$\mathrm{P_{mass}}$	448	0.9926	0.9989	**<0.0001**
PNUE	367	0.8585	0.8664	0.1050
PPUE	173	0.9750	0.9864	0.1105
R_{area}	164	0.2114*	0.2788*	0.0500*
R_{mass}	160	0.9331	0.9578	0.0705

Values in boldface are statistically significant *K*-statistics using the false discovery rate (FDR) corrected *P*-value ($P < 0.0250$). Photosynthesis per unit area (A_{area}; μmol $\mathrm{m^{-2}\ s^{-1}}$) and per unit mass (A_{mass}; μmol $\mathrm{g^{-1}}$ s-^{1}), $\mathrm{CO_2}$ difference between atmosphere and intercellular space (c_a-c_i; ppm), stomatal conductance (g_s; mmol $\mathrm{m^{-1}\ s^{-1}}$), leaf lifespan (LL; $\mathrm{mo^{-1}}$), leaf mass area (LMA; $\mathrm{g/m^2}$), leaf nitrogen and phosphorus per unit area ($\mathrm{N_{area}}$ and $\mathrm{P_{area}}$; $\mathrm{g/m^2}$) and per unit mass ($\mathrm{N_{mass}}$ and $\mathrm{P_{mass}}$; %), photosynthetic nitrogen and phosphorus use efficiencies (PNUE and PPUE; μmol mol $\mathrm{N^{-1}\ s^{-1}}$), respiration per unit area (R_{area}; μmol $\mathrm{m^{-1}\ s^{-1}}$) and per unit mass (R_{mass}; nmol $\mathrm{g^{-1}\ s^{-1}}$). *For R_{area}, all four OU models were equally parsimonious (Appendix I, Table I1) and values for *K*, *K*-star and *P*-values are averages of values for the four OU models.

Table 4.3. Summary of results phylogenetically based comparisons combined with phylogenetic signal (K) for leaf and photosynthetic and traits.

Trait	Differences between lianas and trees due to?
CO_2 difference between atmosphere and intercellular space (c_a-c_i)	Relatedness
Leaf lifespan (LL)	Relatedness
Leaf mass per unit area (LMA)	Relatedness
Foliar nitrogen (N_{area})	Relatedness
Foliar nitrogen (N_{mass})	Relatedness
Photosynthesis (A_{mass})	Growth form
Foliar phosphorus (P_{area})	Growth form
Respiration (R_{area})	Growth form
Respiration (R_{mass})	Growth form
Photosynthesis (A_{area})	NS
Stomatal conductance (g_s)	NS
Foliar phosphorus (P_{mass})	NS
Photosynthetic nitrogen use efficiency (PNUE)	NS
Photosynthetic phosphorus use efficiency (PPUE)	NS

Photosynthesis per unit area (A_{area}; μmol m^{-2} s^{-1}) and per unit mass (A_{mass}; μmol g^{-1} s-^{1}), CO_2 difference between atmosphere and intercellular space (c_a-c_i; ppm), stomatal conductance (g_s; mmol m^{-1} s^{-1}), leaf lifespan (LL; mo^{-1}), leaf mass area (LMA; g/m^2), leaf nitrogen and phosphorus per unit area (N_{area} and P_{area}; g/m^2) and per unit mass (N_{mass} and P_{mass}; %), photosynthetic nitrogen and phosphorus use efficiencies (PNUE and PPUE; μmol mol N^{-1} s^{-1}), respiration per unit area (R_{area}; μmol m^{-1} s^{-1}) and per unit mass (R_{mass}; nmol g^{-1} s^{-1}).

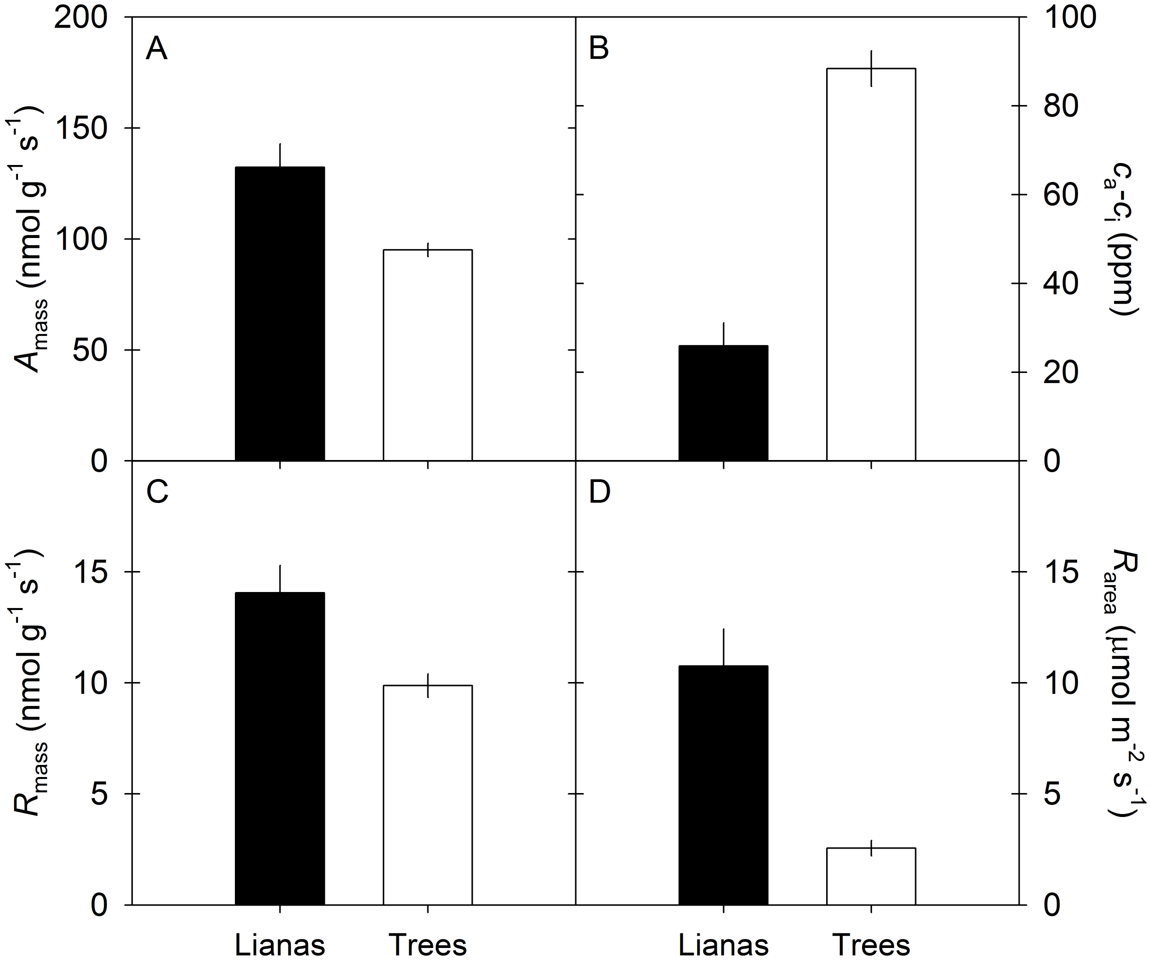

Figure 4.1. Significant differences in photosynthetic traits between trees and lianas using the false discovery rate (FDR) corrected *P*-value ($P < 0.0321$) for **A** maximum photosynthetic rate per leaf mass (A_{mass}), **B** CO_2 difference between atmosphere and intercellular space (c_a-c_i), and **C** respiration rate per leaf mass (R_{mass}) and **D** per leaf area (R_{area}). Bars represent means (± 1 SE).

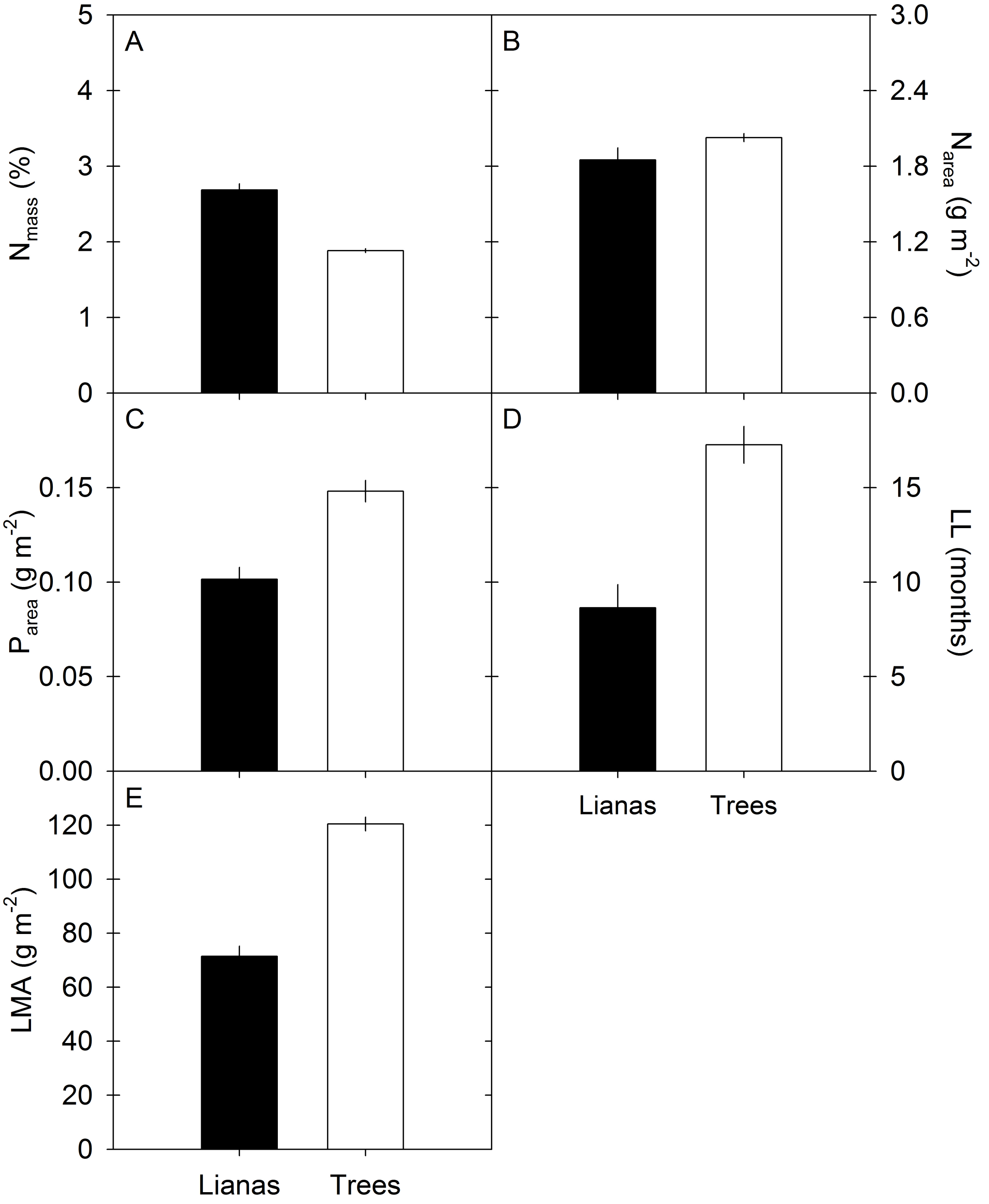

Figure 4.2. Significant differences in leaf traits between trees and lianas using the false discovery rate (FDR) corrected *P*-value ($P < 0.0321$) for **A** foliar nitrogen per leaf mass (N_{mass}) and **B** per leaf area (N_{area}), **C** foliar phosphorus per leaf area (P_{area}), **D** leaf lifespan (LL), and **E** leaf lass per area (LMA). Bars represent means (± 1 SE).

Chapter 5: Conclusion

In the preceding three chapters I addressed the following questions: 1) Do resources other than light limit the growth of woody species, and if so which resources or resource combinations? 2) Are lianas limited more, in terms of photosynthetic processes, by soil resources than trees? and 3) Is there a phylogenetic signal to physiological trait differences between trees and lianas? In Chapter 2, I tested the hypothesis that tree seedlings are limited by nutrients in very low light. The results demonstrated that even in low light environments, understory plants still respond to increases in nutrient availability with increases in photosynthetic processes. Seedlings of *Alseis blackiana* increased maximum photosynthetic CO_2 assimilation rate with nitrogen (N) addition, stomatal conductance with phosphorus (P) addition and with P and potassium (K) in combination, quantum yield of photosystem II with K addition, maximum electron transport rate trended 9% greater with N addition, and saturating photosynthetically active radiation with N addition. Additionally, foliar N concentration increased by 20% with N addition. Foliar P concentration increased by 78% with P addition and decreased by 14% with N addition. Foliar K increased by 8% with K addition. Foliar $\delta^{13}C$ showed no significant responses, and foliar $\delta^{15}N$ decreased strongly with N addition (Pasquini and Santiago 2012). These results demonstrate that increased nutrient availability can enhance woody species performance, even in very low light, which challenges idea that plants only respond to increases in the most limiting resource (Leibig’s Law of the Minimum)

In Chapter 3, I tested the hypothesis that nutrients limit photosynthetic physiology of liana seedlings to a greater degree than tree seedlings. The findings showed that lianas and trees were similarly limited by nutrients, but seedlings of lianas always out-performed seedlings of trees regardless of nutrient addition. Lianas always showed significantly greater photosynthetic capacity, quenching, and saturating light levels compared to trees across all treatments. We found little evidence for nutrient × growth form interactions, indicating that lianas are not more nutrient limited than trees. Tree and liana seedlings also differed in morphology early in ontogeny (Pasquini et al. 2015). Thus there is no evidence that nutrient loading is a mechanism favoring lianas. Our finding that lianas always outperform trees may partially underlie the increase in liana abundance in Neotropical forests.

In Chapter 4, I tested the hypothesis that differences in photosynthetic and leaf traits between trees and lianas are due to inherent differences between the climbing and self-supporting habit versus relatedness. These results demonstrate that important traits did not significantly differ once relatedness was taken into account. Based on the phylogenetic analyses, lianas had greater mass-based photosynthesis and respiration (both area- and mass-based) than trees. These trait differences were found to differ due to inherent properties of the growth-forms. Surprisingly, a suite of traits thought to epitomize the liana growth-form as distinct from trees were found to be due to relatedness rather than the liana habit (low leaf mass per unit area [LMA] and high foliar N). These results run counter to previous conclusions that traits such as LMA and foliar N are inherent characteristics that distinguish the liana habit from trees. Regardless of whether differences between lianas and trees are due to relatedness or growth-form, lianas have much higher rates of photosynthesis, and this key trait alone may partially underlie observed increases in liana abundance throughout the Neotropics. Our findings also predict that lianas will thrive under predicted changes in precipitation (e.g., reduce dry season precipitation) and increases in CO_2.

These three empirical chapters provide important findings that help to form a mechanistic basis for the increase in liana abundance in tropical forests worldwide. This is significant because as lianas replace trees, they store much less carbon in their biomass, and this may have important implications to global carbon budgets.

Literature Cited

Pasquini, S.C., and L.S. Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 168:311-319.

Pasquini, S.C., S.J. Wright, and L.S. Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: Results from a long-term fertilization experiment. Ecology 96:1866-1876.

Appendix A: Map of study site

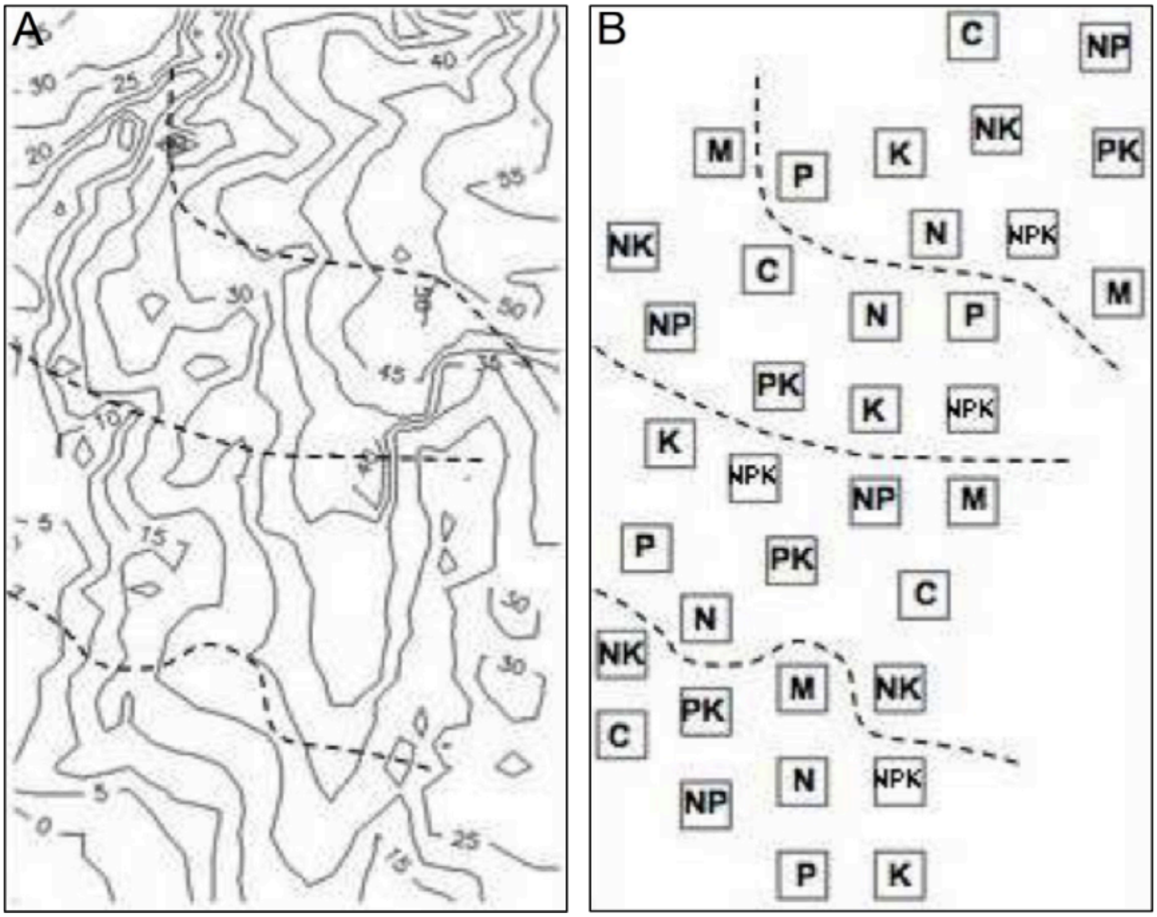

Figure A1. Map of study area showing **A** the topography of the site and **B** the placement of nutrient treatments within the site. Treatments are represented by the combination of added nutrients: nitrogen (N), phosphorus (P), and potassium (K). Control plots (C) and micronutrient plots (M) are also shown. The micronutrient treatment is not addressed in this study. The dashed lines separate four replicates of the full-factorial NPK experiment.

Appendix B: Mixed linear model results comparing model that includes species and model that does not include species

Table B1. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on leaf physiological traits for liana and tree seedlings using statistical model that includes species nested within growth form.

	ETR_{max}		q_P		PFD_{sat}	
Factor	*F*	*P*	*F*	*P*	*F*	*P*
Rep	0.00		0.00		0.00	
Block (Rep)	1.10		0.25		0.57	
Form	13.50	**0.0003**	18.28	**<0.0001**	11.87	**0.0006**
Species (Form)	4.77	**<0.0001**	3.70	**<0.0001**	4.38	**<0.0001**
T_{total}	10.65	**0.0012**	26.20	**<0.0001**	10.41	**0.0014**
N	0.05	0.8286	0.86	0.3554	0.00	0.9483
P	6.25	**0.0129**	4.57	0.0333	0.91	0.3415
K	0.31	0.5808	1.73	0.1896	0.60	0.4405
N × P	3.70	0.0552	1.43	0.2328	2.21	0.1382
N × K	0.16	0.6880	0.00	0.9682	0.17	0.6790
P × K	7.13	**0.0079**	6.51	**0.0112**	6.28	**0.0126**
N × Form	2.19	0.1400	1.04	0.3081	0.62	0.4305
P × Form	0.22	0.6397	1.71	0.1915	0.08	0.7753
K × Form	0.00	0.9657	0.22	0.6398	0.01	0.9068
AIC	1201.6		467.5		1720.9	
Sample size	394		393		394	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0237$). Total light transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), maximum electron transport rate (ETR_{max}; mmol m^{-2} s^{-1}), photochemical quenching (q_P; unitless), and saturating photon flux density (PFD_{sat}; mmol m^{-2} s^{-1}). Rep and Block (Rep) are random effects, and all other variables are fixed effects.

Table B2. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on morphological traits for liana and tree seedlings using statistical model that includes species nested within growth form.

	Relative crown depth		Relative crown area		Leaf thickness		Leaf angle	
Factor	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Rep	3.54		2.72		0.76		21.20	
Block (Rep)	1.63		3.65		0.78		2.44	
Form	20.61	**<0.0001**	5.14	0.0239	21.09	**<0.0001**	7.46	**0.0066**
Species (Form)	8.43	**<0.0001**	11.52	**<0.0001**	12.88	**<0.0001**	3.72	**<0.0001**
T_{total}	0.01	0.9091	0.07	0.7875	0.18	0.6700	1.10	0.2957
N	0.56	0.4538	0.86	0.3545	0.41	0.5213	1.20	0.2738
P	2.98	0.0850	1.04	0.3086	1.24	0.2669	4.01	0.0461
K	0.47	0.4931	0.29	0.5922	0.04	0.8357	4.17	0.0420
N × P	0.15	0.6973	1.14	0.2865	0.13	0.7166	1.37	0.2418
N × K	0.01	0.9349	0.43	0.5107	2.23	0.1359	0.89	0.3454
P × K	0.03	0.8540	0.02	0.8786	1.22	0.2692	14.14	**0.0002**
N × Form	2.14	0.1443	3.37	0.0673	0.01	0.9326	0.09	0.7639
P × Form	0.19	0.6641	2.93	0.0879	0.17	0.6836	1.82	0.1787
K × Form	0.01	0.9091	1.67	0.1972	0.01	0.9299	0.00	0.9715
AIC	72.1		1136.2		-1389.4		3063.9	
Sample size	388		390		381		382	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0115$). Total light transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), relative crown depth (cm), relative crown area (cm^2), leaf thickness (mm), and leaf angle (degrees from main stem). Rep and Block (Rep) are random effects, and all other variables are fixed effects.

Table B3. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on morphological traits for liana and tree seedlings using statistical model that includes species nested within growth form.

	Internode length		Petiole length		SLA	
Factor	*F*	*P*	*F*	*P*	*F*	*P*
Rep	2.74		2.17		0.50	
Block (Rep)	0.58		0.86		0.43	
Form	9.05	**0.0028**	471.37	**<0.0001**	28.84	**<0.0001**
Species (Form)	10.40	**<0.0001**	189.29	**<0.0001**	54.27	**<0.0001**
T_{total}	0.17	0.6846	1.01	0.3155	6.73	**0.0099**
N	0.60	0.4407	1.62	0.2033	0.75	0.3867
P	0.69	0.4054	0.00	0.9743	0.22	0.6409
K	0.57	0.4519	1.33	0.2500	11.73	**0.0007**
N × P	4.78	0.0295	0.02	0.8915	1.73	0.1889
N × K	0.42	0.5180	3.10	0.0793	1.86	0.1729
P × K	0.02	0.8828	0.61	0.4362	1.92	0.1663
N × Form	0.00	0.9454	0.04	0.8491	0.46	0.4990
P × Form	0.30	0.5860	6.87	**0.0091**	2.76	0.0975
K × Form	1.51	0.2206	2.89	0.0901	3.28	0.0710
AIC	2625.9		692.3		2239.7	
Sample size	383		390		393	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0115$). Total light transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), internode length (mm), petiole length (mm), and specific leaf area (SLA; m^2/kg). Rep and Block (Rep) are random effects, and all other variables are fixed effects.

Table B4. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on physiological traits for liana and tree seedlings using statistical model that does not include species.

	ETR_{max}		q_P		PFD_{sat}	
Factor	*F*	*P*	*F*	*P*	*F*	*P*
Rep	0.00		0.00		0.00	
Block (Rep)	1.15		0.27		0.62	
Form	13.04	**0.0003**	17.47	**<0.0001**	11.83	**0.0006**
T_{total}	7.12	**0.0080**	20.91	**<0.0001**	7.33	**0.0071**
N	0.06	0.8108	0.80	0.3715	0.00	0.9906
P	6.20	**0.0132**	4.27	0.0394	0.99	0.3197
K	0.20	0.6576	1.31	0.2538	0.40	0.5260
N × P	3.81	0.0516	1.42	0.2337	2.33	0.1280
N × K	0.17	0.6811	0.03	0.8702	0.21	0.6444
P × K	6.19	**0.0133**	5.52	0.0193	5.76	0.0169
N × Form	2.24	0.1354	1.23	0.2688	0.71	0.4002
P × Form	0.12	0.7330	1.42	0.2344	0.05	0.8171
K × Form	0.01	0.9315	0.29	0.5879	0.08	0.7725
AIC	1240.2		473.3		1771.2	
Sample size	394		393		394	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0144$). Total light transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), maximum electron transport rate (ETR_{max}; mmol m^{-2} s^{-1}), photochemical quenching (q_P; unitless). and saturating photon flux density (PFD_{sat}; mmol m^{-2} s^{-1}). Rep and Block (Rep) are random effects, and all other variables are fixed effects.

Table B5. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects o morphological traits for liana and tree seedlings using statistical model that does not include species.

	Relative crown depth		Relative crown area		Leaf thickness		Leaf angle	
Factor	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Rep	3.17		2.13		0.66		19.42	
Block (Rep)	1.53		2.89		0.50		2.03	
Form	18.01	**<0.0001**	4.59	0.0329	16.66	**<0.0001**	6.83	0.0093
T_{total}	0.14	0.7102	0.00	0.9490	0.87	0.3509	0.72	0.3979
N	0.46	0.4996	0.73	0.3921	0.25	0.6192	1.15	0.2834
P	1.93	0.1658	1.32	0.2509	1.33	0.2504	4.19	0.0413
K	0.49	0.4862	0.13	0.7137	0.10	0.7504	3.88	0.0496
N × P	0.04	0.8377	0.85	0.3565	0.01	0.9392	0.94	0.3330
N × K	0.04	0.8501	0.19	0.6599	1.26	0.2624	0.79	0.3739
P × K	0.00	0.9757	0.01	0.9032	0.49	0.4848	13.78	**0.0002**
N × Form	1.10	0.2954	2.52	0.1135	0.00	0.9893	0.05	0.8181
P × Form	0.14	0.7079	2.93	0.0879	0.12	0.7263	1.81	0.1793
K × Form	0.00	0.9668	1.20	0.2738	0.00	0.9698	0.01	0.9166
AIC	107.5		1227.0		-1358.1		3147.6	
Sample size	388		390		381		382	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0033$). Total ligh transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), relative crown dept (cm), relative crown area (cm^2), leaf thickness (mm), and leaf angle (degrees from main stem). Rep and Block (Rep are random effects, and all other variables are fixed effects.

Table B6. Mixed linear model results of nitrogen (N), phosphorus (P), and potassium (K) fertilization effects on morphological traits for liana and tree seedlings using statistical model that does not include species.

	Internode length		Petiole length		SLA	
Factor	*F*	*P*	*F*	*P*	*F*	*P*
Rep	2.15		0.48		0.29	
Block (Rep)	0.51		0.23		0.21	
Form	8.07	0.0048	71.01	**<0.0001**	11.63	**0.0007**
T_{total}	0.11	0.7439	0.98	0.3219	2.84	0.0927
N	0.85	0.3569	0.09	0.7627	0.39	0.5351
P	0.82	0.3672	0.07	0.7844	0.06	0.8046
K	0.22	0.6396	0.16	0.6872	5.22	0.0229
N × P	2.97	0.0854	0.13	0.7182	0.65	0.4219
N × K	0.17	0.6813	0.32	0.5731	0.86	0.3532
P × K	0.00	0.9590	0.47	0.4937	0.89	0.3472
N × Form	0.02	0.8815	0.01	0.9361	0.10	0.7480
P × Form	0.37	0.5432	1.46	0.2278	1.38	0.2405
K × Form	0.68	0.4111	0.45	0.5015	0.97	0.3242
AIC	2757.9		1367.9		2619.3	
Sample size	383		390		393	

Data presented are *F*-statistics for fixed and random effects and *P*-values for fixed effects. Bolded values are statistically significant *P*-values using False Discovery Rate (FDR) corrected *P*-value ($P < 0.0033$). Total light transmission (T_{total}; proportion of above-canopy ambient), Akaike Information Criterion (AIC), internode length (mm), petiole length (mm), and specific leaf area (SLA; m^2/kg). Rep and Block (Rep) are random effects, and all other variables are fixed effects.

Appendix C: Average of total transmission of light above liana and tree seedlings used in study, and responses to full-factorial nitrogen, phosphorus, and potassium addition compared to unfertilized controls for physiological and morphological traits

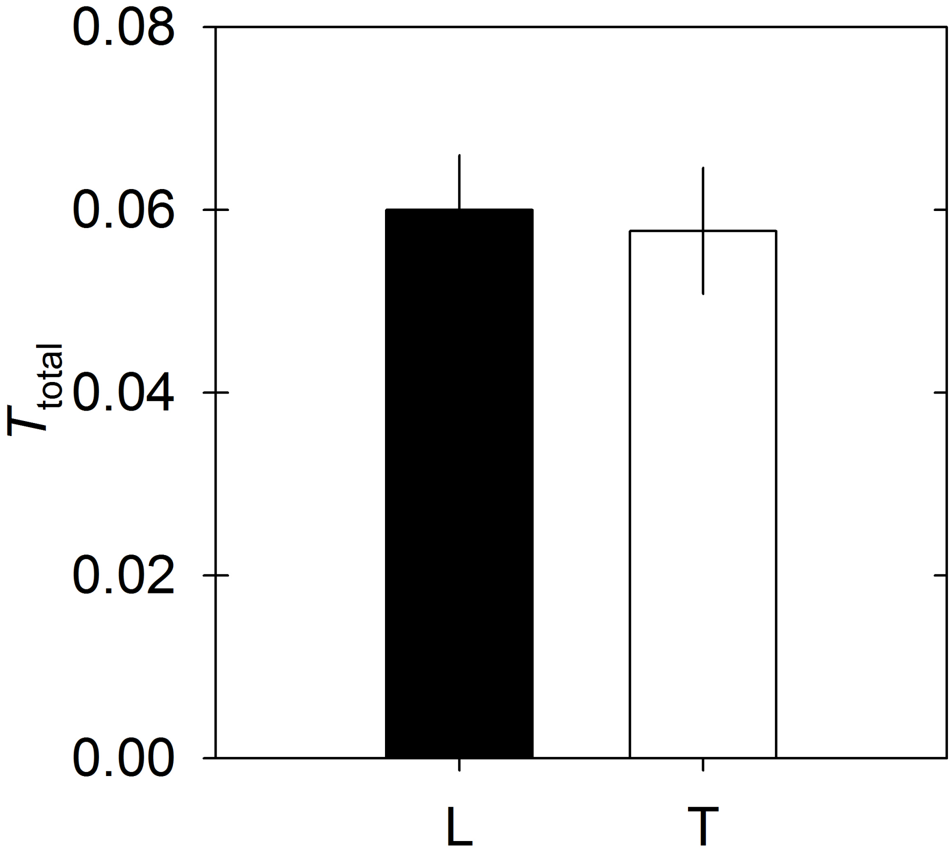

Figure C1. Total transmission of light (T_{total}; proportion of above-canopy ambient) over study seedlings. Liana and tree seedlings are represented by L and black bars, and T and open bars, respectively. All nutrient treatments and controls are pooled. Bars represent means (± 1 SE). There was no significant difference between T_{total} for liana and tree seedlings ($T_{395} = 0.60$, $P = 0.44$).

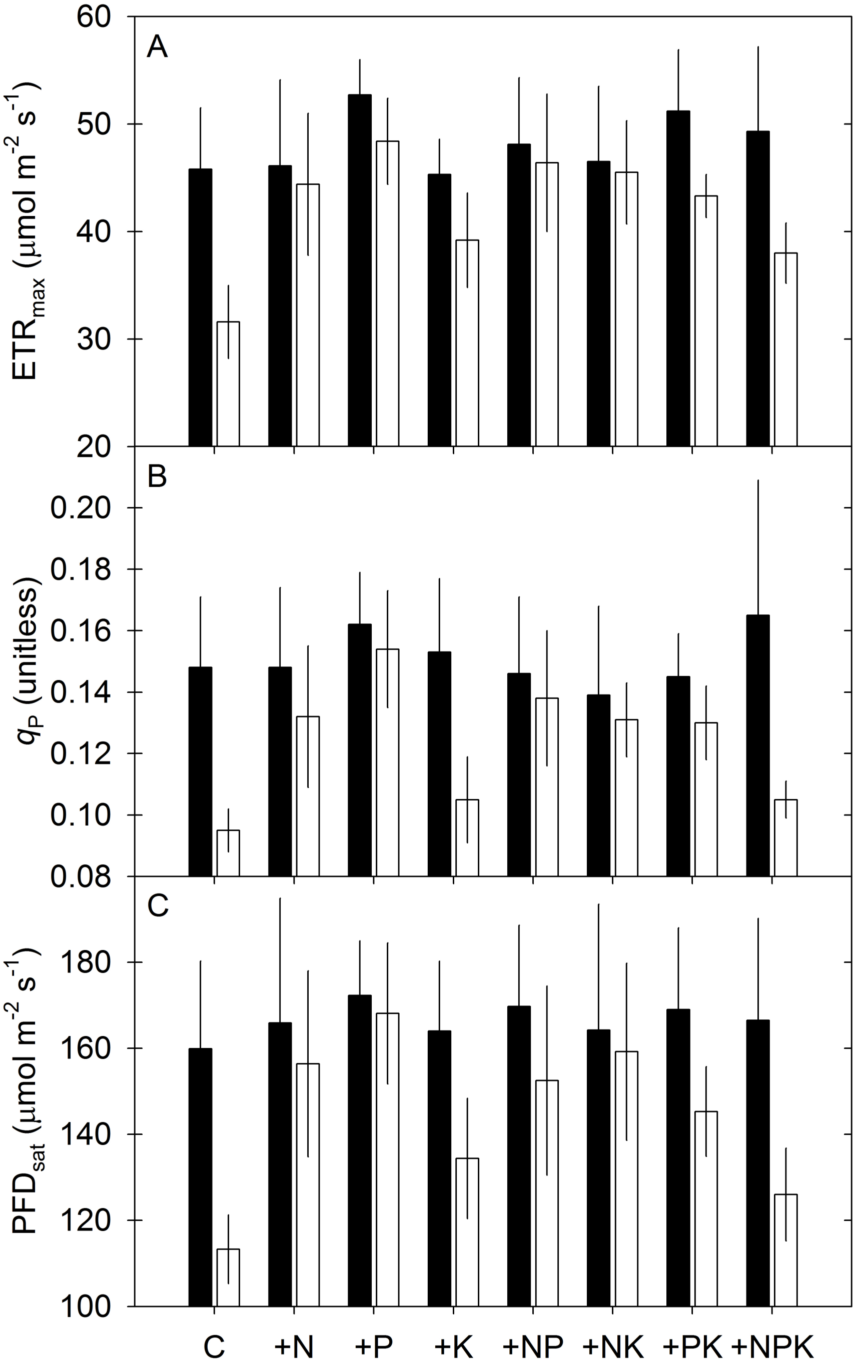

Figure C2. Responses of liana and tree seedlings to full-factorial nitrogen (N), phosphorus (P), potassium (K) addition, and unfertilized controls (C) for **A** maximum electron transport rate (ETR$_{max}$), **B** photochemical quenching coefficient (q_P), and **C** saturating photon flux density (PFD$_{sat}$). Liana and tree seedlings are represented by black bars and open bars, respectively. Bars represent means (± 1 SE; *N* = 4 plots per treatment).

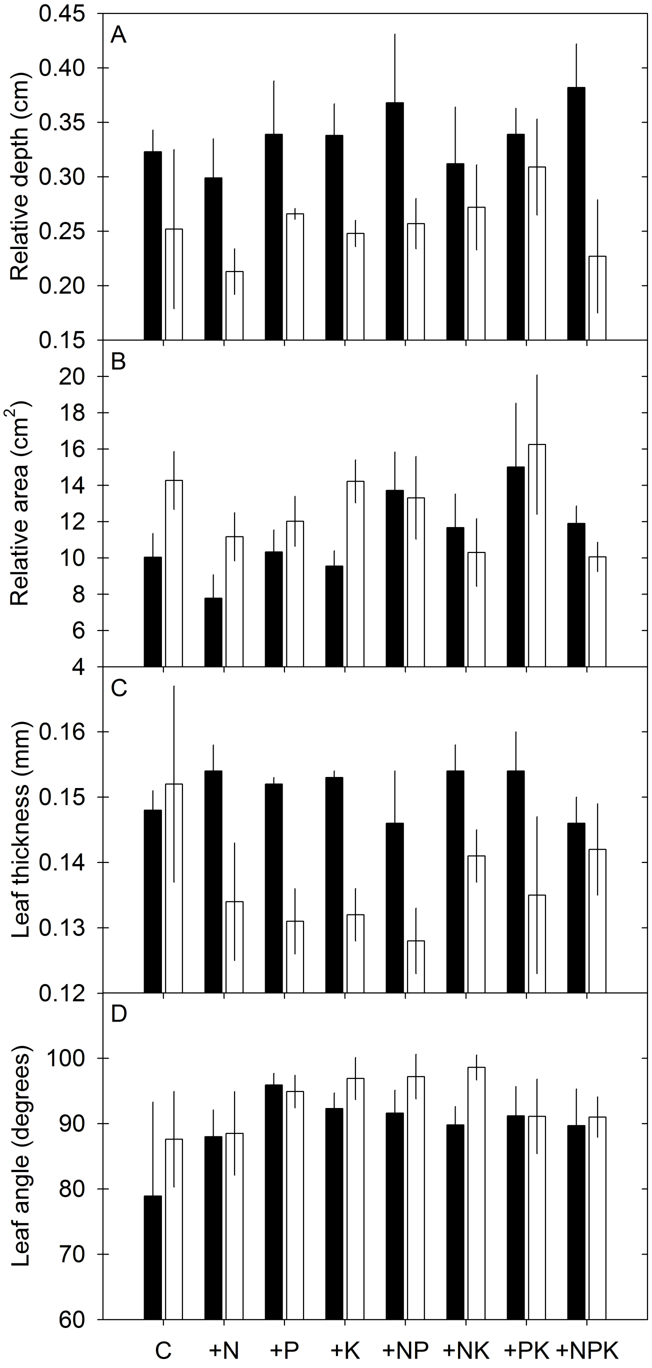

Figure C3. Responses of liana and tree seedlings to full-factorial nitrogen (N), phosphorus (P), potassium (K) addition, and unfertilized controls (C) for **A** relative crown depth, **B** relative crown area, **C** leaf thickness, and **D** leaf angle. Liana and tree seedlings are represented by black bars and open bars, respectively. Bars represent means (± 1 SE; *N* = 4 plots per treatment).

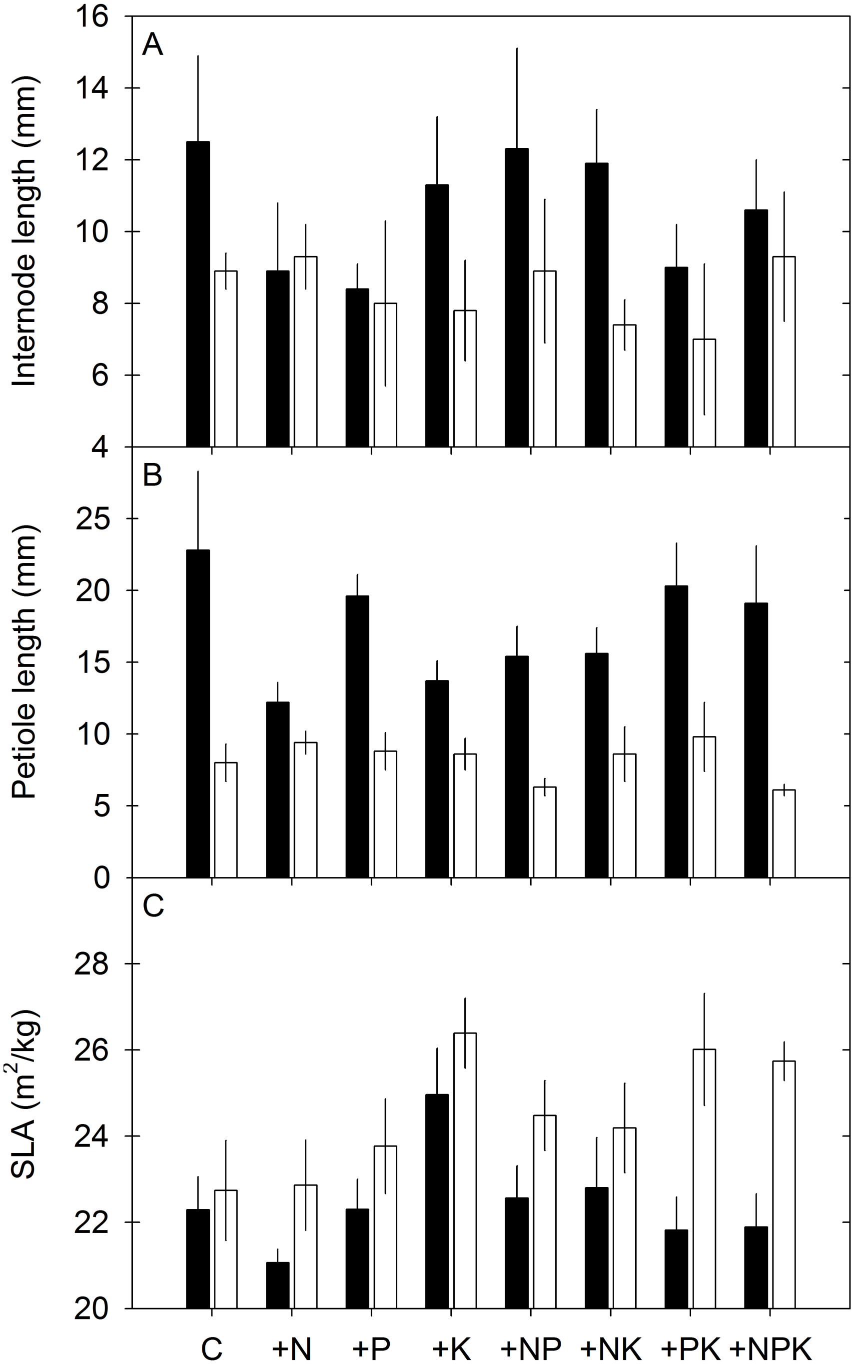

Figure C4. Responses of liana and tree seedlings to full-factorial nitrogen (N), phosphorus (P), potassium (K) addition, and unfertilized controls (C) for **A** internode length, **B** petiole length, and **C** specific leaf area (SLA). Liana and tree seedlings are represented by black bars and open bars, respectively. Bars represent means (± 1 SE; *N* = 4 plots per treatment).

Appendix D: Additions to Glopnet database used in phylogenetic analyses

Table D1. Additional sources of liana and tree leaf and photosynthetic data for phylogenetic analyses.

Reference	Location	Lianas	Trees
Avalos and Mulkey (1999)	Parque Natural Metropolitano, Panama	1	0
Avalos et al. (2007)	Parque Natural Metropolitano, Panama	2	0
Cai (2007)	Xishuangbanna Tropical Botanical Garden, Yunnan, China	29	30
Cai and Bongers (2007)	Xishuangbanna Tropical Botanical Garden, Yunnan, China	12	14
Castellanos et al. (1989)	Estación de Biología Chamela of the Universidad Nacional Autonoma de México, Jalisco, Mexico	28	0
Domingues (2005)	Floresta Nacional do Tapajós, Brazil	6	29
Feild and Balun (2008)	Kau Wildlife Preserve, Papua New Guinea	4	9
Hegarty (1988)	Brisbane Forest Park, Queensland, Australia	39	42
Ichihashi et al. (2010)	Yakushidake National Forest, Japan	5	0
Küppers (1984)	Northern Bavaria, Germany	1	0
Molina-Freaner and Tinoco-Ojanguren (1997)	Centro Ecológico de Sonora, Sonora, Mexico	4	0
Salzer et al. (2004)	Rio San Francisco valley, Ecuador	4	26
Santiago and Wright (2007)	Parque Nacional San Lorenzo, Panama	11	21
Selaya and Anten (2008)	Bolivian Amazon, Bolivia	1	7
Tay et al. (2007)	Pasoh Forest Reserve, Malaysia	1	0
Zhu and Cao (2010)	Xishuangbanna Tropical Botanical Garden, Yunnan, China	7	5
Zotz and Winter (1993)	Barro Colorado Island, Panama	1	4
Totals		**156**	**187**

Literature Cited

Avalos, G., and S.S. Mulkey. 1999. Photosynthetic acclimation of the liana *Stigmaphyllon lindenianum* to light changes in a tropical dry forest canopy. Oecologia 120:475-484.

Avalos, G., S.S. Mulkey, K. Kitajima, and S.J. Wright. 2007. Colonization strategies of two liana species in a tropical dry forest canopy. Biotropica 39:393-399.

Cai, Z.-Q. 2007. Lianas and trees in tropical forests in south China. Ph.D. Dissertation. Wageningen University, Wageningen, The Netherlands.

Cai, Z.-Q., and F. Bongers. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. Journal of Tropical Ecology 23:115-118.

Castellanos, A.E., H.A. Mooney, S.H. Bullock, C. Jones, and R. Robichaux. 1989. Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. Biotropica 21:41-49.

Domingues, T.F. 2005. Photosynthetic gas exchange in eastern Amazonian primary rain forest and pasture ecosystems. Ph.D. Dissertation. University of Utah, Salt Lake City, UT, USA.

Feild, T.S., and L. Balun. 2008. Xylem hydraulic and photosynthetic function of *Gnetum* (Gnetales) species from Papua New Guinea. New Phytologist 177:665-675.

Hegarty, E.E. 1988. Canopy dynamics of lianes and trees in subtropical rainforest. Ph.D. Dissertation. University of Queensland, St. Lucia, Australia.

Ichihashi, R., H. Nagashima, and M. Tateno. 2010. Biomass allocation between extension- and leaf display-oriented shoots in relation to habitat differentiation among five deciduous liana species in a Japanese cool-temperate forest. Plant Ecology 211:181-190.

Küppers, M. 1984. Carbon relations and competition between woody species in a central European hedgerow II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. Oecologia 64:344-354.

Molina-Freaner, F., and C. Tinoco-Ojanguren. 1997. Vines of a desert plant community in central Senora, México. Biotropica 29:46-56.

Salzer, J. 2004. Structural and nutritional differences between climbers and their supporting trees in a montane rainforest in South-Ecuador. Dr. rer. nat. Dissertation. University of Ulm, Ulm, Germany.

Santiago, L.S., and S.J. Wright. 2007. Leaf functional traits of tropical forest plants in relation to growth form. Functional Ecology 21:19-27.

Selaya, N.G., and N.P.R. Anten. 2008. Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. Functional Ecology 22:30-39.

Tay, A.C., A.M. Abdullah, M. Awang, and A. Furukawa. 2007. Midday depression of photosynthesis in *Enkleia malaccensis*, a woody climber in a tropical rainforest. Photosynthetica 45:189-193.

Zhu, S.-D., and K.-F. Cao. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rainforest in southwestern China. Oecologia 163:591-599.

Zotz, G., and K. Winter. 1993. Short-term photosynthesis measurements predict leaf carbon balance in tropical rain-forest canopy plants. Planta 191:409-412.

Appendix E: Plant families in phylogenetic analyses

Table E1. Plant families included in phylogenetic analyses with numbers of tree and liana species, and references (if any) used to resolve tree.

Family	Code	Trees	Lianas	Total	References
Acanthaceae	AC	1	0	1	
Achariaceae	AH	1	0	1	
Actinidiaceae	AT	0	1	1	
Aextoxicaceae	AX	1	0	1	
Altingiaceae	AL	1	0	1	
Alzateaceae	A2	1	0	1	
Anacardiaceae	AN	21	0	21	Pell (2004), Yi et al. (2004b), Pan et al. (2008)
Annonaceae	AO	13	5	18	Bakker and Gerritsen (1992), Doyle et al. (2004), Mols et al. (2004), Richardson et al. (2004), Pirie et al. (2006), Chatrou et al. (2009), Zhou et al. (2010); L.W. Chatrou *personal communication*
Apocynaceae	AP	13	10	23	Bolzani et al. (1987), Potgieter and Albert (2001), Livshultz et al. (2007), Simoes et al. (2007)
Aquifoliaceae	AQ	6	0	6	Cuénoud et al. (2000), Manen et al. (2002)
Araceae	AR	0	1	1	
Araliaceae	AA	10	1	11	Wen et al. (2001), Yi et al. (2004a), Plunkett et al. (2005), Fiaschi and Plunkett (2011)
Araucariaceae	AU	1	0	1	
Arecaceae	AE	8	1	9	Gunn (2004), Asmussen et al. (2006), Baker et al. (2011)
Aristolochiaceae	A3	0	1	1	
Asteraceae	AS	7	4	11	Goertzen et al. (2003), Panero and Funk (2008)
Atherospermataceae	AM	2	0	2	
Berberidaceae	BE	1	0	1	
Betulaceae	BT	23	0	23	Chen et al. (1999), Yoo and Wen (2002), Chen and Li (2004), Jarvinen et al. (2004), Schenk et al. (2008)
Bignoniaceae	BG	11	8	19	Lohmann (2006), Olmstead et al. (2009)
Bixaceae	BI	2	0	2	
Boraginaceae	BO	6	0	6	Gottschling et al. (2005), Weeks et al. (2010)
Burseraceae	BU	7	0	7	Weeks et al. (2005)

Table E1 (continued)

Family	Code	Trees	Lianas	Total	References
Buxaceae	BX	1	0	1	
Cactaceae	CA	1	0	1	
Calophyllaceae	CL	5	0	5	Gustafsson et al. (2002)
Cannabaceae	CN	6	0	6	Sattarian (2006)
Capparaceae	CP	7	0	7	Stern et al. (1963), Hall et al. (2002), Rankin Rodríguez and Greuter (2004), Hall (2008)
Caprifoliaceae	C7	1	2	3	
Cardiopteridaceae	CR	2	1	3	
Caryocaraceae	CY	1	0	1	
Casuarinaceae	CS	1	0	1	
Celastraceae	CE	6	5	11	Simmons and Hedin (1999), McKenna et al. (2011)
Cercidiphyllaceae	CC	1	0	1	
Chloranthaceae	CH	1	0	1	
Chrysobalanaceae	CB	5	0	5	Chappill (1992)
Clethraceae	CT	2	0	2	
Clusiaceae	CI	7	0	7	Sweeney (2008), Abdullah et al. (2012)
Combretaceae	CO	15	1	16	Maurin et al. (2010)
Connaraceae	C1	1	0	1	
Convolvulaceae	CV	0	4	4	Stefanovic et al. (2002)
Cornaceae	C2	6	0	6	Fan and Xiang (2003), Xiang et al. (2006)
Coulaceae	C3	1	0	1	
Cucurbitaceae	CU	0	4	4	Kocyan et al. (2007)
Cunoniaceae	C4	5	0	5	Bradford and Barnes (2001), Bradford (2002)
Cupressaceae	C5	9	0	9	Gadek et al. (2000), Mao et al. (2010)
Curtisiaceae	C6	1	0	1	
Dilleniaceae	DI	2	1	3	Horn (2009)
Dioscoreaceae	DO	0	1	1	
Dipterocarpaceae	DP	6	0	6	Dayanandan et al. (1999), Kamiya et al. (2005)
Ebenaceae	EB	13	0	13	Duangjai et al. (2009), Geeraerts et al. (2009)
Elaeagnaceae	EL	1	0	1	
Elaeocarpaceae	EA	3	0	3	
Ericaceae	ER	12	0	12	Kron et al. (1999), Hileman et al. (2001), Gillespie and Kron (2010)
Erythroxylaceae	EY	3	0	3	Emche et al. (2011)
Escalloniaceae	ES	1	0	1	

Table E1 (continued)

Family	Code	Trees	Lianas	Total	References
Euphorbiaceae	EU	25	3	28	Wurdack et al. (2005), Kulju et al. (2007), van Ee et al. (2008), Baier et al. (2009), Riina et al. (2009), Sierra et al. (2010)
Eupomatiaceae	EP	1	0	1	
Fabaceae	FA	77	16	93	Zhi (1985), Bruneau (1996), Luckow and Grimes (1997), Hu et al. (2000), Bruneau et al. (2001), Kajita et al. (2001), Pennington et al. (2001), Hao et al. (2003), Herendeen et al. (2003), Luckow et al. (2003), Pardo et al. (2004), Wojciechowski et al. (2004), Schrire et al. (2005), McMahon and Sanderson (2006), Brown et al. (2008), Bruneau et al. (2008), Sinou et al. (2009), Sousa (2009), Bouchenak-Khelladi et al. (2010), Mackinder and Pennington (2011), Trytsman et al. (2011), da Silva et al. (2012), Manzanilla and Bruneau (2012)
Fagaceae	FG	51	0	51	Manos et al. (1999), Ohyama et al. (1999), Manos and Stanford (2001), Manos et al. (2001), Denk (2003), Cavender-Bares et al. (2004), Oh and Manos (2008), Denk and Grimm (2009), Pearse and Hipp (2009), Hipp et al. (2010)
Flagellariaceae	FL	0	1	1	Price (1996), Won and Renner (2006)
Gentianaceae	GE	2	0	2	
Gnetaceae	GN	2	3	5	
Goupiaceae	GO	2	0	2	
Griseliniaceae	GR	1	0	1	
Hamamelidaceae	HA	2	0	2	
Humiriaceae	HU	1	0	1	
Hydrangeaceae	HY	0	1	1	Fan and Xiang (2003)
Hypericaceae	HP	2	0	2	
Icacinaceae	IC	1	1	2	
Ixonanthaceae	IX	1	0	1	
Juglandaceae	JU	9	0	9	Manos and Stone (2001), Aradhya et al. (2007), Manos et al. (2007)
Lamiaceae	LA	5	0	5	Steane et al. (2004), Bendiksby et al. (2011)
Lardizabalaceae	LR	0	1	1	
Lauraceae	LU	25	0	25	Chanderbali et al. (2001), Rohwer et al. (2009)

Table E1 (continued).

Family	Code	Trees	Lianas	Total	References
Lecythidaceae	LE	5	0	5	Mori et al. (2007)
Loganiaceae	LG	4	0	4	Frasier (2008)
Loranthaceae	LO	1	0	1	
Lythraceae	LY	3	0	3	
Magnoliaceae	MA	7	0	7	Azuma et al. (1999), Azuma et al. (2001), Kim et al. (2001)
Malpighiaceae	MP	1	7	8	Davis and Anderson (2010)
Malvaceae	MV	39	1	40	Alverson et al. (1999), Bayer et al. (1999), Whitlock et al. (2001), Tate et al. (2005), Wilkie et al. (2006), Clark (2009), Duarte et al. (2011)
Melastomataceae	ME	15	1	16	Clausing and Renner (2001), Michelangeli et al. (2004), Goldenberg et al. (2008), Amorim et al. (2009)
Meliaceae	ML	14	0	14	Muellner et al. (2003), Muellner et al. (2008), Muellner et al. (2009)
Menispermaceae	MN	0	9	9	Ortiz et al. (2007)
Monimiaceae	MO	2	1	3	Renner (1998)
Moraceae	MR	31	3	34	Datwyler and Weiblen (2004), Rønsted et al. (2008), van Noort and Rasplus (2012)
Myricaceae	MY	3	0	3	Steeves (2011)
Myristicaceae	MI	4	0	4	
Myrtaceae	MT	55	0	55	Hill (2004), van der Merwe et al. (2005), Wilson et al. (2005), Lucas et al. (2007), Ochieng et al. (2007), Biffin et al. (2010), Craven and Biffin (2010), Soh and Parnell (2011), Steane et al. (2011); E. Biffin personal communication
Nothofagaceae	NO	6	0	6	Swenson et al. (2001)
Nyctaginaceae	NY	1	0	1	
Ochnaceae	OC	2	0	2	
Olacaceae	OL	1	1	2	
Oleaceae	OE	16	0	16	Wallander and Albert (2000), Wallander (2008), Besnard et al. (2009)
Passifloraceae	PA	2	4	6	Muschner et al. (2003), Stevens (2012), Tokuoka (2012)
Penaeaceae	PE	1	0	1	

Table E1 (continued).

Family	Code	Trees	Lianas	Total	References
Pennantiaceae	PN	1	0	1	
Pentaphylacaceae	PT	4	0	4	Martínez-Millán et al. (2009)
Phyllanthaceae	PH	15	2	17	Bodegom et al. (2001), Kathriarachchi et al. (2005)
Pinaceae	PI	27	0	27	Eckert and Hall (2006), Ran et al. (2006), Gernandt et al. (2008)
Piperaceae	PP	1	1	2	
Platanaceae	PL	1	0	1	
Poaceae	PO	1	0	1	
Podocarpaceae	PD	10	0	10	Knopf et al. (2012)
Polygalaceae	PG	1	1	2	
Polygonaceae	PY	1	1	2	
Primulaceae	PR	8	2	10	Stahl (1996)
Proteaceae	PC	12	0	12	Mast and Givnish (2002), Barker et al. (2007), Sauquet et al. (2009)
Putranjivaceae	PU	2	0	2	
Ranunculaceae	RA	0	3	3	Miikeda et al. (2006), Xie and Li (2012)
Rhamnaceae	RH	6	3	9	Richardson et al. (2000), Islam and Simmons (2006), Li et al. (2010)
Rhipogonaceae	RI	0	2	2	
Rhizophoraceae	RZ	6	0	6	Setoguchi et al. (1999)
Rosaceae	RO	21	4	25	Alice and Campbell (1999), Potter et al. (2007), Chin et al. (2010), Wang et al. (2011)
Rubiaceae	RU	28	5	33	Persson (1996), Nepokroeff et al. (1999), Paz et al. (1999), Andreasen and Bremer (2000), Faivre and McDade (2001), Bremer and Eriksson (2009), Kainulainen et al. (2010), Manns and Bremer (2010)
Rutaceae	RT	16	0	16	Poon et al. (2007), Trinder-Smith et al. (2007), Groppo et al. (2008), Martyn et al. (2009)
Salicaceae	SA	24	0	24	Eckenwalder (1996), Argus (1997), Chase et al. (2002), Cervera et al. (2005), Williams (2012)
Santalaceae	SN	2	0	2	
Sapindaceae	SP	28	3	31	Suh et al. (2000), Harrington et al. (2005), Li et al. (2006), Renner et al. (2007), Buerki et al. (2009)
Sapotaceae	SO	20	0	20	Bartish et al. (2005), Smedmark et al. (2006), Swenson et al. (2008), Armstrong (2010), Petersen et al. (2012)

Table E1 (continued).

Family	Code	Trees	Lianas	Total	References
Schisandraceae	SC	1	1	2	
Scrophulariaceae	SR	2	0	2	
Simaroubaceae	SI	2	0	2	
Smilacaceae	SM	1	4	5	Chen et al. (2006)
Solanaceae	SL	1	1	2	
Staphyleaceae	ST	2	0	2	
Styracaceae	S1	1	0	1	
Symplocaceae	SY	1	0	1	
Taxaceae	TA	1	0	1	
Theaceae	TH	3	0	3	
Thymelaeaceae	TY	1	1	2	
Ulmaceae	UL	9	0	9	Wiegrefe et al. (1994), Sytsma et al. (2002), Hipp et al. (2008)
Urticaceae	UR	9	0	9	Sytsma et al. (2002), Hadiah et al. (2008)
Verbenaceae	VE	1	1	2	
Violaceae	VI	4	0	4	Tokuoka (2008)
Vitaceae	VT	2	10	12	Rossetto et al. (2002), Wen et al. (2007), Tröndle et al. (2010), Ren et al. (2011)
Vochysiaceae	VO	4	0	4	
Winteraceae	WI	1	0	1	
Xanthorrhoeaceae	XA	0	1	1	
Zygophyllaceae	ZY	2	0	2	

Literature Cited

Abdullah, N.A.P., A.J. Richards, and K. Wolff. 2012. Molecular evidence in identifying parents of *Garcinia mangostana* L. Pertanika Journal of Tropical Agricultural Science 35:257-270.

Alice, L.A., and C.S. Campbell. 1999. Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. American Journal of Botany 86:81-97.

Alverson, W.S., B.A. Whitlock, R. Nyffeler, C. Bayer, and D.A. Baum. 1999. Phylogeny of the core Malvales: Evidence from *ndhF* sequence data. American Journal of Botany 86:1474-1486.

Amorim, A.M., R. Goldenberg, and F.A. Michelangeli. 2009. A new species of *Physeterostemon* (Melastomataceae) from Bahia, Brazil, with notes on the phylogeny of the genus. Systematic Botany 34:324-329.

Andreasen, K., and B. Bremer. 2000. Combined phylogenetic analysis in the Rubiaceae-Ixoroideae: Morphology, nuclear and chloroplast DNA data. American Journal of Botany 87:1731-1748.

Aradhya, M.K., D. Potter, F. Gao, and C.J. Simon. 2007. Molecular phylogeny of *Juglans* (Juglandaceae): A biogeographic perspective. Tree Genetics & Genomes 3:363-378.

Argus, G.W. 1997. Infrageneric classification of *Salix* (Salicaceae) in the New World. Systematic Botany Monographs 52:1-121.

Armstrong, K. 2010. Systematics and biogeography of the pantropical genus *Manilkara* Adans. (Sapotaceae). Ph.D. Dissertation. University of Edinburgh & Royal Botanic Garden Edinburgh, Edinburgh, UK.

Asmussen, C.B., J. Dransfield, V. Deickmann, A.S. Barfod, J.C. Pintaud, and W.J. Baker. 2006. A new subfamily classification of the palm family (Arecaceae): Evidence from plastid DNA phylogeny. Botanical Journal of the Linnean Society 151:15-38.

Azuma, H., J.G. Garcia-Franco, V. Rico-Gray, and L.B. Thien. 2001. Molecular phylogeny of the Magnoliaceae: The biogeography of tropical and temperate disjunctions. American Journal of Botany 88:2275-2285.

Azuma, H., L.B. Thien, and S. Kawano. 1999. Molecular phylogeny of *Magnolia* (Magnoliaceae) inferred from cpDNA sequences and evolutionary divergence of the floral scents. Journal of Plant Research 112:291-306.

Baier, C., D. Guicking, K. Prinz, C. Fey-Wagner, T. Wohrmann, K. Weising, T. Debener, S. Schie, and F.R. Blattner. 2009. Isolation and characterization of 11 new microsatellite markers for *Macaranga* (Euphorbiaceae). Molecular Ecology Resources 9:1049-1052.

Baker, W.J., M.V. Norup, J.J. Clarkson, T.L.P. Couvreur, J.L. Dowe, C.E. Lewis, J.C. Pintaud, V. Savolainen, T. Wilmot, and M.W. Chase. 2011. Phylogenetic relationships among arecoid palms (Arecaceae: Arecoideae). Annals of Botany 108:1417-1432.

Bakker, M.E., and A.F. Gerritsen. 1992. Oil and mucilage cells in *Annona* (Annonaceae) and their systematic significance. Blumea 36:411-438.

Barker, N.P., P.H. Weston, F. Rutschmann, and H. Sauquet. 2007. Molecular dating of the 'Gondwanan' plant family Proteaceae is only partially congruent with the timing of the break-up of Gondwana. Journal of Biogeography 34:2012-2027.

Bartish, I.V., U. Swenson, J. Munzinger, and A.A. Anderberg. 2005. Phylogenetic relationships among New Caledonian Sapotaceae (Ericales): Molecular evidence for generic polyphyly and repeated dispersal. American Journal of Botany 92:667-673.

Bayer, C., M.F. Fay, P.Y. De Bruijn, V. Savolainen, C.M. Morton, K. Kubitzki, W.S. Alverson, and M.W. Chase. 1999. Support for an expanded family concept of Malvaceae within a recircumscribed order Malvales: A combined analysis of plastid *atp*B and *rbc*L DNA sequences. Botanical Journal of the Linnean Society 129:267-303.

Bendiksby, M., L. Thorbek, A.C. Scheen, C. Lindqvist, and O. Ryding. 2011. An updated phylogeny and classification of Lamiaceae subfamily Lamioideae. Taxon 60:471-484.

Besnard, G., R. Rubio de Casas, P.-A. Christin, and P. Vargas. 2009. Phylogenetics of *Olea* (Oleaceae) based on plastid and nuclear ribosomal DNA sequences: Tertiary climatic shifts and lineage differentiation times. Annals of Botany 104:143-160.

Biffin, E., E.J. Lucas, L.A. Craven, I.R. da Costa, M.G. Harrington, and M.D. Crisp. 2010. Evolution of exceptional species richness among lineages of fleshy-fruited Myrtaceae. Annals of Botany 106:79-93.

Bodegom, S., R. Haegens, B.J. Van Heuven, and P. Baas. 2001. Systematic leaf anatomy of *Baccaurea*, *Distichirhops*, and *Nothobaccaurea* (Euphorbiaceae). Blumea 46:485-497.

Bolzani, V.D., L.M. Serur, F.J.D. Matos, and O.R. Gottlieb. 1987. Indole alkaloid evolution in *Aspidosperma*. Biochemical Systematics and Ecology 15:187-200.

Bouchenak-Khelladi, Y., O. Maurin, J. Hurter, and M. van der Bank. 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): An emphasis on African acacias. Molecular Phylogenetics and Evolution 57:495-508.

Bradford, J.C. 2002. Molecular phylogenetics and morphological evolution in Cunonieae (Cunoniaceae). Annals of the Missouri Botanical Garden 89:491-503.

Bradford, J.C., and R.W. Barnes. 2001. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. Systematic Botany 26:354-385.

Bremer, B., and T. Eriksson. 2009. Time tree of Rubiaceae: Phylogeny and dating the family, subfamilies, and tribes. International Journal of Plant Sciences 170:766-793.

Brown, G.K., D.J. Murphy, J.T. Miller, and P.Y. Ladiges. 2008. *Acacia* s.s. and its relationship among tropical legumes, tribe Ingeae (Leguminosae: Mimosoideae). Systematic Botany 33:739-751.

Bruneau, A. 1996. Phylogenetic and biogeographical patterns in *Erythrina* (Leguminosae: Phaseoleae) as inferred from morphological and chloroplast DNA characters. Systematic Botany 21:587-605.

Bruneau, A., F. Forest, P.S. Herendeen, B.B. Klitgaard, and G.P. Lewis. 2001. Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast *trnL* intron sequences. Systematic Botany 26:487-514.

Bruneau, A., M. Mercure, G.P. Lewis, and P.S. Herendeen. 2008. Phylogenetic patterns and diversification in the caesalpinioid legumes. Botany-Botanique 86:697-718.

Buerki, S., F. Forest, P. Acevedo-Rodriguez, M.W. Callmander, J.A.A. Nylander, M. Harrington, I. Sanmartin, P. Kuepfer, and N. Alvarez. 2009. Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). Molecular Phylogenetics and Evolution 51:238-258.

Cavender-Bares, J., D.D. Ackerly, D.A. Baum, and F.A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. American Naturalist 163:823-843.

Cervera, M.T., V. Storme, A. Soto, B. Ivens, M. Van Montagu, O.P. Rajora, and W. Boerjan. 2005. Intraspecific and interspecific genetic and phylogenetic relationships in the genus *Populus* based on AFLP markers. Theoretical and Applied Genetics 111:1440-1456.

Chanderbali, A.S., H. van der Werff, and S.S. Renner. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. Annals of the Missouri Botanical Garden 88:104-134.

Chappill, J.A. 1992. Cladistics and the Chrysobalanaceae. Taxon 41:211-223.

Chase, M.W., S. Zmarzty, M.D. Lledó, K.J. Wurdack, S.M. Swensen, and M.F. Fay. 2002. When in doubt, put it in Flacourtiaceae: A molecular phylogenetic analysis based on plastic *rbcL* DNA sequences. Kew Bulletin 57:141-181.

Chatrou, L.W., M.P. Escribano, M.A. Viruel, J.W. Maas, J.E. Richardson, and J.I. Hormaza. 2009. Flanking regions of monomorphic microsatellite loci provide a new source of data for plant species-level phylogenetics. Molecular Phylogenetics and Evolution 53:726-733.

Chen, S.C., Y.X. Qiu, A.L. Wang, K.M. Cameron, and C.X. Fu. 2006. A phylogenetic analysis of the Smilacaceae based on morphological data. Acta Phytotaxonomica Sinica 44:113-125.

Chen, Z.D., and J.H. Li. 2004. Phylogenetics and biogeography of *Alnus* (Betulaceae) inferred from sequences of nuclear ribosomal DNA its region. International Journal of Plant Sciences 165:325-335.

Chen, Z.D., S.R. Manchester, and H.Y. Sun. 1999. Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology, and paleobotany. American Journal of Botany 86:1168-1181.

Chin, S.-W., J. Wen, G. Johnson, and D. Potter. 2010. Merging *Maddenia* with the morphologically diverse *Prunus* (Rosaceae). Botanical Journal of the Linnean Society 164:236-245.

Clark, J.Y. 2009. Neural networks and cluster analysis for unsupervised classification of cultivated species of *Tilia* (Malvaceae). Botanical Journal of the Linnean Society 159:300-314.

Clausing, G., and S.S. Renner. 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. American Journal of Botany 88:486-498.

Craven, L.A., and E. Biffin. 2010. An infrageneric classification of *Syzygium* (Myrtaceae). Blumea 55:94-99.

Cuénoud, P., M.A.D. Martinez, P.A. Loizeau, R. Spichiger, S. Andrews, and J.F. Manen. 2000. Molecular phylogeny and biogeography of the genus *Ilex* L. (Aquifoliaceae). Annals of Botany 85:111-122.

da Silva, M.J., L.P. de Queiroz, A. Tozzi, G.P. Lewis, and A.P. de Sousa. 2012. Phylogeny and biogeography of *Lonchocarpus* sensu lato and its allies in the tribe Millettieae (Leguminosae, Papilionoideae). Taxon 61:93-108.

Datwyler, S.L., and G.D. Weiblen. 2004. On the origin of the fig: Phylogenetic relationships of Moraceae from *ndhF* sequences. American Journal of Botany 91:767-777.

Davis, C.C., and W.R. Anderson. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. American Journal of Botany 97:2031-2048.

Dayanandan, S., P.S. Ashton, S.M. Williams, and R.B. Primack. 1999. Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide sequences of the chloroplast *rbcL* gene. American Journal of Botany 86:1182-1190.

Denk, T. 2003. Phylogeny of *Fagus* L. (Fagaceae) based on morphological data. Plant Systematics and Evolution 240:55-81.

Denk, T., and G.W. Grimm. 2009. Significance of pollen characteristics for infrageneric classification and phylogeny in *Quercus* (Fagaceae). International Journal of Plant Sciences 170:926-940.

Doyle, J.A., H. Sauquet, T. Scharaschkin, and A. Le Thomas. 2004. Phylogeny, molecular and fossil dating, and biogeographic history of Annonaceae and Myristicaceae (Magnoliales). International Journal of Plant Sciences 165:S55-S67.

Duangjai, S., R. Samuel, J. Munzinger, F. Forest, B. Wallnofer, M.H.J. Barfuss, G. Fischer, and M.W. Chase. 2009. A multi-locus plastid phylogenetic analysis of the pantropical genus *Diospyros* (Ebenaceae), with an emphasis on the radiation and biogeographic origins of the New Caledonian endemic species. Molecular Phylogenetics and Evolution 52:602-620.

Duarte, M.C., G.L. Esteves, M.L.F. Salatino, K.C. Walsh, and D.A. Baum. 2011. Phylogenetic analyses of *Eriotheca* and related genera (Bombacoideae, Malvaceae). Systematic Botany 36:690-701.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus* Pages 7-32 *in* R.F. Stettler, H.D. Bradshaw Jr, P.E. Heilman, and T.M. Hinckley, editors. Biology of *Populus* and its implications for management and conservation. NRC Research Press, Ottawa, Canada.

Eckert, A.J., and B.D. Hall. 2006. Phylogeny, historical biogeography, and patterns of diversification for *Pinus* (Pinaceae): Phylogenetic tests of fossil-based hypotheses. Molecular Phylogenetics and Evolution 40:166-182.

Emche, S.D., D. Zhang, M.B. Islam, B.A. Bailey, and L.W. Meinhardt. 2011. AFLP phylogeny of 36 *Erythroxylum* species. Tropical Plant Biology 4:123-133.

Faivre, A.E., and L.A. McDade. 2001. Population-level variation in the expression of heterostyly in three species of Rubiaceae: Does reciprocal placement of anthers and stigmas characterize heterostyly? American Journal of Botany 88:841-853.

Fan, C.Z., and Q.Y. Xiang. 2003. Phylogenetic analyses of Cornales based on 26S rRNA and combined 26S rDNA-*matK*-*rbcL* sequence data. American Journal of Botany 90:1357-1372.

Fiaschi, P., and G.M. Plunkett. 2011. Monophyly and phylogenetic relationships of Neotropical *Schefflera* (Araliaceae) based on plastid and nuclear markers. Systematic Botany 36:806-817.

Frasier, C.L. 2008. Evolution and systematics of the angiosperm order Gentianales with an in-depth focus on Loganiaceae and its species-rich and toxic genus *Strychnos*. Ph.D. Dissertation. Rutgers University, New Brunswick, NJ, USA.

Gadek, P.A., D.L. Alpers, M.M. Heslewood, and C.J. Quinn. 2000. Relationships within Cupressaceae sensu lato: A combined morphological and molecular approach. American Journal of Botany 87:1044-1057.

Geeraerts, A., J.A.M. Raeymaekers, S. Vinckier, A. Pletsers, E. Smets, and S. Huysmans. 2009. Systematic palynology in Ebenaceae with focus on Ebenoideae: Morphological diversity and character evolution. Review of Palaeobotany and Palynology 153:336-353.

Gernandt, D.S., S. Magallon, G.G. Lopez, O.Z. Flores, A. Willyard, and A. Liston. 2008. Use of simultaneous analyses to guide fossil-based calibrations of Pinaceae phylogeny. International Journal of Plant Sciences 169:1086-1099.

Gillespie, E., and K. Kron. 2010. Molecular phylogenetic relationships and a revised classification of the subfamily Ericoideae (Ericaceae). Molecular Phylogenetics and Evolution 56:343-354.

Goertzen, L.R., J.J. Cannone, R.R. Gutell, and R.K. Jansen. 2003. ITS secondary structure derived from comparative analysis: Implications for sequence alignment and phylogeny of the Asteraceae. Molecular Phylogenetics and Evolution 29:216-234.

Goldenberg, R., D.S. Penneys, F. Almeda, W.S. Judd, and F.A. Michelangeli. 2008. Phylogeny of *Miconia* (Melastomataceae): Patterns of stamen diversification in a megadiverse Neotropical genus. International Journal of Plant Sciences 169:963-979.

Gottschling, M., J.S. Miller, M. Weigend, and H.H. Hilger. 2005. Congruence of a phylogeny of Cordiaceae (Boraginales) inferred from ITS1 sequence data with morphology, ecology,and biogeography. Annals of the Missouri Botanical Garden 92:425-437.

Groppo, M., J.R. Pirani, M.L.F. Salatino, S.R. Blanco, and J.A. Kallunki. 2008. Phylogeny of Rutaceae based on two noncoding regions from cpDNA. American Journal of Botany 95:985-1005.

Gunn, B.F. 2004. The phylogeny of the Cocoeae (Arecaceae) with emphasis on *Cocos nucifera*. Annals of the Missouri Botanical Garden 91:505-522.

Gustafsson, M.H.G., V. Bittrich, and P.F. Stevens. 2002. Phylogeny of Clusiaceae based on *rbc*L sequences. International Journal of Plant Sciences 163:1045-1054.

Hadiah, J.T., B.J. Conn, and C.J. Quinn. 2008. Infra-familial phylogeny of Urticaceae, using chloroplast sequence data. Australian Systematic Botany 21:375-385.

Hall, J.C. 2008. Systematics of Capparaceae and Cleomaceae: An evaluation of the generic delimitations of *Capparis* and *Cleome* using plastid DNA sequence data. Botany-Botanique 86:682-696.

Hall, J.C., K.J. Sytsma, and H.H. Iltis. 2002. Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. American Journal of Botany 89:1826-1842.

Hao, G., D.X. Zhang, M.Y. Zhang, L.X. Guo, and S.J. Li. 2003. Phylogenetics of *Bauhinia* subgenus *Phanera* (Leguminosae : Caesalpinioideae) based on ITS sequences of nuclear ribosomal DNA. Botanical Bulletin of Academia Sinica 44:223-228.

Harrington, M.G., K.J. Edwards, S.A. Johnson, M.W. Chase, and P.A. Gadek. 2005. Phylogenetic inference in Sapindaceae sensu lato using plastid *matK* and *rbcL* DNA sequences. Systematic Botany 30:366-382.

Herendeen, P.S., G.P. Lewis, and A. Bruneau. 2003. Floral morphology in Caesalpinioid legumes: Testing the monophyly of the "*Umtiza* clade". International Journal of Plant Sciences 164:S393-S407.

Hileman, L.C., M.C. Vasey, and V.T. Parker. 2001. Phylogeny and biogeography of the Arbutoideae (Ericaceae): Implications for the Madrean-Tethyan Hypothesis. Systematic Botany 26:131-143.

Hill, K.D. 2004. EucaLink: A web guide to the eucalypts. Community Acces to Natural Resource Information (CANRI), Parramatta, Australia.

Hipp, A.L., L. Gog, J.A. Weber, and A.B. Giesler. 2008. Evaluating the taxonomy of elms (*Ulmus*) using DNA sequence data. Botany 2008, Vancouver, Canada.

Hipp, A.L., J.A. Weber, and A. Srivastava. 2010. Who am I this time? The affinities and misbehaviors of Hill's oak (*Quercus ellipsoidalis*). International Oak Journal 21:27-36.

Horn, J.W. 2009. Phylogenetics of Dilleniaceae using sequence data from four plastid loci (*rbcL*, *infA*, *rps4*, *rpl16* intron). International Journal of Plant Sciences 170:794-813.

Hu, J.M., M. Lavin, M.F. Wojciechowski, and M.J. Sanderson. 2000. Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast *trnK*/*matK* sequences and its implications for evolutionary patterns in Papilionoideae. American Journal of Botany 87:418-430.

Islam, M.B., and M.P. Simmons. 2006. A thorny dilemma: Testing alternative intrageneric classifications within *Ziziphus* (Rhamnaceae). Systematic Botany 31:826-842.

Jarvinen, P., A. Palme, L.O. Morales, M. Lannenpaa, M. Keinanen, T. Sopanen, and M. Lascoux. 2004. Phylogenetic relationships of *Betula* species (Betulaceae) based on nuclear *ADH* and chloroplast *matK* sequences. American Journal of Botany 91:1834-1845.

Kainulainen, K., C. Persson, T. Eriksson, and B. Bremer. 2010. Molecular systematics and morphological character evolution of the Condamineeae (Rubiaceae). American Journal of Botany 97:1961-1981.

Kajita, T., H. Ohashi, Y. Tateishi, C.D. Bailey, and J.J. Doyle. 2001. *rbcL* and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and allies. Systematic Botany 26:515-536.

Kamiya, K., K. Harada, H. Tachida, and P.S. Ashton. 2005. Phylogeny of *PgiC* gene in *Shorea* and its closely related genera (Dipterocarpaceae), the dominant trees in Southeast Asian tropical rain forests. American Journal of Botany 92:775-788.

Kathriarachchi, H., P. Hoffmann, R. Samuel, K.J. Wurdack, and M.W. Chase. 2005. Molecular phylogenetics of Phyllanthaceae inferred from five genes (plastid *atpB*, *matK*, 3 ' *ndhF*, r*bcL*,and nuclear *PHYC*). Molecular Phylogenetics and Evolution 36:112-134.

Kim, S., C.W. Park, Y.D. Kim, and Y. Suh. 2001. Phylogenetic relationships in family Magnoliaceae inferred from *ndhF* sequences. American Journal of Botany 88:717-728.

Knopf, P., C. Schulz, D.P. Little, T. Stuetzel, and D.W. Stevenson. 2012. Relationships within Podocarpaceae based on DNA sequence, anatomical, morphological, and biogeographical data. Cladistics 28:271-299.

Kocyan, A., L.B. Zhang, H. Schaefer, and S.S. Renner. 2007. A multi-locus chloroplast phylogeny for the Cucurbitaceae and its implications for character evolution and classification. Molecular Phylogenetics and Evolution 44:553-577.

Kron, K.A., W.S. Judd, and D.M. Crayn. 1999. Phylogenetic analyses of Andromedeae (Ericaceae subfam. Vaccinioideae). American Journal of Botany 86:1290-1300.

Kulju, K.K.M., S.E.C. Sierra, S.G.A. Draisma, R. Samuel, and P.C. van Welzen. 2007. Molecular phylogeny of *Macaranga*, *Mallotus*, and related genera (Euphorbiaceae s.s.): insights from plastid and nuclear DNA sequence data. American Journal of Botany 94:1726-1743.

Li, J., J. Yue, and S. Shoup. 2006. Phylogenetics of *Acer* (Aceroideae, Sapindaceae) based on nucleotide sequences of two chloroplast non-coding regions. Harvard Papers in Botany 11:101-115.

Li, L., J.-y. Peng, and R.-x. Bai. 2010. Analysis of the genetic relationships in Chinese *Ziziphus* with SRAP markers. Agricultural Sciences in China 9:1278-1284.

Livshultz, T., D.J. Middleton, M.E. Endress, and J.K. Williams. 2007. Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). Annals of the Missouri Botanical Garden 94:324-359.

Lohmann, L.G. 2006. Untangling the phylogeny of Neotropical lianas (Bignonieae, Bignoniaceae). American Journal of Botany 93:304-318.

Lucas, E.J., S.A. Harris, F.F. Mazine, S.R. Bellsham, E.M.N. Lughadha, A. Telford, P.E. Gasson, and M.W. Chase. 2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). Taxon 56:1105-1128.

Luckow, M., and J. Grimes. 1997. A survey of anther glands in the mimosoid legume tribes Parkieae and Mimoseae. American Journal of Botany 84:285-297.

Luckow, M., J.T. Miller, D.J. Murphy, and T. Livshultz. 2003. A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. Pages 197-220 *in* B.B. Klitgaard and A. Bruneau, editors. Advances in legume systematics, Part 10, Higher level systematics. Royal Botanic Gardens, Kew, London, UK.

Mackinder, B.A., and R.T. Pennington. 2011. Monograph of *Berlinia* (Leguminosae). Systematic Botany Monographs 91:1-117.

Manen, J.F., M.C. Boulter, and Y. Naciri-Graven. 2002. The complex history of the genus *Ilex* L. (Aquifoliaceae): Evidence from the comparison of plastid and nuclear DNA sequences and from fossil data. Plant Systematics and Evolution 235:79-98.

Manns, U., and B. Bremer. 2010. Towards a better understanding of intertribal relationships and stable tribal delimitations within Cinchonoideae s.s. (Rubiaceae). Molecular Phylogenetics and Evolution 56:21-39.

Manos, P.S., J.J. Doyle, and K.C. Nixon. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). Molecular Phylogenetics and Evolution 12:333-349.

Manos, P.S., P.S. Soltis, D.E. Soltis, S.R. Manchester, S.H. Oh, C.D. Bell, D.L. Dilcher, and D.E. Stone. 2007. Phylogeny of extant and fossil Juglandaceae inferred from the integration of molecular and morphological data sets. Systematic Biology 56:412-430.

Manos, P.S., and A.M. Stanford. 2001. The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. International Journal of Plant Sciences 162:S77-S93.

Manos, P.S., and D.E. Stone. 2001. Evolution, phylogeny, and systematics of the Juglandaceae. Annals of the Missouri Botanical Garden 88:231-269.

Manos, P.S., Z.K. Zhou, and C.H. Cannon. 2001. Systematics of Fagaceae: Phylogenetic tests of reproductive trait evolution. International Journal of Plant Sciences 162:1361-1379.

Manzanilla, V., and A. Bruneau. 2012. Phylogeny reconstruction in the Caesalpinieae grade (Leguminosae) based on duplicated copies of the sucrose synthase gene and plastid markers. Molecular Phylogenetics and Evolution 65:149-162.

Mao, K.S., G. Hao, J.Q. Liu, R.P. Adams, and R.I. Milne. 2010. Diversification and biogeography of *Juniperus* (Cupressaceae): Variable diversification rates and multiple intercontinental dispersals. New Phytologist 188:254-272.

Martínez-Millán, M., W.L. Crepet, and K.C. Nixon. 2009. *Pentapetalum trifasciculandricus* gen. et sp. nov., a Thealean fossil flower from the Raritan Formation, New Jersey, USA (Turonian, Late Cretaceous). American Journal of Botany 96:933-949.

Martyn, A.J., L.U. Seed, M.K. Ooi, and C.A. Offord. 2009. Seed fill, variability and germination of NSW species in the family Rutaceae. Cunninghamia 11:203-212.

Mast, A.R., and T.J. Givnish. 2002. Historical biogeography and the origin of stomatal distributions in *Banksia* and *Dryandra* (Proteaceae) based on their cpDNA phylogeny. American Journal of Botany 89:1311-1323.

Maurin, O., M.W. Chase, M. Jordaan, and M. Van Der Bank. 2010. Phylogenetic relationships of Combretaceae inferred from nuclear and plastid DNA sequence data: Implications for generic classification. Botanical Journal of the Linnean Society 162:453-476.

McKenna, M.J., M.P. Simmons, C.D. Bacon, and J.A. Lombardi. 2011. Delimitation of the segregate genera of *Maytenus* s. l. (Celastraceae) based on morphological and molecular characters. Systematic Botany 36:922-932.

McMahon, M.M., and M.J. Sanderson. 2006. Phylogenetic supermatrix analysis of GenBank sequences from 2228 papilionoid legumes. Systematic Biology 55:818-836.

Michelangeli, F.A., D.S. Penneys, J. Giza, D. Soltis, M.H. Hils, and J.D. Skean. 2004. A preliminary phylogeny of the tribe Miconieae (Melastomataceae) based on nrITS sequence data and its implications on inflorescence position. Taxon 53:279-290.

Miikeda, O., K. Kita, T. Handa, and T. Yukawa. 2006. Phylogenetic relationships of *Clematis* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. Botanical Journal of the Linnean Society 152:153-168.

Mols, J.B., B. Gravendeel, L.W. Chatrou, M.D. Pirie, P.C. Bygrave, M.W. Chase, and P.J.A. Kessler. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. American Journal of Botany 91:590-600.

Mori, S.A., C.H. Tsou, C.C. Wu, B. Cronholm, and A.A. Anderberg. 2007. Evolution of Lecythidaceae with an emphasis on the circumscription of neotropical genera: Information from combined *ndhF* and *trnL-F* sequence data. American Journal of Botany 94:289-301.

Muellner, A.N., H. Greger, and C.M. Pannell. 2009. Genetic diversity and geographic structure in *Aglaia elaeagnoidea* (Meliaceae, Sapindales), a morphologically complex tree species, near the two extremes of its distribution. Blumea 54:207-216.

Muellner, A.N., R. Samuel, M.W. Chase, A. Coleman, and T.F. Stuessy. 2008. An evaluation of tribes and generic relationships in Melioideae (Meliaceae) based on nuclear ITS ribosomal DNA. Taxon 57:98-108.

Muellner, A.N., R. Samuel, S.A. Johnson, M. Cheek, T.D. Pennington, and M.W. Chase. 2003. Molecular phylogenetics of Meliaceae (Sapindales) based on nuclear and plastid DNA sequences. American Journal of Botany 90:471-480.

Muschner, V.C., A.P. Lorenz, A.C. Cervi, S.L. Bonatto, T.I. Souza-Chies, F.M. Salzano, and L.B. Freitas. 2003. A first molecular phylogenetic analysis of *Passiflora* (Passifloraceae). American Journal of Botany 90:1229-1238.

Nepokroeff, M., B. Bremer, and K.J. Sytsma. 1999. Reorganization of the genus *Psychotria* and tribe Psychotrieae (Rubiaceae) inferred from ITD and *rbcL* sequence data. Systematic Botany 24:5-27.

Ochieng, J.W., R.J. Henry, P.R. Baverstock, D.A. Steane, and M. Shepherd. 2007. Nuclear ribosomal pseudogenes resolve a corroborated monophyly of the eucalypt genus *Corymbia* despite misleading hypotheses at functional ITS paralogs. Molecular Phylogenetics and Evolution 44:752-764.

Oh, S.-H., and P.S. Manos. 2008. Molecular phylogenetics and cupule evolution in Fagaceae as inferred from nuclear *CRABS CLAW* sequences. Taxon 57:434-451.

Ohyama, M., K. Baba, and T. Itoh. 1999. Possibility of grouping of *Cyclobalanopsis* species (Fagaceae) grown in Japan based on an analysis of several regions of chloroplast DNA. Journal of Wood Science 45:498-501.

Olmstead, R.G., M.L. Zjhra, L.G. Lohmann, S.O. Grose, and A.J. Eckert. 2009. A molecular phylogeny and classification of Bignoniaceae. American Journal of Botany 96:1731-1743.

Ortiz, R.D.C., E.A. Kellogg, and H. Van Der Werff. 2007. Molecular phylogeny of the moonseed family (Menispermaceae): Implications for morphological diversification. American Journal of Botany 94:1425-1438.

Pan, Y.Z., X. Gong, and Y. Yang. 2008. Phylogenetic position of the genus *Dobinea*: Evidence from nucleotide sequences of the chloroplast gene *rbc*L and the nuclear ribosomal ITS region. Journal of Systematics and Evolution 46:586-594.

Panero, J.L., and V.A. Funk. 2008. The value of sampling anomalous taxa in phylogenetic studies: Major clades of the Asteraceae revealed. Molecular Phylogenetics and Evolution 47:757-782.

Pardo, C., P. Cubas, and H. Tahiri. 2004. Molecular phylogeny and systematics of *Genista* (Leguminosae) and related genera based on nucleotide sequences of nrDNA (ITS region) and cpDNA (*trn*L-t*rn*F intergenic spacer). Plant Systematics and Evolution 244:93-119.

Paz, H., S.J. Mazer, and M. Martinez-Ramos. 1999. Seed mass, seedling emergence, and environmental factors in seven rain forest *Psychotria* (Rubiaceae). Ecology 80:1594-1606.

Pearse, I.S., and A.L. Hipp. 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. Proceedings of the National Academy of Sciences of the United States of America 106:18097-18102.

Pell, S.K. 2004. Molecular systematics of the cashew family (Anacardiaceae). Ph.D. Dissertation. Louisiana State University, Baton Rouge, LA, USA.

Pennington, R.T., M. Lavin, H. Ireland, B. Klitgaard, J. Preston, and J.M. Hu. 2001. Phylogenetic relationships of basal papilionoid legumes based upon sequences of the chloroplast *trnL* intron. Systematic Botany 26:537-556.

Persson, C. 1996. Phylogeny of the Gardenieae (Rubiaceae). Botanical Journal of the Linnean Society 121:91-109.

Petersen, J.J., I.M. Parker, and D. Potter. 2012. Origins and close relatives of a semi-domesticated Neotropical fruit tree: *Chrysophyllum cainito* (Sapotaceae). American Journal of Botany 99:585-604.

Pirie, M.D., L.W. Chatrou, J.B. Mols, R.H.J. Erkens, and J. Oosterhof. 2006. 'Andean-centred' genera in the short-branch clade of Annonaceae: Testing biogeographical hypotheses using phylogeny reconstruction and molecular dating. Journal of Biogeography 33:31-46.

Plunkett, G.M., P.P. Lowry, D.G. Frodin, and J. Wen. 2005. Phylogeny and geography of *Schefflera*: Pervasive polyphyly in the largest genus of Araliaceae. Annals of the Missouri Botanical Garden 92:202-224.

Poon, W.S., P.C. Shaw, M.P. Simmons, and P.P.H. But. 2007. Congruence of molecular, morphological, and biochemical profiles in Rutaceae: A cladistic analysis of the subfamilies Rutoideae and Toddalioideae. Systematic Botany 32:837-846.

Potgieter, K., and V.A. Albert. 2001. Phylogenetic relationships within Apocynaceae s.l. based on *trn*L intron and *trn*L-F spacer sequences and propagule characters. Annals of the Missouri Botanical Garden 88:523-549.

Potter, D., T. Eriksson, R.C. Evans, S. Oh, J.E.E. Smedmark, D.R. Morgan, M. Kerr, K.R. Robertson, M. Arsenault, T.A. Dickinson, and C.S. Campbell. 2007. Phylogeny and classification of Rosaceae. Plant Systematics and Evolution 266:5-43.

Price, R.A. 1996. Systematics of the Gnetales: A review of morphological and molecular evidence. International Journal of Plant Sciences 157:S40-S49.

Ran, J.-H., X.-X. Wei, and X.-Q. Wang. 2006. Molecular phylogeny and biogeography of *Picea* (Pinaceae): Implications for phylogeographical studies using cytoplasmic haplotypes. Molecular Phylogenetics and Evolution 41:405-419.

Rankin Rodríguez, R., and W. Greuter. 2004. A study of differentiation patterns in *Capparis* sect. Breyniastrum in Cuba, with a nomenclatural and taxonomic survey of Cuban *Capparis* (*Capparaceae*). Willdenowia 34:259-276.

Ren, H., L.M. Lu, A. Soejima, Q. Luke, D.X. Zhang, Z.D. Chen, and J. Wen. 2011. Phylogenetic analysis of the grape family (Vitaceae) based on the noncoding plastid *trnC-petN*, *trnH-psbA*, and *trnL-F* sequences. Taxon 60:629-637.

Renner, S.S. 1998. Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences. Perspectives in Plant Ecology Evolution and Systematics 1:61-77.

Renner, S.S., L. Beenken, G.W. Grimm, A. Kocyan, and R.E. Ricklefs. 2007. The evolution of dioecy, heterodichogamy, and labile sex expression in *Acer*. Evolution 61:2701-2719.

Richardson, J.E., L.W. Chatrou, J.B. Mols, R.H.J. Erkens, and M.D. Pirie. 2004. Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. Philosophical Transactions of the Royal Society Series B 359:1495-1508.

Richardson, J.E., M.F. Fay, Q.C.B. Cronk, D. Bowman, and M.W. Chase. 2000. A phylogenetic analysis of Rhamnaceae using *rbcL* and *trnL-F* plastid DNA sequences. American Journal of Botany 87:1309-1324.

Riina, R., P.E. Berry, and B.W. van Ee. 2009. Molecular phylogenetics of the dragon's blood *Croton* section Cyclostigma (Euphorbiaceae): A polyphyletic assemblage unraveled. Systematic Botany 34:360-374.

Rohwer, J.G., J. Li, B. Rudolph, S.A. Schmidt, H. van der Werff, and H.W. Li. 2009. Is *Persea* (Lauraceae) monophyletic? Evidence from nuclear ribosomal ITS sequences. Taxon 58:1153-1167.

Rønsted, N., G.D. Weiblen, W.L. Clement, N.J.C. Zerega, and V. Savolainen. 2008. Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of the fig pollination mutualism. Symbiosis 45:45-55.

Rossetto, M., B.R. Jackes, K.D. Scott, and R.J. Henry. 2002. Is the genus *Cissus* (Vitaceae) monophyletic? Evidence from plastid and nuclear ribosomal DNA. Systematic Botany 27:522-533.

Sattarian, A. 2006. Contribution to the biosystematics of *Celtis* L. (Celtidaceae) with special emphasis on the African species. Ph.D. Dissertation. Wageningen University, Wageningen, The Netherlands.

Sauquet, H., P.H. Weston, N.P. Barker, C.L. Anderson, D.J. Cantrill, and V. Savolainen. 2009. Using fossils and molecular data to reveal the origins of the Cape proteas (subfamily Proteoideae). Molecular Phylogenetics and Evolution 51:31-43.

Schenk, M.F., C.-N. Thienpont, W.J.M. Koopman, L.J.W.J. Gilissen, and M.J.M. Smulders. 2008. Phylogenetic relationships in *Betula* (Betulaceae) based on AFLP markers. Tree Genetics & Genomes 4:911-924.

Schrire, B.D., G.P. Lewis, and M. Lavin, editors. 2005. Biogeography of the Leguminosae. Royal Botanic Gardens, Kew, London, UK.

Setoguchi, H., K. Kosuge, and H. Tobe. 1999. Molecular phylogeny of Rhizophoraceae based on *rbcL* gene sequences. Journal of Plant Research 112:443-455.

Sierra, S.E.C., K.K.M. Kulju, Z. Fiser, M. Aparicio, and P.C. van Welzen. 2010. The phylogeny of *Mallotus* s. str. (Euphorbiaceae) inferred from DNA sequence and morphological data. Taxon 59:101-116.

Simmons, M.P., and J.P. Hedin. 1999. Relationships and morphological character change among genera of Celastraceae sensu lato (including Hippocrateaceae). Annals of the Missouri Botanical Garden 86:723-757.

Simoes, A.O., T. Livshultz, E. Conti, and M.E. Endress. 2007. Phylogeny and systematics of the Rauvolfioideae (Apocynaceae) based on molecular and morphological evidence. Annals of the Missouri Botanical Garden 94:268-297.

Sinou, C., F. Forest, G.P. Lewis, and A. Bruneau. 2009. The genus *Bauhinia* s.l. (Leguminosae): A phylogeny based on the plastid *trn*L-*trn*F region. Botany-Botanique 87:947-960.

Smedmark, J.E.E., U. Swenson, and A.A. Anderberg. 2006. Accounting for variation of substitution rates through time in Bayesian phylogeny reconstruction of Sapotoideae (Sapotaceae). Molecular Phylogenetics and Evolution 39:706-721.

Soh, W.K., and J. Parnell. 2011. Comparative leaf anatomy and phylogeny of *Syzygium* Gaertn. Plant Systematics and Evolution 297:1-32.

Sousa, M.S. 2009. *Standleyi* una nueva sección del género *Lonchocarpus* (Leguminosae), nuevas especies y subespecie para Mesoamérica y Sudamérica. Acta Botanica Mexicana 86:39-69.

Stahl, B. 1996. The relationships of *Heberdenia bahamensis* and *H. penduliflora* (Myrsinaceae). Botanical Journal of the Linnean Society 122:315-333.

Steane, D.A., R.P.J. de Kok, and R.G. Olmstead. 2004. Phylogenetic relationships between *Clerodendrum* (Lamiaceae) and other Ajugoid genera inferred from nuclear and chloroplast DNA sequence data. Molecular Phylogenetics and Evolution 32:39-45.

Steane, D.A., D. Nicolle, C.P. Sansaloni, C.D. Petroli, J. Carling, A. Kilian, A.A. Myburg, D. Grattapaglia, and R.E. Vaillancourt. 2011. Population genetic analysis and phylogeny reconstruction in *Eucalyptus* (Myrtaceae) using high-throughput, genome-wide genotyping. Molecular Phylogenetics and Evolution 59:206-224.

Steeves, R.A.D. 2011. An introgeneric and intraspecific study of morphological and genetic variation in the Neotropical *Compsoneura* and *Virola* (Myristicaceae). Ph.D. Dissertation. University of Guelph, Guelph, Canada.

Stefanovic, S., L. Krueger, and R.G. Olmstead. 2002. Monophyly of the Convolvulaceae and circumscription of their major lineages based on DNA sequences of multiple chloroplast loci. American Journal of Botany 89:1510-1522.

Stern, W.L., G.K. Brizicky, and F.N. Tamolang. 1963. The woods and flora of the Florida Keys: Capparaceae. Smithsonian Institution, Washington, DC, USA.

Stevens, P.F. 2012. Angiosperm phylogeny website, version 12, July 2012. Missouri Botanical Garden, St. Louis, MO, USA.

Suh, Y., K. Heo, and C.W. Park. 2000. Phylogenetic relationships of maples (*Acer* L.; Aceraceae) implied by nuclear ribosomal ITS sequences. Journal of Plant Research 113:193-202.

Sweeney, P.W. 2008. Phylogeny and floral diversity in the genus *Garcinia* (Clusiaceae) and relatives. International Journal of Plant Sciences 169:1288-1303.

Swenson, U., R.S. Hill, and S. McLoughlin. 2001. Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. Taxon 50:1025-1041.

Swenson, U., J.E. Richardson, and I.V. Bartish. 2008. Multi-gene phylogeny of the pantropical subfamily Chrysophylloideae (Sapotaceae): Evidence of generic polyphyly and extensive morphological homoplasy. Cladistics 24:1006-1031.

Sytsma, K.J., J. Morawetz, J.C. Pires, M. Nepokroeff, E. Conti, M. Zjhra, J.C. Hall, and M.W. Chase. 2002. Urticalean rosids: Circumscription, rosid ancestry, and phylogenetics based on *rbcL*, *trnL-F*, and *ndhF* sequences. American Journal of Botany 89:1531-1546.

Tate, J.A., J.F. Aguilar, S.J. Wagstaff, J.C. La Duke, T.A.B. Slotta, and B.B. Simpson. 2005. Phylogenetic relationships within the tribe Malveae (Malvaceae, subfamily Malvoideae) as inferred from its sequence data. American Journal of Botany 92:584-602.

Tokuoka, T. 2008. Molecular phylogenetic analysis of Violaceae (Malpighiales) based on plastid and nuclear DNA sequences. Journal of Plant Research 121:253-260.

Tokuoka, T. 2012. Molecular phylogenetic analysis of Passifloraceae sensu lato (Malpighiales) based on plastid and nuclear DNA sequences. Journal of Plant Research 125:489-497.

Trinder-Smith, T.H., H.P. Linder, T. Van der Niet, G.A. Verboom, and T.L. Nowell. 2007. Plastid DNA sequences reveal generic paraphyly within Diosmeae (Rutoideae, Rutaceae). Systematic Botany 32:847-855.

Tröndle, D., S. Schröder, H.H. Kassemeyer, C. Kiefer, M.A. Koch, and P. Nick. 2010. Molecular phylogeny of the genus *Vitis* (Vitaceae) based on plastic markers. American Journal of Botany 97:1168-1178.

Trytsman, M., A.E. van Wyk, and E.L. Masemola. 2011. Systematics, diversity and forage value of indigenous legumes of South Africa, Lesotho and Swaziland. African Journal of Biotechnology 10:13773-13779.

van der Merwe, M.M., A.E. van Wyk, and A.M. Botha. 2005. Molecular phylogenetic analysis of *Eugenia* L. (Myrtaceae), with emphasis on southern African taxa. Plant Systematics and Evolution 251:21-34.

van Ee, B.W., P.E. Berry, R. Riina, and J.E.G. Amaro. 2008. Molecular phylogenetics and biogeography of the Caribbean-centered *Croton* subgenus Moacroton (Euphorbiaceae s.s.). Botanical Review 74:132-165.

van Noort, S., and J.-Y. Rasplus. 2012. Figweb. Iziko South African Museum, Cape Town, South Africa.

Wallander, E. 2008. Systematics of *Fraxinus* (Oleaceae) and evolution of dioecy. Plant Systematics and Evolution 273:25-49.

Wallander, E., and V.A. Albert. 2000. Phylogeny and classification of Oleaceae based on *rps16* and *trnL-F* sequence data. American Journal of Botany 87:1827-1841.

Wang, G., M. Zhang, G.X. Wang, and M.L. Zhang. 2011. A molecular phylogeny of *Sorbus* (Rosaceae) based on ITS sequence. Acta Horticulturae Sinica 38:2387-2394.

Weeks, A., K.E. Baird, and C.K. McMullen. 2010. Origin and evolution of endemic Galapagos *Varronia* species (Cordiaceae). Molecular Phylogenetics and Evolution 57:948-954.

Weeks, A., D.C. Daly, and B.B. Simpson. 2005. The phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. Molecular Phylogenetics and Evolution 35:85-101.

Wen, J., Z.-L. Nie, A. Soejima, and Y. Meng. 2007. Phylogeny of Vitaceae based on the nuclear *GAI1* gene sequences. Canadian Journal of Botany 85:144-167.

Wen, J., G.M. Plunkett, A.D. Mitchell, and S.J. Wagstaff. 2001. The evolution of Araliaceae: a phylogenetic analysis based on ITS sequences of nuclear ribosomal DNA. Systematic Botany 26:144-167.

Whitlock, B.A., C. Bayer, and D.A. Baum. 2001. Phylogenetic relationships and floral evolution of the Byttnerioideae ("Sterculiaceae" or Malvaceae s.l.) based on sequences of the chloroplast gene, *ndhF*. Systematic Botany 26:420-437.

Wiegrefe, S.J., K.J. Sytsma, and R.P. Guries. 1994. Phylogeny of elms (*Ulmus*, Ulmaceae): Molecular evidence for a sectional classification. Systematic Botany 19:590-612.

Wilkie, P., A. Clark, R.T. Pennington, M. Cheek, C. Bayer, and C.C. Wilcock. 2006. Phylogenetic relationships within the subfamily Sterculioideae (Malvaceae/Sterculiaceae-Sterculieae) using the chloroplast gene *ndhF*. Systematic Botany 31:160-170.

Williams, C.N. 2012. A phylogeny of Samydaceae based on nuclear GBSSI and EMB2765 DNA sequences. B.S. Honors Thesis. University of Southern Mississippi, Hattiesburg, MS, USA.

Wilson, P.G., M.M. O'Brien, M.M. Heslewood, and C.J. Quinn. 2005. Relationships within Myrtaceae sensu lato based on a *mat*K phylogeny. Plant Systematics and Evolution 251:3-19.

Wojciechowski, M.F., M. Lavin, and M.J. Sanderson. 2004. A phylogeny of legumes (Leguminosae) based on analyses of the plastid *matK* gene resolves many well-supported subclades within the family. American Journal of Botany 91:1846-1862.

Won, H., and S.S. Renner. 2006. Dating dispersal and radiation in the gymnosperm *Gnetum* (Gnetales) - Clock calibration when outgroup relationships are uncertain. Systematic Biology 55:610-622.

Wurdack, K.J., P. Hoffmann, and M.W. Chase. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcL* and *trnL-F* DNA sequences. American Journal of Botany 92:1397-1420.

Xiang, Q.Y.J., D.T. Thomas, W.H. Zhang, S.R. Manchester, and Z. Murrell. 2006. Species level phylogeny of the genus *Cornus* (Cornaceae) based on molecular and morphological evidence - Implications for taxonomy and Tertiary intercontinental migration. Taxon 55:9-30.

Xie, L., and L.Q. Li. 2012. Variation of pollen morphology, and its implications in the phylogeny of *Clematis* (Ranunculaceae). Plant Systematics and Evolution 298:1437-1453.

Yi, T.S., P.P. Lowry, G.M. Plunkett, and J. Wen. 2004a. Chromosomal evolution in Araliaceae and close relatives. Taxon 53:987-1005.

Yi, T.S., A.J. Miller, and J. Wen. 2004b. Phylogenetic and biogeographic diversification of *Rhus* (Anacardiaceae) in the Northern Hemisphere. Molecular Phylogenetics and Evolution 33:861-879.

Yoo, K.O., and J. Wen. 2002. Phylogeny and biogeography of *Carpinus* and subfamily Coryloideae (Betulaceae). International Journal of Plant Sciences 163:641-650.

Zhi, W. 1985. A revision of the Chinese *Millettia* (Papilionoideae). Acta Phytotaxonomica Sinica 23:196-208.

Zhou, L.L., Y.C.F. Su, P. Chalermglin, and R.M.K. Saunders. 2010. Molecular phylogenetics of *Uvaria* (Annonaceae): Relationships with *Balonga*, *Dasoclema* and Australian species of *Melodorum*. Botanical Journal of the Linnean Society 163:33-43.

Appendix F: Maximally resolved phylogenetic tree

Newick tree notation for maximally resolved phylogenetic tree.

(((((((((((((((((((((C7_Viburnum_sp.,(C7_Lonicera_periclymenum,C7_Lonicera_hispidula))CAPRIFOLIACEAE,(((AA_Cephalaralia_cephalobotrys,((AA_Cussonia_spicata,AA_Cheirodendron_trigynum),(((AA_Polyscias_elegans,AA_Polyscias_murrayi),AA_Arthrophyllum_diversifolium),((AA_Schefflera_morototoni,AA_Schefflera_macrocarpa,AA_Schefflera_vinosa),AA_Dendropanax_arboreus,AA_Oreopanax_xalapensis))))ARALIACEAE,GR_Griselinia_littoralis),PN_Pennantia_cunninghamii)),ES_Polyosma_cunninghamii),(((((AS_Pentacalia_sp.,((AS_Baccharis_angustifolia,AS_Baccharis_macrantha),((AS_Bidens_reptans,AS_Lasianthaea_ceanothifolia),AS_Ageratina_dendroides))),(AS_Sinclairia_caducifolia,AS_Piptocarpha_rotundifolia)),AS_Brachylaena_neriifolia),AS_Gochnatia_floribunda),AS_Dasyphyllum_diacanthoides)ASTERACEAE),((AQ_Ilex_canariensis,(AQ_Ilex_opaca,(AQ_Ilex_mitis,(AQ_Ilex_anomala,(AQ_Ilex_aquifolium,AQ_Ilex_perado)))))AQUIFOLIACEAE,(CR_Citronella_moorei,(CR_Leptaulus_daphnoides,CR_Gonocaryum_sp.))CARDIOPTERIDACEAE)),((((((SR_Freylinia_lanceolata,SR_Myoporum_sandwicense)SCROPHULARIACEAE,((BG_Pandorea_pandorana,(BG_Jacaranda_copaia,((BG_Chilopsis_linearis,(((BG_Kigelia_africana,BG_Markhamia_lutea),(BG_Mayodendron_igneum,BG_Spathodea_campanulata)),(((BG_Amphitecna_tuxtlensis,BG_Crescentia_cujete),(BG_Handronathus_chrysanthus,BG_Handroanthus_billbergii)),BG_Tabebuia_rosea))),((BG_Adenocalymma_tanaeciicarpum,BG_Memora_sp.),((BG_Fridericia_schumanniana,BG_Fridericia_prancei),(BG_Pleonotoma_variabilis,(BG_Mansoa_verrucifera,BG_Bignonia_corymbosa)))))))BIGNONIACEAE,(AC_Avicennia_marina,((((LA_Aegiphila_costaricensis,LA_Aegiphila_lhotzkiana),(LA_Gmelina_leichardtii,LA_Tectona_grandis)),LA_Vitex_pinnata)LAMIACEAE,(VE_Citharexylum_macradenium,VE_Lantana_camara)VERBENACEAE)))),(((((OE_Olea_paniculata,(OE_Olea_europaea,(OE_Olea_woodiana,OE_Olea_capensis))),(OE_Chionanthus_virginicus,OE_Chionanthus_peglerae)),(OE_Phillyrea_angustifolia,OE_Picconia_excelsa)),((OE_Fraxinus_americana,OE_Fraxinus_pennsylvanica),(OE_Fraxinus_ornus,(OE_Fraxinus_nigra,(OE_Fraxinus_mandshurica,(OE_Fraxinus_angustifolia,OE_Fraxinus_excelsior)))))),OE_Nyctanthes_arbortristis)OLEACEAE),(BO_Bourreria_cumanensis,((BO_Cordia_caffra,BO_Cordia_dichotoma),(BO_Cordia_bicolor,BO_Cordia_megalantha,BO_Cordia_alliodora)))BORAGINACEAE),((((CV_Bonamia_trichantha,CV_Maripa_panamensis),(CV_Convolvulus_nodiflorus,CV_Merremia_quinquefolia))CONVOLVULACEAE,(SL_Solanum_refractum,SL_Solanum_stramoniifolium)SOLANACEAE),((((((((AP_Wrightia_natalensis,(AP_Wrightia_pubescens,AP_Wrightia_arborea)),(((AP_Urceola_rosea,AP_Beaumontia_grandiflora),(((AP_Marsdenia_lanata,AP_Pergularia_rostrata),AP_Polystemma_guatemalense),(AP_Parsonsia_fulva,(AP_Parsonsia_lilacina,AP_Parsonsia_ventricosa)))),AP_Funtumia_africana)),(AP_Cerbera_manghas,AP_Cascabela_thevetia)),(AP_Melodinus_australis,AP_Melodinus_cochinchinensis)),((AP_Stemmadenia_donnellsmithii,(AP_Kopsia_arborea,AP_Rauvolfia_vomitoria)),((AP_Aspidosperma_desmanthum,AP_Aspidosperma_album),(AP_Aspidosperma_tomentosum,AP_Aspidosperma_megalocarpon))))APOCYNACEAE,((LG_Strychnos_nuxvomica,(LG_Strychnos_decussata,LG_Strychnos_madagascariensis)),LG_Strychnos_henningsii)LOGANIACEAE),(GE_Fagraea_fragrans,GE_Macrocarpaea_sidiroana)GENTIANACEAE),((((RU_Faramea_occidentalis,RU_Faramea_platyneura),RU_Coussarea_albescens),(RU_Coprosma_ochracea,(RU_Morinda_jasminoides,((RU_Palicourea_guianensis,((RU_Psychotria_faxlucens,RU_Psychotria_chiapensis),RU_Palicourea_sp.)),(RU_Psychotria_capensis,(RU_Psychotria_simiarum,RU_Psychotria_flava)))))),(((RU_Pittoniotis_trichantha,(RU_Haldina_cordifolia,(RU_Mitragyna_parvifolia,(RU_Neolamarckia_cadamba,(RU_Uncaria_guianensis,RU_Uncaria_tomentosa,RU_Uncaria_macrophylla,RU_Uncaria_rhynchophylla))))),RU_Remijia_morilloi),(((RU_Chimarrhis_turbinata,RU_Alseis_blackiana),RU_Macrocnemum_roseum),((RU_Retiniphyllum_concolor,RU_Retiniphyllum_truncatum),(RU_Scyphiphora_hydrophylacea,(RU_Diplospora_malaccensis,(RU_Hyperacanthus_amoenus,(RU_Rothmannia_globosa,(RU_Gardenia_latifolia,(RU_Tamilnadia_uliginosa,RU_Tocoyena_formosa))))))))))RUBIACEAE))),(IC_Apodytes_dim idiata,IC_Iodes_vitiginea)ICACINACEAE)),((((((AT_Actinidia_arguta,((CT_Clethra_mexicana,CT_Purdiaea_nutans)CLETHRACEAE,((((((ER_Chamaedaphne_latifolia,(ER_Kalmia_angustifolia,ER_Kalmia_polifolia)),ER_Bejaria_aestuans),(ER_Hymenanthes_maxima,ER_Erica_arborea)),ER_Oxydendrum_arboreum),(ER_Vaccinium_floribundum,ER_Vaccinium_sp.)),(ER_Arbutus_menziesii,(ER_Arbutus_canariensis,ER_Arbutus_unedo)))ERICACEAE)),(S1_Styrax_camporum,SY_Symplocos_sumuntia)),(TH_Camellia_japonica,(TH_Schima_brevifolia,TH_Schima_superba))THEACEAE),(PT_Adinandra_dumosa,(PT_Cleyera_japonica,(PT_Eurya_japonica,PT_Visnea_mocanera)))PENTAPHYLACACEAE),((((PR_Jacquinia_pungens,PR_Jacquinia_armillaris),(PR_Parathesis_amplifolia,(((PR_Myrsine_seguinii,PR_Myrsine_andina),(PR_Rapanea_lessertiana,PR_Rapanea_melanophloeos)),(PR_Heberdenia_bahamensis,(PR_Embelia_australiana,PR_Cybianthus_marginatus)))))PRIMULACEAE,((((((((EB_Diospyros_malabarica,EB_Diospyros_kerrii,EB_Diospyros_nutans,EB_Diospyros_melanoxylon),(EB_Diospyros_inhacaensis,EB_Diospyros_dendo)),EB_Diospyros_cauliflora),(EB_Diospyros_natalensis,EB_Diospyros_hoyleana)),EB_Diospyros_pentamera),EB_Diospyros_maingayi),EB_Diospyros_whyteana),EB_Euclea_divinorum)EBENACEAE),(((SO_Madhuca_longifolia,SO_Madhuca_sp.),(SO_Sideroxylon_inerme,(SO_Inhambanella_henriquezii,((SO_Mimusops_elengi,SO_Mimusops_obovata),(SO_Manilkara_hexandra,(SO_Manilkara_huberi,SO_Manilkara_bidentata)))))),(SO_Englerophytum_natalense,(((SO_Micropholis_sp.,SO_Micropholis_maguirei),SO_Chrysophyllum_argenteum),((SO_Niemeyera_chartacea,SO_Planchonella_obovata),(SO_Pouteria_venosa,SO_Pouteria_macrophylla,SO_Pouteria_reticulata,SO_Pouteria_rhynchocarpa,SO_Pouteria_durlandii)))))SAPOTACEAE)),(((LE_Lecythis_sp.,LE_Lecythis_lurida),LE_Couratari_guianensis),(LE_Barringtonia_macrostachya,LE_Planchonia_careya))LECYTHIDACEAE)),((((C2_Alangium_chinensis,C2_Alangium_villosum),((C2_Cornus_controversa,C2_Cornus_alternifolia),C2_Cornus_florida)),C2_Nyssa_sylvatica)CORNACEAE,(C6_Curtisia_dentata,HY_Schizophragma_hydrangeoides))),((CA_Pereskia_guamacho,NY_Neea_obovata),(PY_Antigonon_flavescens,PY_Coccoloba_hondurensis)POLYGONACEAE)),AX_Aextoxicon_punctatum),(C3_Coula_edulis,((OL_Heisteria_scandens,OL_Strombosia_scheffleri)OLACACEAE,((SN_Exocarpos_aphyllus,SN_Santalum_acuminatum)SANTALACEAE,LO_Nuytsia_floribunda)))),(DI_Davilla_rugosa,(DI_Doliocarpus_dentatus,DI_Dillenia_indica))DILLENIACEAE),((((((((CP_Cladostemon_kirkii,(((CP_Capparis_odoratissima,CP_Morisonia_americana),(CP_Capparis_baducca,CP_Capparis_pachaca)),(CP_Capparis_linearis,CP_Capparis_flexuosa)))CAPPARACEAE,(((((MV_Byttneria_aspera,MV_Kleinhovia_hospita),(MV_Commersonia_bartramia,((MV_Apeiba_glabra,MV_Apeiba_membranacea,MV_Apeiba_tibourbou),(MV_Heliocarpus_appendiculatus,(MV_Luehea_seemannii,((MV_Trichospermum_mexicanum,MV_Trichospermum_pleiostigma),MV_Grewia_asiatica)))))),(((MV_Brachychiton_discolor,MV_Brachychiton_populneus,MV_Brachychiton_megaphyllus),((MV_Firmiana_colorata,MV_Pterygota_alata),(MV_Heritiera_actinophylla,MV_Heritiera_trifoliolata))),(((MV_Tilia_maximowicziana,MV_Tilia_americana),(MV_Tilia_cordata,MV_Tilia_japonica)),(((MV_Pterospermum_acerifolium,MV_Dombeya_kirkii),(MV_Cola_greenwayi,MV_Mortoniodendron_guatemalense)),((((MV_Quararibea_asterolepis,MV_Quararibea_yunckeri),(((MV_Hampea_nutricia,MV_Thespesia_populnea),MV_Robinsonella_mirandae),(MV_Hibiscus_sp.,MV_Hibiscus_tiliaceus))),(MV_Catostemma_sp.,((MV_Pseudobombax_septenatum,MV_Ceiba_pentandra),(MV_Bombax_ceiba,(MV_Pachira_sordida,MV_Pachira_humilis))))),MV_Ochroma_pyramidale))))),(TY_Enkleia_malaccensis,TY_Ovidia_pillopillo)THYMELAEACEAE),((DP_Monotes_glaber,(DP_Dipterocarpus_sublamellatus,((DP_Shorea_argentifolia,DP_Shorea_robusta),(DP_Parashorea_malaanonan,DP_Parashorea_chinensis))))DIPTEROCARPACEAE,(BI_Cochlospermum_fraseri,BI_Cochlospermum_vitifolium)BIXACEAE))),(((((ML_Toona_australis,(ML_Carapa_guianensis,(ML_Soymida_febrifuga,ML_Swietenia_mahagoni))),(ML_Azadirachta_indica,(ML_Ekebergia_capensis,((ML_Trichilia_cipo,ML_Trichilia_martiana),(((((ML_Guarea_guidonia,ML_Guarea_glabra),ML_Dysoxylum_rufum),ML_Amoora_rohituka),ML_Synoum_glandulosum),ML_Anthocarpa_nitidula)))))MELIACEAE,(((((((RT_Pelea_sp.,RT_Acronychia_pedunculata),((RT_Vepris_undulata,RT_Vepris_nobilis),(RT_Teclea_gerrardii,RT_Teclea_natalensis))),(RT_Tetradium_trichotomum,(RT_Geijera_parviflora,(RT_Zanthoxylum_capense,(RT_Zanthoxylum_kellermanii,(RT_Zanthoxylum_ekmanii,RT_Zanthoxylum_panamense)))))),RT_Calodendrum_capense),(RT_Aegle_marmelos,RT_Clausena_anisata)),RT_Ptaeroxylon_obliquum)RUTACEAE,(SI_Eurycoma_longifolia,SI_Simar ouba_amara)SIMAROUBACEAE)),(((((((SP_Acer_negundo,(SP_Acer_pensylvanicum,((SP_Acer_platanoides,SP_Acer_campestre),SP_Acer_mono))),SP_Acer_rubrum),((SP_Acer_saccharum,(SP_Acer_opalus,SP_Acer_monspessulanum)),SP_Acer_palmatum)),SP_Acer_pseudoplatanus),(SP_Aesculus_californica,SP_Aesculus_hippocastanum)),SP_Hippobromus_pauciflorus),(((SP_Litchi_chinensis,(SP_Pancovia_golungensis,SP_Pancovia_turbinata)),(((SP_Diploglottis_cunninghamii,SP_Elattostachys_nervosa),((SP_Cupania_dentata,SP_Cupania_rufescens,SP_Cupania_sylvatica),SP_Mischocarpus_australis)),((SP_Sapindus_mukorossi,SP_Sapindus_saponaria),((SP_Allophylus_camptostachys,SP_Allophylus_zeylanicus),(SP_Cardiospermum_halicacabum,(SP_Serjania_brachycarpa,SP_Paullinia_fibrigera)))))),SP_Schleichera_oleosa))SAPINDACEAE),(((AN_Spondias_pinnata,AN_Spondias_radlkoferi),((AN_Harpephyllum_caffrum,(AN_Tapirira_guianensis,(AN_Lannea_coromandelica,AN_Lannea_schweinfurthii))),((AN_Rhus_chirindensis,AN_Searsia_tomentosa),((AN_Buchanania_cochinchinensis,AN_Buchanania_obovata),(AN_Astronium_graveolens,(((AN_Anacardium_excelsum,(AN_Mangifera_foetida,AN_Mangifera_indica)),(AN_Trichoscypha_patens,AN_Semecarpus_anacardium)),((AN_Pistacia_lentiscus,AN_Pistacia_terebinthus),(AN_Toxicodendron_succedaneum,(AN_Rhus_typhina,AN_Rhus_sandwicensis)))))))))ANACARDIACEAE,((((BU_Protium_tenuifolium,BU_Protium_puncticulatum,BU_Protium_spruceanum),BU_Tetragastris_panamensis),BU_Bursera_simaruba),(BU_Boswellia_serrata,BU_Trattinnickia_aspera))BURSERACEAE))),(ST_Turpinia_insignis,ST_Turpinia_occidentalis)STAPHYLEACEAE),(((((A2_Alzatea_sp.,PE_Olinia_ventosa),((ME_Mouriri_uncitheca,ME_Mouriri_brachyanthera),(((((ME_Clidemia_sericea,(ME_Miconia_acinodendron,ME_Miconia_dispar,ME_Miconia_media,ME_Miconia_rivetii,(ME_Miconia_albicans,((ME_Miconia_minutiflora,ME_Miconia_ligustroides),ME_Miconia_argentea)))),ME_Graffenrieda_sp.),ME_Topobea_sp.),(ME_Macairea_rufescens,ME_Tibouchina_stenocarpa)),ME_Bellucia_grossularioides))MELASTOMATACEAE),(((VO_Qualea_dichotoma,VO_Qualea_grandiflora),(VO_Vochysia_ferruginea,VO_Vochysia_guatemalensis))VOCHYSIACEAE,(((((((((MT_Campomanesia_aromatica,MT_Psidium_guajava),MT_Amomyrtus_luma),(MT_Eugenia_mabaeoides,MT_Eugenia_casearioides,MT_Eugenia_woodii)),(MT_Myrceugenia_planipes,MT_Luma_apiculata)),MT_Rhodamnia_cinerea),((MT_Tristaniopsis_clementis,MT_Tristaniopsis_whiteana),((((((MT_Syzygium_crebrinerve,MT_Syzygium_jambos),MT_Syzygium_cumini),MT_Syzygium_eucalyptoides,MT_Syzygium_suborbiculare),((MT_Syzygium_stapfianum,MT_Syzygium_zeylanicum),MT_Syzygium_corynanthum)),MT_Syzygium_confertum,MT_Syzygium_houttuynii,MT_Syzygium_ingens,MT_Syzygium_megacarpum,MT_Syzygium_rugosum,MT_Syzygium_urophyllum),MT_Meterosideros_polymorpha))),((((MT_Corymbia_clavigera,MT_Corymbia_confertiflora),(MT_Corymbia_nesophila,(MT_Corymbia_porrecta,(MT_Corymbia_gummifera,((MT_Corymbia_terminalis,MT_Corymbia_foelscheana),MT_Corymbia_bleeseri))))),((MT_Eucalyptus_baxteri,MT_Eucalyptus_haemastoma,MT_Eucalyptus_obliqua,MT_Eucalyptus_umbra),((MT_Eucalyptus_brevifolia,MT_Eucalyptus_dumosa,MT_Eucalyptus_foecunda,MT_Eucalyptus_globulus,MT_Eucalyptus_incrassata,MT_Eucalyptus_intertexta,MT_Eucalyptus_paniculata,MT_Eucalyptus_pruinosa,MT_Eucalyptus_socialis,MT_Eucalyptus_tectifica),(MT_Eucalyptus_miniata,MT_Eucalyptus_tetrodonta)))),MT_Syncarpia_glomulifera)),(MT_Melaleuca_leucadendra,MT_Melaleuca_viridiflora)),(MT_Lophostemon_lactifluus,MT_Xanthostemon_paradoxus))MYRTACEAE)),((LY_Lagerstroemia_parviflora,LY_Lagerstroemia_speciosa),LY_Sonneratia_alba)LYTHRACEAE),(CO_Lumnitzera_littorea,(((CO_Combretum_apiculatum,CO_Combretum_fruticosum),CO_Combretum_latifolium),(((CO_Terminalia_arjuna,CO_Terminalia_alata),(CO_Anogeissus_latifolia,CO_Terminalia_chebula)),(CO_Pteleopsis_myrtifolia,(CO_Terminalia_bellirica,((CO_Terminalia_catappa,CO_Terminalia_arostrata,CO_Terminalia_microcarpa,CO_Terminalia_ferdinandiana,CO_Terminalia_canescens),CO_Terminalia_sericea))))))COMBRETACEAE)),(((((((((((((((BT_Alnus_incana,BT_Alnus_hirsuta),BT_Alnus_glutinosa),BT_Alnus_rhombifolia),BT_Alnus_japonica),BT_Alnus_maximowiczii),(BT_Betula_nigra,(BT_Betula_alleghaniensis,(BT_Betula_maximowicziana,((BT_Betula_ermanii,BT_Betula_davurica),(BT_Betula_pubescens,(BT_Betula_populifolia,((BT_Betula_pendula,BT_Betula_platyphylla),(BT_Betula_pumila,BT_Betula_papyrifera)))))))))),(BT_Corylus_avellana,(((BT_Carpinus_caroliniana,BT_Carpinus_betulus),BT_Carpinus_cordata),(BT_Ostrya_japonica,BT_Ostrya_virginiana))))BETULACEAE,CS_Allocasuarina_sp.),((JU_Engelhardtia_roxburghiana,((JU_Carya_cordiformis,((JU_Carya_alba,JU_Carya_glabra),JU_Carya_ovata)),(((JU_Juglans_nigr

```
a,JU_Juglans_cinerea),JU_Juglans_ailanthifolia),JU_Juglans_regia)))JUGLANDACEAE,(MY_Co
mptonia_peregrina,(MY_Myrica_esculenta,MY_Myrica_faya))MYRICACEAE)),(((FG_Fagus_cren
ata,FG_Fagus_sylvatica),FG_Fagus_grandifolia),(FG_Trigonobalanus_verticillata,(FG_Lithocarp
us_havilandii,(((FG_Castanopsis_indica,FG_Castanopsis_sieboldii),(FG_Castanea_dentata,FG_
Castanea_sativa)),(((((((FG_Quercus_robur,FG_Quercus_faginea),FG_Quercus_mongolica),FG_
Quercus_petraea,FG_Quercus_pubescens,FG_Quercus_pyrenaica),((FG_Quercus_michauxii,(F
G_Quercus_stellata,(FG_Quercus_margarettiae,(FG_Quercus_austrina,FG_Quercus_chapmanii
)))),(FG_Quercus_alba,FG_Quercus_lobata),FG_Quercus_douglasii,FG_Quercus_turbinella,FG_
Quercus_macrocarpa))Quercus,(FG_Quercus_virginiana,(FG_Quercus_geminata,FG_Quercus_
minima))Virentes),((FG_Quercus_incana,(((FG_Quercus_falcata,FG_Quercus_laevis),((FG_Quer
cus_nigra,FG_Quercus_hemisphaerica),FG_Quercus_laurifolia)),(FG_Quercus_shumardii,(FG_
Quercus_pumila,FG_Quercus_myrtifolia)))),(FG_Quercus_rubra,(FG_Quercus_velutina,(FG_Que
rcus_ellipsoidalis,FG_Quercus_coccinea))),FG_Quercus_agrifolia,FG_Quercus_kelloggii,FG_Qu
ercus_xalapensis)Lobatae),(((FG_Quercus_salicina,FG_Quercus_acuta),FG_Quercus_myrsinifol
ia)yclobalanopsisis,((FG_Quercus_Ilex,FG_Quercus_rotundifolia),(FG_Quercus_cerris,FG_Quer
cus_suber))Cerris_&_Ilex))))))FAGACEAE),(NO_Nothofagus_menziesii,(NO_Nothofagus_dombe
yi,((NO_Nothofagus_antarctica,NO_Nothofagus_pumilio),(NO_Nothofagus_betuloides,NO_Notho
fagus_nitida))))NOTHOFAGACEAE),(((CU_Dieterlea_fusiformis,CU_Doyerea_emetocathartica),
CU_Cayaponia_granatensis),CU_Nothoalsomitra_suberosa)CUCURBITACEAE),(((((((((MR_Arto
carpus_heterophyllus,MR_Artocarpus_lakoocha),MR_Clarisia_biflora),(MR_Trophis_mexicana,M
R_Morus_alba)),(((((MR_Castilla_elastica,MR_Poulsenia_armata),MR_Perebea_mollis),(MR_Ps
eudolmedia_laevis,MR_Pseudolmedia_glabrata)),(((((MR_Ficus_watkinsiana,(MR_Ficus_bengha
lensis,MR_Ficus_rumphii)),(MR_Ficus_obtusifolia,MR_Ficus_aurea)),MR_Ficus_fistulosa),((MR_
Ficus_religiosa,MR_Ficus_superba),((MR_Ficus_callosa,(MR_Ficus_racemosa,MR_Ficus_auricu
lata)),(MR_Ficus_carica,(((MR_Ficus_scobina,MR_Ficus_cyrtophylla),MR_Ficus_subulata),(MR_
Ficus_hirta,MR_Ficus_grossularioides)))))),MR_Ficus_yoponensis)),(MR_Cudrania_cochinchinen
sis,(MR_Alchornea_scandens,(MR_Trilepisium_madagascariense,((MR_Brosimum_alicastrum,M
R_Brosimum_utile),MR_Brosimum_lactescens))))))MORACEAE,(((UR_Cecropia_ficifolia,(UR_Ce
cropia_longipes,(UR_Cecropia_obtusifolia,UR_Cecropia_insignis))),(UR_Pipturus_albidus,UR_P
ourouma_bicolor)),(UR_Urera_caracasana,(UR_Dendrocnide_excelsa,UR_Dendrocnide_photinip
hylla)))URTICACEAE),(((CN_Celtis_africana,CN_Celtis_occidentalis),CN_Celtis_gomphophylla),(
CN_Trema_orientalis,(CN_Trema_micrantha,CN_Trema_tomentosa)))CANNABACEAE),(UL_Ch
aetachme_aristata,(UL_Holoptelea_integrifolia,(((UL_Ulmus_glabra,(UL_Ulmus_laciniata,UL_Ul
mus_davidiana)),UL_Ulmus_rubra),(UL_Ulmus_thomasii,(UL_Ulmus_americana,UL_Ulmus_laevi
s)))))ULMACEAE),(EL_Elaeagnus_angustifolia,((RH_Frangula_dodonei,RH_Rhamnus_glandulos
a),((RH_Ventilago_viminalis,RH_Ventilago_denticulata),(RH_Hovenia_acerba,((RH_Ziziphus_att
opensis,RH_Ziziphus_glaberrima),(RH_Ziziphus_jujuba,RH_Ziziphus_mucronata)))))RHAMNAC
EAE)),((((((RO_Cerasus_vulgaris,RO_Padus_avium),RO_Prunus_pensylvanica),RO_Cerasus_s
achailnensis),(RO_Cerasus_lusitanica,(RO_Prunus_serotina,(RO_Padus_ssiori,RO_Padus_virgi
niana)))),(((((RO_Pyrus_bourgaeana,RO_Pyrus_pyraster),RO_Stranvaesia_davidiana),(RO_Mal
us_domestica,RO_Malus_sylvestris)),(RO_Crataegus_monogyna,RO_Amelanchier_sanguinea)),
((RO_Sorbus_alnifolia,RO_Sorbus_intermedia),(RO_Sorbus_commixta,RO_Sorbus_aucuparia),
RO_Sorbus_aria))),(((RO_Rubus_corylifolius,(RO_Rubus_hispidus,RO_Rubus_fruticosus)),RO_
Rubus_moluccanus),RO_Rosa_arvensis))ROSACEAE)),((PG_Securidaca_inappendiculata,PG_
Xanthophyllum_stipitatum)POLYGALACEAE,((((FA_Bauhinia_variegata,(FA_Bauhinia_multinervi
a,FA_Bauhinia_rufa)),(FA_Lysiphyllum_cunninghamii,(FA_Bauhinia_racemosa,FA_Bauhinia_gla
uca,FA_Bauhinia_yunnanensis))),(((((FA_Copaifera_duckei,(FA_Eperua_leucantha,FA_Eperua_
purpurea)),(FA_Colophospermum_mopane,FA_Hardwickia_binata)),FA_Prioria_copaifera),(FA_
Saraca_indica,(((((FA_Anthonotha_graciliflora,FA_Anthonotha_macrophylla),FA_Berlinia_auricul
ata),FA_Brachystegia_spiciformis,FA_Julbernardia_globiflora),FA_Librevillea_klainei),FA_Cynom
etra_retusa))),((FA_Dialium_guianense,FA_Dialium_schlechteri),((FA_Umtiza_listeriana,FA_Cera
tonia_siliqua),(((FA_Caesalpinia_granadillo,FA_Caesalpinia_scortechinii),(FA_Cassia_fistula,FA_
Cassia_grandis)),(((FA_Tachigali_versicolor,FA_Tachigali_myrmecophila),FA_Sclerolobium_para
```

```
ense,FA_Burkea_africana),((((((((((FA_Acacia_holosericea,FA_Acacia_auriculiformis,FA_Acacia
_floribunda,FA_Acacia_mimula),(FA_Pithecellobium_dulce,FA_Pithecellobium_lanceolatum)),(FA
_Inga_punctata,FA_Inga_quaternata)),(FA_Chloroleucon_mangense,(FA_Albizia_saman,(FA_Al
bizia_adianthifolia,FA_Albizia_antunesiana)))),FA_Acacia_nigrescens),(FA_Mimosa_albida,FA_
Mimosa_micheliana)),(FA_Acacia_karroo,FA_Acacia_robusta)),(FA_Prosopis_glandulosa,FA_Pr
osopis_juliflora)),FA_Newtonia_hildebrandtii),((FA_Erythrophleum_chlorostachys,FA_Erythrophle
um_lasianthum)Caesalpinioideae,FA_Entada_polystachya))Mimosoideae))))))Caesalpinioideae,((
((FA_Vatairea_lundellii,((FA_Nissolia_leiogyne,((FA_Pterocarpus_marsupium,FA_Pterocarpus_r
ohrii),(FA_Dalbergia_melanoxylon,FA_Dalbergia_armata,FA_Dalbergia_sissoo))),((((((((FA_Millet
tia_dielsiana,(FA_Millettia_leptobotrya,FA_Millettia_pachycarpa)),FA_Millettia_dura,FA_Pongami
a_pinnata),(FA_Derris_involuta,(FA_Lonchocarpus_dipteroneurus,(FA_Lonchocarpus_guatemale
nsis,FA_Lonchocarpus_heptaphyllus)))),FA_Galactia_acapulcensis),(FA_Mucuna_macrocarpa,((
(FA_Erythrina_excelsa,FA_Erythrina_caffra),FA_Erythrina_folkersii),(FA_Spatholobus_suberectu
s,FA_Butea_monosperma)))),FA_Craspedolobium_schochii),(FA_Callerya_cinerea,(FA_Courseti
a_ferruginea,FA_Robinia_pseudoacacia))),(FA_Poecilanthe_effusa,(FA_Laburnum_anagyroides,
(FA_Bowdichia_virgilioides,(FA_Bolusanthus_speciosus,(FA_Sophora_chrysophylla,FA_Maackia
_amurensis)))))))),FA_Andira_inermis),(FA_Dussia_mexicana,FA_Dussia_munda)),FA_Swartzia
_simplex)Papilioloideae)FABACEAE)),(ZY_Balanites_maughamii,ZY_Bulnesia_arborea)ZYGOP
HYLLACEAE),(((((((IX_Ixonanthes_reticulata,((((((((PH_Baccaurea_racemosa,PH_Baccaurea_pa
rviflora,PH_Baccaurea_ramiflora),PH_Baccaurea_reticulata),(PH_Aporosa_lunata,PH_Aporosa_
subcaudata,PH_Aporosa_microstachya)),PH_Protomegabaria_stapfiana),(PH_Hyeronima_alche
ornoides,PH_Hymenocardia_ulmoides)),PH_Uapaca_staudtii),PH_Bischofia_javanica),((PH_Acte
phila_lindleyi,PH_Phyllanthus_flexuosus),(PH_Cleistanthus_schlechteri,(PH_Bridelia_insulana,P
H_Bridelia_retusa))))PHYLLANHACEAE),(((EU_Alchornea_costaricensis,EU_Discoglypremna_c
aloneura),((EU_Ptychopyxis_caputmedusae,(((EU_Macaranga_heynei,(EU_Macaranga_hypoleu
ca,EU_Macaranga_triloba)),EU_Macaranga_lowii),(EU_Mallotus_nesophilus,(EU_Mallotus_panic
ulatus,EU_Mallotus_philippensis)))),(EU_Dalechampia_scandens,(EU_Acalypha_skutchii,EU_Cl
aoxylon_indicum)))),((EU_Suregada_zanzibariensis,(((EU_Micrandra_sprucei,EU_Manihot_chlor
osticta),EU_Elateriospermum_tapos),(EU_Dodecastigma_uleanum,(((EU_Croton_billbergianus,E
U_Croton_schiedeanus),EU_Croton_steenkampianus),EU_Croton_draco)))),(EU_Omphalea_olei
fera,((EU_Dichostemma_glaucenscens,EU_Euphorbia_colletioides),(EU_Sapium_glandulosum,(
EU_Triadica_cochinchinensis,EU_Homalanthus_novoguineensis))))))EUPHORBIACEAE),((((MP
_Cottsia_scandens,MP_Cottsia_linearis),MP_Gaudichaudia_macvaughii),MP_Stigmaphyllon_lind
enianum),(((MP_Heteropterys_palmeri,MP_Heteropteris_sp.),MP_Tetrapterys_sp.),MP_Mascagn
ia_macroptera))MALPIGHIACEAE),(HU_Humiria_balsamifera,(AH_Kiggelaria_africana,(((GO_Go
upia_glabra,GO_Iryanthera_sagotiana)GOUPIACEAE,(VI_Rinorea_neglecta,(VI_Rinoreocarpus_
ulei,(VI_Amphirrhox_longifolia,VI_Orthion_oblanceolatum)))VIOLACEAE),((PA_Barteria_fistulosa
,(PA_Efulensia_clematoides,(((PA_Passiflora_edulis,PA_Passiflora_subpeltata),PA_Passiflora_f
oetida),PA_Passiflora_juliana)))PASSIFLORACEAE,(((SA_Casearia_arborea,SA_Casearia_sylv
estris),(((SA_Scolopia_mundii,SA_Scolopia_zeyheri),(SA_Pleuranthodendron_lindenii,SA_Dovya
lis_longispina)),(((((SA_Populus_maximowiczii,(SA_Populus_balsamifera,(SA_Populus_heteroph
ylla,SA_Populus_sieboldii))),SA_Populus_deltoides),SA_Populus_fremontii),(SA_Populus_alba,(
SA_Populus_tremuloides,SA_Populus_tremula))),((SA_Salix_glauca,(SA_Salix_caprea,SA_Salix
_planifolia)),(SA_Salix_laevigata,(SA_Salix_pentandra,(SA_Salix_fragilis,SA_Salix_alba))))))),(S
A_Zuelania_guidonia,SA_Lunania_mexicana))SALICACEAE))))),((((OC_Lophira_alata,OC_Ochn
a_natalitia)OCHNACEAE,((((CB_Hirtella_punctillata,CB_Hirtella_triandra),(CB_Licania_arborea,
CB_Licania_heteromorpha)),CB_Parinari_excelsa)CHRYSOBALANACEAE,(PU_Drypetes_argut
a,PU_Drypetes_natalensis)PUTRANJIVACEAE)),(CY_Caryocar_brasiliense,((((CI_Garcinia_oval
ifolia,CI_Garcinia_intermedia),(CI_Garcinia_mannii,(CI_Garcinia_bancana,CI_Garcinia_malacce
nsis))),(CI_Clusia_elliptica,CI_Clusia_multiflora))CLUCIACEAE,((((CL_Caraipa_heterocarpa,CL_
Kielmeyera_coriacea),(CL_Calophyllum_polyanthum,CL_Calophyllum_longifolium)),CL_Mamme
a_africana)CALOPHYLLACEAE,(HP_Vismia_japurensis,HP_Vismia_lauriformis)HYPERICACEA
E)))),((EY_Erythroxylum_densum,EY_Erythroxylum_cumanense,EY_Erythroxylum_orinocense)E
```

RYTHROXYLACEAE,(RZ_Cassipourea_ruwensorensis,(RZ_Carallia_brachiata,(RZ_Bruguiera_cylindrica,(RZ_Ceriops_tagal,(RZ_Rhizophora_apiculata,RZ_Rhizophora_mucronata)))))RHIZOPHORACEAE))),(C1_Connarus_suberosus,((C4_Pseudoweinmannia_lachnocarpa,(C4_Eucryphia_cordifolia,(C4_Cunonia_capensis,(C4_Weinmannia_sp.,C4_Weinmannia_trichosperma))))CUNONIACEAE,((EA_Elaeocarpus_angustifolius,EA_Elaeocarpus_sylvestris),EA_Sloanea_woollsii)ELAEOCARPACEAE))),(((((CE_Celastrus_orbiculatus,CE_Celastrus_paniculatus),(CE_Cassine_schinoides,CE_Euonymus_europaeus)),CE_Maytenus_magellanica),(CE_Maytenus_acuminata,CE_Maytenus_oleoides)),(CE_Prionostemma_aspera,(CE_Tontelea_ovalifolia,(CE_Salacia_leptoclada,CE_Salacia_cordata))))CELASTRACEAE))),(VT_Leea_asiatica,((((VT_Cissus_antarctica,VT_Cissus_hypoglauca),VT_Vitis_vinifera),(VT_Rhoicissus_tomentosa,(((VT_Cayratia_clematidea,VT_Cayratia_eurynema),(VT_Tetrastigma_nitens,VT_Tetrastigma_planicaule)),(VT_Cissus_verticillata,VT_Cissus_producta)))),VT_Nothocissus_sterculiifolia))VITACEAE),((AL_Liquidambar_styraciflua,(HA_Trichocladus_crinitus,HA_Trichocladus_ellipticus)HAMAMELIDACEAE),CC_Cercidiphyllum_japonicum))),BX_Buxus_macowanii),(PL_Platanus_occidentalis,((PC_Persoonia_linearis,PC_Faurea_macnaughtonii),((PC_Brabejum_stellatifolium,PC_Gevuina_avellana),((PC_Banksia_attenuata,PC_Banksia_menziesii),((PC_Xylomelum_pyriforme,PC_Helicia_glabriflora),(PC_Embothrium_coccineum,((PC_Hakea_arborescens,PC_Hakea_leucoptera),PC_Lomatia_hirsuta))))))PROTEACEAE)PROTEACEAE),(((BE_Berberis_ilicifolia,((RA_Clematis_vitalba,RA_Clematis_lasiantha),RA_Clematis_glycinoides)RANUNCULACEAE),(((MN_Stephania_japonica,MN_Cissampelos_pareira),(((MN_Anomospermum_reticulatum,(MN_Abuta_rufescens,MN_Abuta_panamensis)),MN_Cocculus_moorei),MN_Sarcopetalum_harveyanum)),(MN_Tinospora_sp.,MN_Tinomiscium_tonkinense))MENISPERMACECAE),LR_Akebia_trifoliata)),(AR_Pothos_longipes,(DO_Dioscorea_transversa,(((RI_Rhipogonum_elseyanum,RI_Rhipogonum_album)RHIPOGONACEAE,(SM_Smilax_australis,(SM_Smilax_aspera,(SM_Smilax_microphylla,(SM_Smilax_corbularia,SM_Smilax_hypoglauca))))SMILACACEAE),(XA_Geitonoplesium_cymosum,((AE_Calamus_muelleri,(AE_Livistona_humilis,((AE_Socratea_exorrhiza,AE_Dictyocaryum_sp.),(((AE_Archontophoenix_cunninghamiana,AE_Oenocarpus_mapora),AE_Astrocaryum_mexicanum),(AE_Chamaedorea_alternans,AE_Chamaedorea_pinnatifrons)))))ARECACEAE,(FL_Flagellaria_indica,PO_Bambusa_bambos))))))),(CH_Hedyosmum_mexicanum,((((((((((AO_Polyalthia_longifolia,(AO_Guamia_sp.,AO_Desmopsis_panamensis)),(AO_Polyalthia_pendula,AO_Miliusa_tomentosa)),AO_Monocarpia_marginalis),((AO_Fissistigma_polyanthoides,AO_Fissistigma_polyanthum),AO_Melodorum_leichhardtii)),((((AO_Annona_spraguei,(AO_Annona_coriacea,AO_Annona_squamosa)),AO_Monanthotaxis_caffra),(AO_Cymbopetalum_baillonii,(AO_Duguetia_furfuracea,AO_Duguetia_cadaverica))),(AO_Guatteria_dumentorum,AO_Artabotrys_honkongensis)))ANNONACEAE,EP_Eupomatia_laurina),(MA_Liriodendron_tulipifera,((MA_Magnolia_fraseri,(MA_Magnolia_grandiflora,MA_Magnolia_schiedeana)),(MA_Magnolia_obovata,(MA_Magnolia_nilagirica,MA_Magnolia_floribunda))))MAGNOLIACEAE),(MI_Horsfieldia_sp.,((MI_Virola_sebifera,MI_Virola_elongata),MI_Virola_surinamensis))MYRICACEAE),((AM_Daphnandra_micrantha,AM_Laureliopsis_philippiana)ATHEROSPERMATACEAE,((((LU_Cryptocarya_alba,LU_Cryptocarya_erythroxylon,LU_Cryptocarya_densiflora),(LU_Beilschmiedia_obtusifolia,LU_Endiandra_muelleri)),((((LU_Apollonias_barbujana,LU_Alseodaphne_petiolaris),LU_Machilus_thunbergii),(LU_Persea_lingue,LU_Persea_indica)),((LU_Laurus_azorica,(LU_Litsea_panamanja,(LU_Actinodaphne_ambigua,(LU_Neolitsea_dealbata,LU_Neolitsea_sericea)))),(((LU_Cinnamomum_oliveri,LU_Cinnamomum_tenuifolium),LU_Cinnamomum_barbeyanum),(((LU_Ocotea_esmeraldana,(LU_Nectandra_ambigens,LU_Nectandra_purpurea)),(LU_Licaria_brasiliensis,LU_Ocotea_aciphylla)),(LU_Ocotea_bullata,LU_Agathophyllum_perso onianum))))))LAURACEAE,(MO_Palmeria_scandens,(MO_Xymalos_monospora,MO_Kibara_macrophylla))MONIMIACEAE))),(((PP_Piper_amalago,PP_Piper_novaehollandiae')PIPERACEAE,A3_Aristolochia_taliscana),WI_Drimys_winteri)))),(SC_Illicium_anisatum,SC_Schisandra_repanda)SCHISANDRACEAE),(((GN_Gnetum_costatum,GN_Gnetum_gnemon),((GN_Gnetum_latifolium,GN_Gnetum_pendulum),GN_Gnetum_parvifolium))GNETACEAE,((((PI_Abies_alba,PI_Abies_lasiocarpa),PI_Tsuga_canadensis),((PI_Pseudotsuga_menziesii,(PI_Larix_decidua,PI_Larix_laricina)),((PI_Picea_sitchensis,((PI_Picea_glauca,PI_Picea_engelmannii),(PI_Picea_abies,PI_Picea_mariana))),(((((PI_Pinus_nigra,PI_Pinus_resinosa),PI_Pinus_sylvestris),((PI_Pinus_pinaster,PI_Pinus _canariensis),PI_Pinus_halepensis)),(PI_Pinus_banksiana,((PI_Pinus_ponderosa,PI_Pinus_jeffreyi),(PI_Pinus_palustris,(PI_Pinus_rigida,PI_Pinus_serotina))))),((PI_Pinus_monophylla,PI_Pinus_edulis),(PI_Pinus_flexilis,PI_Pinus_strobus))))))PINACEAE,((AU_Araucaria_araucana,(PD_Saxegothaea_conspicua,(PD_Prumnopitys_andina,(PD_Dacrydium_beccarii,(PD_Afrocarpus_falcatus,((PD_Podocarpus_neriifolius,PD_Podocarpus_elatus),(PD_Podocarpus_salignus,(PD_Podocarpus_nubigenus,(PD_Podocarpus_latifolius,PD_Podocarpus_elongatus))))))))PODOCARPACEAE),(TA_Taxus_baccata,((((C5_Juniperus_communis,(C5_Juniperus_phoenicea,(C5_Juniperus_virginiana,(C5_Juniperus_osteosperma,C5_Juniperus_monosperma)))),C5_Thuja_occidentalis),(C5_Callitris_columellaris,C5_Austrocedrus_chilensis)),C5_Taxodium_distichum)CUPRESSACEAE))))));

Appendix G: Conservatively resolved phylogenetic tree

Newick tree notation for conservatively resolved phylogenetic tree.

(((((((((((((((((((((C7_Viburnum_sp.,(C7_Lonicera_periclymenum,C7_Lonicera_hispidula))CAPRIFOLIACEAE,(((AA_Cephalaralia_cephalobotrys,((AA_Cussonia_spicata,AA_Cheirodendron_trigynum),(((AA_Polyscias_elegans,AA_Polyscias_murrayi),AA_Arthrophyllum_diversifolium),((AA_Schefflera_morototoni,AA_Schefflera_macrocarpa,AA_Schefflera_vinosa),AA_Dendropanax_arboreus,AA_Oreopanax_xalapensis))))ARALIACEAE,GR_Griselinia_littoralis),PN_Pennantia_cunninghamii)),ES_Polyosma_cunninghamii),(((((AS_Pentacalia_sp.,((AS_Baccharis_angustifolia,AS_Baccharis_macrantha),((AS_Bidens_reptans,AS_Lasianthaea_ceanothifolia),AS_Ageratina_dendroides))),(AS_Sinclairia_caducifolia,AS_Piptocarpha_rotundifolia)),AS_Brachylaena_neriifolia),AS_Gochnatia_floribunda),AS_Dasyphyllum_diacanthoides)ASTERACEAE),((AQ_Ilex_canariensis,(AQ_Ilex_opaca,(AQ_Ilex_mitis,(AQ_Ilex_anomala,(AQ_Ilex_aquifolium,AQ_Ilex_perado)))))AQUIFOLIACEAE,(CR_Citronella_moorei,(CR_Leptaulus_daphnoides,CR_Gonocaryum_sp.))CARDIOPTERIDACEAE)),((((((SR_Freylinia_lanceolata,SR_Myoporum_sandwicense)SCROPHULARIACEAE,((BG_Pandorea_pandorana,(BG_Jacaranda_copaia,((BG_Chilopsis_linearis,(((BG_Kigelia_africana,BG_Markhamia_lutea),(BG_Mayodendron_igneum,BG_Spathodea_campanulata)),(((BG_Amphitecna_tuxtlensis,BG_Crescentia_cujete),(BG_Handronathus_chrysanthus,BG_Handroanthus_billbergii)),BG_Tabebuia_rosea))),((BG_Adenocalymma_tanaeciicarpum,BG_Memora_sp.),((BG_Fridericia_schumanniana,BG_Fridericia_prancei),(BG_Pleonotoma_variabilis,(BG_Mansoa_verrucifera,BG_Bignonia_corymbosa)))))))BIGNONIACEAE,(AC_Avicennia_marina,((((LA_Aegiphila_costaricensis,LA_Aegiphila_lhotzkiana),(LA_Gmelina_leichardtii,LA_Tectona_grandis)),LA_Vitex_pinnata)LAMIACEAE,(VE_Citharexylum_macradenium,VE_Lantana_camara)VERBENACEAE)))),(((((OE_Olea_paniculata,(OE_Olea_europaea,(OE_Olea_woodiana,OE_Olea_capensis))),(OE_Chionanthus_virginicus,OE_Chionanthus_peglerae)),(OE_Phillyrea_angustifolia,OE_Picconia_excelsa)),((OE_Fraxinus_americana,OE_Fraxinus_pennsylvanica),(OE_Fraxinus_ornus,(OE_Fraxinus_nigra,(OE_Fraxinus_mandshurica,(OE_Fraxinus_angustifolia,OE_Fraxinus_excelsior)))))),OE_Nyctanthes_arbortristis)OLEACEAE),(BO_Bourreria_cumanensis,((BO_Cordia_caffra,BO_Cordia_dichotoma),(BO_Cordia_bicolor,BO_Cordia_megalantha,BO_Cordia_alliodora)))BORAGINACEAE),((((CV_Bonamia_trichantha,CV_Maripa_panamensis),(CV_Convolvulus_nodiflorus, CV_Merremia_quinquefolia))CONVOLVULACEAE,(SL_Solanum_refractum,SL_Solanum_stramoniifolium)SOLANACEAE),((((((((AP_Wrightia_natalensis,(AP_Wrightia_pubescens,AP_Wrightia_arborea)),(((AP_Urceola_rosea,AP_Beaumontia_grandiflora),(((AP_Marsdenia_lanata,AP_Pergularia_rostrata),AP_Polystemma_guatemalense),(AP_Parsonsia_fulva,(AP_Parsonsia_lilacina,AP_Parsonsia_ventricosa)))),AP_Funtumia_africana)),(AP_Cerbera_manghas,AP_Cascabela_thevetia)),(AP_Melodinus_australis,AP_Melodinus_cochinchinensis)),((AP_Stemmadenia_donnellsmithii,(AP_Kopsia_arborea,AP_Rauvolfia_vomitoria)),((AP_Aspidosperma_desmanthum,AP_Aspidosperma_album),(AP_Aspidosperma_tomentosum,AP_Aspidosperma_megalocarpon))))APOCYNACEAE,((LG_Strychnos_nuxvomica,(LG_Strychnos_decussata,LG_Strychnos_madagascariensis)),LG_Strychnos_henningsii)LOGANIACEAE),(GE_Fagraea_fragrans,GE_Macrocarpaea_sidiroana)GENTIANACEAE),((((RU_Faramea_occidentalis,RU_Faramea_platyneura),RU_Coussarea_albescens),(RU_Coprosma_ochracea,(RU_Morinda_jasminoides,((RU_Palicourea_guianensis,((RU_Psychotria_faxlucens,RU_Psychotria_chiapensis),RU_Palicourea_sp.)),(RU_Psychotria_capensis,(RU_Psychotria_simiarum,RU_Psychotria_flava)))))),(((RU_Pittoniotis_trichantha,(RU_Haldina_cordifolia,(RU_Mitragyna_parvifolia,(RU_Neolamarckia_cadamba,(RU_Uncaria_guianensis,RU_Uncaria_tomentosa,RU_Uncaria_macrophylla,RU_Uncaria_rhynchophylla))))),RU_Remijia_morilloi),(((RU_Chimarrhis_turbinata,RU_Alseis_blackiana),RU_Macrocnemum_roseum),((RU_Retiniphyllum_concolor,RU_Retiniphyllum_truncatum),(RU_Scyphiphora_hydrophylacea,(RU_Diplospora_malaccensis,(RU_Hyperacanthus_amoenus,(RU_Rothmannia_globosa,(RU_Gardenia_latifolia,(RU_Tamilnadia_uliginosa,RU_Tocoyena_formosa))))))))))RUBIACEAE))),(IC_Apodytes_dim idiata,IC_Iodes_vitiginea)ICACINACEAE)),((((((AT_Actinidia_arguta,((CT_Clethra_mexicana,CT_Purdiaea_nutans)CLETHRACEAE,((((((ER_Chamaedaphne_latifolia,(ER_Kalmia_angustifolia,ER_Kalmia_polifolia)),ER_Bejaria_aestuans),(ER_Hymenanthes_maxima,ER_Erica_arborea)),ER_Oxydendrum_arboreum),(ER_Vaccinium_floribundum,ER_Vaccinium_sp.)),(ER_Arbutus_menziesii,(ER_Arbutus_canariensis,ER_Arbutus_unedo)))ERICACEAE)),(S1_Styrax_camporum,SY_Symplocos_sumuntia)),(TH_Camellia_japonica,(TH_Schima_brevifolia,TH_Schima_superba))THEACEAE),(PT_Adinandra_dumosa,(PT_Cleyera_japonica,(PT_Eurya_japonica,PT_Visnea_mocanera)))PENTAPHYLACACEAE),((((PR_Jacquinia_pungens,PR_Jacquinia_armillaris),(PR_Parathesis_amplifolia,(((PR_Myrsine_seguinii,PR_Myrsine_andina),(PR_Rapanea_lessertiana,PR_Rapanea_melanophloeos)),(PR_Heberdenia_bahamensis,(PR_Embelia_australiana,PR_Cybianthus_marginatus)))))PRIMULACEAE,((((((((EB_Diospyros_malabarica,EB_Diospyros_kerrii,EB_Diospyros_nutans,EB_Diospyros_melanoxylon),(EB_Diospyros_inhacaensis,EB_Diospyros_dendo)),EB_Diospyros_cauliflora),(EB_Diospyros_natalensis,EB_Diospyros_hoyleana)),EB_Diospyros_pentamera),EB_Diospyros_maingayi),EB_Diospyros_whyteana),EB_Euclea_divinorum)EBENACEAE),(((SO_Madhuca_longifolia,SO_Madhuca_sp.),(SO_Sideroxylon_inerme,(SO_Inhambanella_henriquezii,((SO_Mimusops_elengi,SO_Mimusops_obovata),(SO_Manilkara_hexandra,(SO_Manilkara_huberi,SO_Manilkara_bidentata)))))),(SO_Englerophytum_natalense,(((SO_Micropholis_sp.,SO_Micropholis_maguirei),SO_Chrysophyllum_argenteum),((SO_Niemeyera_chartacea,SO_Planchonella_obovata),(SO_Pouteria_venosa,SO_Pouteria_macrophylla,SO_Pouteria_reticulata,SO_Pouteria_rhynchocarpa,SO_Pouteria_durlandii)))))SAPOTACEAE)),(((LE_Lecythis_sp.,LE_Lecythis_lurida),LE_Couratari_guianensis),(LE_Barringtonia_macrostachya,LE_Planchonia_careya))LECYTHIDACEAE)),((((C2_Alangium_chinensis,C2_Alangium_villosum),((C2_Cornus_controversa,C2_Cornus_alternifolia),C2_Cornus_florida)),C2_Nyssa_sylvatica)CORNACEAE,(C6_Curtisia_dentata,HY_Schizophragma_hydrangeoides))),((CA_Pereskia_guamacho,NY_Neea_obovata),(PY_Antigonon_flavescens,PY_Coccoloba_hondurensis)POLYGONACEAE)),AX_Aextoxicon_punctatum),(C3_Coula_edulis,((OL_Heisteria_scandens,OL_Strombosia_scheffleri)OLACACEAE,((SN_Exocarpos_aphyllus,SN_Santalum_acuminatum)SANTALACEAE,LO_Nuytsia_floribunda)))),(DI_Davilla_rugosa,(DI_Doliocarpus_dentatus,DI_Dillenia_indica))DILLENIACEAE),((((((((CP_Cladostemon_kirkii,(((CP_Capparis_odoratissima,CP_Morisonia_americana),(CP_Capparis_baducca,CP_Capparis_pachaca)),(CP_Capparis_linearis,CP_Capparis_flexuosa)))CAPPARACEAE,(((((MV_Byttneria_aspera,MV_Kleinhovia_hospita),(MV_Commersonia_bartramia,((MV_Apeiba_glabra,MV_Apeiba_membranacea,MV_Apeiba_tibourbou),(MV_Heliocarpus_appendiculatus,(MV_Luehea_seemannii,((MV_Trichospermum_mexicanum,MV_Trichospermum_pleiostigma),MV_Grewia_asiatica)))))),(((MV_Brachychiton_discolor,MV_Brachychiton_populneus,MV_Brachychiton_megaphyllus),((MV_Firmiana_colorata,MV_Pterygota_alata),(MV_Heritiera_actinophylla,MV_Heritiera_trifoliolata))),(((MV_Tilia_maximowicziana,MV_Tilia_americana),(MV_Tilia_cordata,MV_Tilia_japonica)),(((MV_Pterospermum_acerifolium,MV_Dombeya_kirkii),(MV_Cola_greenwayi,MV_Mortoniodendron_guatemalense)),((((MV_Quararibea_asterolepis,MV_Quararibea_yunckeri),(((MV_Hampea_nutricia,MV_Thespesia_populnea),MV_Robinsonella_mirandae),(MV_Hibiscus_sp.,MV_Hibiscus_tiliaceus))),(MV_Catostemma_sp.,((MV_Pseudobombax_septenatum,MV_Ceiba_pentandra),(MV_Bombax_ceiba,(MV_Pachira_sordida,MV_Pachira_humilis))))),MV_Ochroma_pyramidale))))),(TY_Enkleia_malaccensis,TY_Ovidia_pillopillo)THYMELAEACEAE),((DP_Monotes_glaber,(DP_Dipterocarpus_sublamellatus,((DP_Shorea_argentifolia,DP_Shorea_robusta),(DP_Parashorea_malaanonan,DP_Parashorea_chinensis))))DIPTEROCARPACEAE,(BI_Cochlospermum_fraseri,BI_Cochlospermum_vitifolium)BIXACEAE))),(((((ML_Toona_australis,(ML_Carapa_guianensis,(ML_Soymida_febrifuga,ML_Swietenia_mahagoni))),(ML_Azadirachta_indica,(ML_Ekebergia_capensis,((ML_Trichilia_cipo,ML_Trichilia_martiana),(((((ML_Guarea_guidonia,ML_Guarea_glabra),ML_Dysoxylum_rufum),ML_Amoora_rohituka),ML_Synoum_glandulosum),ML_Anthocarpa_nitidula)))))MELIACEAE,(((((((RT_Pelea_sp.,RT_Acronychia_pedunculata),((RT_Vepris_undulata,RT_Vepris_nobilis),(RT_Teclea_gerrardii,RT_Teclea_natalensis))),(RT_Tetradium_trichotomum,(RT_Geijera_parviflora,(RT_Zanthoxylum_capense,(RT_Zanthoxylum_kellermanii,(RT_Zanthoxylum_ekmanii,RT_Zanthoxylum_panamense)))))),RT_Calodendrum_capense),(RT_Aegle_marmelos,RT_Clausena_anisata)),RT_Ptaeroxylon_obliquum)RUTACEAE,(SI_Eurycoma_longifolia,SI_Simar ouba_amara)SIMAROUBACEAE)),(((((((SP_Acer_negundo,(SP_Acer_pensylvanicum,((SP_Acer_platanoides,SP_Acer_campestre),SP_Acer_mono))),SP_Acer_rubrum),((SP_Acer_saccharum,(SP_Acer_opalus,SP_Acer_monspessulanum)),SP_Acer_palmatum)),SP_Acer_pseudoplatanus),(SP_Aesculus_californica,SP_Aesculus_hippocastanum)),SP_Hippobromus_pauciflorus),(((SP_Litchi_chinensis,(SP_Pancovia_golungensis,SP_Pancovia_turbinata)),(((SP_Diploglottis_cunninghamii,SP_Elattostachys_nervosa),((SP_Cupania_dentata,SP_Cupania_rufescens,SP_Cupania_sylvatica),SP_Mischocarpus_australis)),((SP_Sapindus_mukorossi,SP_Sapindus_saponaria),((SP_Allophylus_camptostachys,SP_Allophylus_zeylanicus),(SP_Cardiospermum_halicacabum,(SP_Serjania_brachycarpa,SP_Paullinia_fibrigera)))))),SP_Schleichera_oleosa))SAPINDACEAE),(((AN_Spondias_pinnata,AN_Spondias_radlkoferi),((AN_Harpephyllum_caffrum,(AN_Tapirira_guianensis,(AN_Lannea_coromandelica,AN_Lannea_schweinfurthii))),((AN_Rhus_chirindensis,AN_Searsia_tomentosa),((AN_Buchanania_cochinchinensis,AN_Buchanania_obovata),(AN_Astronium_graveolens,(((AN_Anacardium_excelsum,(AN_Mangifera_foetida,AN_Mangifera_indica)),(AN_Trichoscypha_patens,AN_Semecarpus_anacardium)),((AN_Pistacia_lentiscus,AN_Pistacia_terebinthus),(AN_Toxicodendron_succedaneum,(AN_Rhus_typhina,AN_Rhus_sandwicensis)))))))))ANACARDIACEAE,((((BU_Protium_tenuifolium,BU_Protium_puncticulatum,BU_Protium_spruceanum),BU_Tetragastris_panamensis),BU_Bursera_simaruba),(BU_Boswellia_serrata,BU_Trattinnickia_aspera))BURSERACEAE))),(ST_Turpinia_insignis,ST_Turpinia_occidentalis)STAPHYLEACEAE),(((((A2_Alzatea_sp.,PE_Olinia_ventosa),((ME_Mouriri_uncitheca,ME_Mouriri_brachyanthera),(((((ME_Clidemia_sericea,(ME_Miconia_acinodendron,ME_Miconia_dispar,ME_Miconia_media,ME_Miconia_rivetii,ME_Miconia_albicans,ME_Miconia_minutiflora,ME_Miconia_ligustroides,ME_Miconia_argentea)),ME_Graffenrieda_sp.),ME_Topobea_sp.),(ME_Macairea_rufescens,ME_Tibouchina_stenocarpa)),ME_Bellucia_grossularioides))MELASTOMATACEAE),(((VO_Qualea_dichotoma,VO_Qualea_grandiflora),(VO_Vochysia_ferruginea,VO_Vochysia_guatemalensis))VOCHYSIACEAE,(((((((((MT_Campomanesia_aromatica,MT_Psidium_guajava),MT_Amomyrtus_luma),(MT_Eugenia_mabaeoides,MT_Eugenia_casearioides,MT_Eugenia_woodii)),(MT_Myrceugenia_planipes,MT_Luma_apiculata)),MT_Rhodamnia_cinerea),((MT_Tristaniopsis_clementis,MT_Tristaniopsis_whiteana),((MT_Syzygium_crebrinerve,MT_Syzygium_jambos,MT_Syzygium_cumini,MT_Syzygium_eucalyptoides,MT_Syzygium_suborbiculare,MT_Syzygium_stapfianum,MT_Syzygium_zeylanicum,MT_Syzygium_corynanthum,MT_Syzygium_confertum,MT_Syzygium_houttuynii,MT_Syzygium_ingens,MT_Syzygium_megacarpum,MT_Syzygium_rugosum,MT_Syzygium_urophyllum),MT_Meterosideros_polymorpha))),((((MT_Corymbia_clavigera,MT_Corymbia_confertiflora),(MT_Corymbia_nesophila,(MT_Corymbia_porrecta,(MT_Corymbia_gummifera,((MT_Corymbia_terminalis,MT_Corymbia_foelscheana),MT_Corymbia_bleeseri))))),((MT_Eucalyptus_baxteri,MT_Eucalyptus_haemastoma,MT_Eucalyptus_obliqua,MT_Eucalyptus_umbra),((MT_Eucalyptus_brevifolia,MT_Eucalyptus_dumosa,MT_Eucalyptus_foecunda,MT_Eucalyptus_globulus,MT_Eucalyptus_incrassata,MT_Eucalyptus_intertexta,MT_Eucalyptus_paniculata,MT_Eucalyptus_pruinosa,MT_Eucalyptus_socialis,MT_Eucalyptus_tectifica),(MT_Eucalyptus_miniata,MT_Eucalyptus_tetrodonta)))),MT_Syncarpia_glomulifera)),(MT_Melaleuca_leucadendra,MT_Melaleuca_viridiflora)),(MT_Lophostemon_lactifluus,MT_Xanthostemon_paradoxus))MYRTACEAE)),((LY_Lagerstroemia_parviflora,LY_Lagerstroemia_speciosa),LY_Sonneratia_alba)LYTHRACEAE),(CO_Lumnitzera_littorea,(((CO_Combretum_apiculatum,CO_Combretum_fruticosum),CO_Combretum_latifolium),(((CO_Terminalia_arjuna,CO_Terminalia_alata),(CO_Anogeissus_latifolia,CO_Terminalia_chebula)),(CO_Pteleopsis_myrtifolia,(CO_Terminalia_bellirica,((CO_Terminalia_catappa,CO_Terminalia_arostrata,CO_Terminalia_microcarpa,CO_Terminalia_ferdinandiana,CO_Terminalia_canescens),CO_Terminalia_sericea))))))COMBRETACEAE)),(((((((((((((((BT_Alnus_incana,BT_Alnus_hirsuta),BT_Alnus_glutinosa),BT_Alnus_rhombifolia),BT_Alnus_japonica),BT_Alnus_maximowiczii),(BT_Betula_nigra,(BT_Betula_alleghaniensis,(BT_Betula_maximowicziana,((BT_Betula_ermanii,BT_Betula_davurica),(BT_Betula_pubescens,(BT_Betula_populifolia,((BT_Betula_pendula,BT_Betula_platyphylla),(BT_Betula_pumila,BT_Betula_papyrifera))))))))),(BT_Corylus_avellana,(((BT_Carpinus_caroliniana,BT_Carpinus_betulus),BT_Carpinus_cordata),(BT_Ostrya_japonica,BT_Ostrya_virginiana))))BETULACEAE,CS_Allocasuarina_sp.),((JU_Engelhardtia_roxburghiana,((JU_Carya_cordiformis,((JU_Carya_alba,JU_Carya_glabra),JU_Carya_ovata)),(((JU_Juglans_nigra,JU_Jug

```
lans_cinerea),JU_Juglans_ailanthifolia),JU_Juglans_regia)))JUGLANDACEAE,(MY_Comptonia_
peregrina,(MY_Myrica_esculenta,MY_Myrica_faya))MYRICACEAE)),(((FG_Fagus_crenata,FG_F
agus_sylvatica),FG_Fagus_grandifolia),(FG_Trigonobalanus_verticillata,(FG_Lithocarpus_havila
ndii,(((FG_Castanopsis_indica,FG_Castanopsis_sieboldii),(FG_Castanea_dentata,FG_Castanea
_sativa)),(((((FG_Quercus_robur,FG_Quercus_faginea,FG_Quercus_mongolica,FG_Quercus_pe
traea,FG_Quercus_pubescens,FG_Quercus_pyrenaica),(FG_Quercus_michauxii,FG_Quercus_s
tellata,FG_Quercus_margarettiae,FG_Quercus_austrina,FG_Quercus_chapmanii,FG_Quercus_a
lba,FG_Quercus_lobata,FG_Quercus_douglasii,FG_Quercus_turbinella,FG_Quercus_macrocarp
a))Quercus,(FG_Quercus_virginiana,(FG_Quercus_geminata,FG_Quercus_minima))Virentes),(F
G_Quercus_incana,FG_Quercus_falcata,FG_Quercus_laevis,FG_Quercus_nigra,FG_Quercus_h
emisphaerica,FG_Quercus_laurifolia,FG_Quercus_shumardii,FG_Quercus_pumila,FG_Quercus_
myrtifolia,FG_Quercus_rubra,FG_Quercus_velutina,FG_Quercus_ellipsoidalis,FG_Quercus_cocc
inea,FG_Quercus_agrifolia,FG_Quercus_kelloggii,FG_Quercus_xalapensis)Lobatae),(((FG_Quer
cus_salicina,FG_Quercus_acuta),FG_Quercus_myrsinifolia)yclobalanopsisis,((FG_Quercus_Ilex,
FG_Quercus_rotundifolia),(FG_Quercus_cerris,FG_Quercus_suber))Cerris_&_Ilex))))))FAGACE
AE),(NO_Nothofagus_menziesii,(NO_Nothofagus_dombeyi,((NO_Nothofagus_antarctica,NO_Not
hofagus_pumilio),(NO_Nothofagus_betuloides,NO_Nothofagus_nitida))))NOTHOFAGACEAE),(((
CU_Dieterlea_fusiformis,CU_Doyerea_emetocathartica),CU_Cayaponia_granatensis),CU_Notho
alsomitra_suberosa)CUCURBITACEAE),(((((((((MR_Artocarpus_heterophyllus,MR_Artocarpus_l
akoocha),MR_Clarisia_biflora),(MR_Trophis_mexicana,MR_Morus_alba)),(((((MR_Castilla_elasti
ca,MR_Poulsenia_armata),MR_Perebea_mollis),(MR_Pseudolmedia_laevis,MR_Pseudolmedia_
glabrata)),(((((MR_Ficus_watkinsiana,(MR_Ficus_benghalensis,MR_Ficus_rumphii)),(MR_Ficus_
obtusifolia,MR_Ficus_aurea)),MR_Ficus_fistulosa),((MR_Ficus_religiosa,MR_Ficus_superba),((M
R_Ficus_callosa,(MR_Ficus_racemosa,MR_Ficus_auriculata)),(MR_Ficus_carica,(((MR_Ficus_s
cobina,MR_Ficus_cyrtophylla),MR_Ficus_subulata),(MR_Ficus_hirta,MR_Ficus_grossularioides))
)))),MR_Ficus_yoponensis)),(MR_Cudrania_cochinchinensis,(MR_Alchornea_scandens,(MR_Tril
episium_madagascariense,((MR_Brosimum_alicastrum,MR_Brosimum_utile),MR_Brosimum_lact
escens))))))MORACEAE,(((UR_Cecropia_ficifolia,(UR_Cecropia_longipes,(UR_Cecropia_obtusif
olia,UR_Cecropia_insignis))),(UR_Pipturus_albidus,UR_Pourouma_bicolor)),(UR_Urera_caracas
ana,(UR_Dendrocnide_excelsa,UR_Dendrocnide_photiniphylla)))URTICACEAE),(((CN_Celtis_af
ricana,CN_Celtis_occidentalis),CN_Celtis_gomphophylla),(CN_Trema_orientalis,(CN_Trema_mic
rantha,CN_Trema_tomentosa)))CANNABACEAE),(UL_Chaetachme_aristata,(UL_Holoptelea_int
egrifolia,(((UL_Ulmus_glabra,(UL_Ulmus_laciniata,UL_Ulmus_davidiana)),UL_Ulmus_rubra),(UL
_Ulmus_thomasii,(UL_Ulmus_americana,UL_Ulmus_laevis)))))ULMACEAE),(EL_Elaeagnus_ang
ustifolia,((RH_Frangula_dodonei,RH_Rhamnus_glandulosa),((RH_Ventilago_viminalis,RH_Ventil
ago_denticulata),(RH_Hovenia_acerba,((RH_Ziziphus_attopensis,RH_Ziziphus_glaberrima),(RH
_Ziziphus_jujuba,RH_Ziziphus_mucronata)))))RHAMNACEAE)),((((((RO_Cerasus_vulgaris,RO_
Padus_avium),RO_Prunus_pensylvanica),RO_Cerasus_sachailnensis),(RO_Cerasus_lusitanica,
(RO_Prunus_serotina,(RO_Padus_ssiori,RO_Padus_virginiana)))),(((((RO_Pyrus_bourgaeana,R
O_Pyrus_pyraster),RO_Stranvaesia_davidiana),(RO_Malus_domestica,RO_Malus_sylvestris)),(
RO_Crataegus_monogyna,RO_Amelanchier_sanguinea)),(RO_Sorbus_alnifolia,RO_Sorbus_inte
rmedia,RO_Sorbus_commixta,RO_Sorbus_aucuparia,RO_Sorbus_aria))),(((RO_Rubus_corylifoli
us,(RO_Rubus_hispidus,RO_Rubus_fruticosus)),RO_Rubus_moluccanus),RO_Rosa_arvensis))
ROSACEAE)),((PG_Securidaca_inappendiculata,PG_Xanthophyllum_stipitatum)POLYGALACEA
E,((((FA_Bauhinia_variegata,(FA_Bauhinia_multinervia,FA_Bauhinia_rufa)),(FA_Lysiphyllum_cun
ninghamii,(FA_Bauhinia_racemosa,FA_Bauhinia_glauca,FA_Bauhinia_yunnanensis))),(((((FA_C
opaifera_duckei,(FA_Eperua_leucantha,FA_Eperua_purpurea)),(FA_Colophospermum_mopane,
FA_Hardwickia_binata)),FA_Prioria_copaifera),(FA_Saraca_indica,(((((FA_Anthonotha_graciliflor
a,FA_Anthonotha_macrophylla),FA_Berlinia_auriculata),FA_Brachystegia_spiciformis,FA_Julber
nardia_globiflora),FA_Librevillea_klainei),FA_Cynometra_retusa))),((FA_Dialium_guianense,FA_
Dialium_schlechteri),((FA_Umtiza_listeriana,FA_Ceratonia_siliqua),(((FA_Caesalpinia_granadillo,
FA_Caesalpinia_scortechinii),(FA_Cassia_fistula,FA_Cassia_grandis)),(((FA_Tachigali_versicolo
r,FA_Tachigali_myrmecophila),FA_Sclerolobium_paraense,FA_Burkea_africana),((((((((((FA_Aca
```

cia_holosericea,FA_Acacia_auriculiformis,FA_Acacia_floribunda,FA_Acacia_mimula),(FA_Pithecellobium_dulce,FA_Pithecellobium_lanceolatum)),(FA_Inga_punctata,FA_Inga_quaternata)),(FA_Chloroleucon_mangense,(FA_Albizia_saman,(FA_Albizia_adianthifolia,FA_Albizia_antunesiana)))),FA_Acacia_nigrescens),(FA_Mimosa_albida,FA_Mimosa_micheliana)),(FA_Acacia_karroo,FA_Acacia_robusta)),(FA_Prosopis_glandulosa,FA_Prosopis_juliflora)),FA_Newtonia_hildebrandtii),((FA_Erythrophleum_chlorostachys,FA_Erythrophleum_lasianthum)Caesalpinioideae,FA_Entada_polystachya))Mimosoideae))))))Caesalpinioideae,((((FA_Vatairea_lundellii,((FA_Nissolia_leiogyne,((FA_Pterocarpus_marsupium,FA_Pterocarpus_rohrii),(FA_Dalbergia_melanoxylon,FA_Dalbergia_armata,FA_Dalbergia_sissoo))),(((((((FA_Millettia_dielsiana,FA_Millettia_leptobotrya,FA_Millettia_pachycarpa,FA_Millettia_dura,FA_Pongamia_pinnata),(FA_Derris_involuta,(FA_Lonchocarpus_dipteroneurus,(FA_Lonchocarpus_guatemalensis,FA_Lonchocarpus_heptaphyllus)))),FA_Galactia_acapulcensis),(FA_Mucuna_macrocarpa,(((FA_Erythrina_excelsa,FA_Erythrina_caffra),FA_Erythrina_folkersii),(FA_Spatholobus_suberectus,FA_Butea_monosperma)))),FA_Craspedolobium_schochii),(FA_Callerya_cinerea,(FA_Coursetia_ferruginea,FA_Robinia_pseudoacacia))),(FA_Poecilanthe_effusa,(FA_Laburnum_anagyroides,(FA_Bowdichia_virgilioides,(FA_Bolusanthus_speciosus,(FA_Sophora_chrysophylla,FA_Maackia_amurensis)))))))),FA_Andira_inermis),(FA_Dussia_mexicana,FA_Dussia_munda)),FA_Swartzia_simplex)Papilioloideae)FABACEAE)),(ZY_Balanites_maughamii,ZY_Bulnesia_arborea)ZYGOPHYLLACEAE),(((((((IX_Ixonanthes_reticulata,((((((((PH_Baccaurea_racemosa,PH_Baccaurea_parviflora,PH_Baccaurea_ramiflora),PH_Baccaurea_reticulata),(PH_Aporosa_lunata,PH_Aporosa_subcaudata,PH_Aporosa_microstachya)),PH_Protomegabaria_stapfiana),(PH_Hyeronima_alcheornoides,PH_Hymenocardia_ulmoides)),PH_Uapaca_staudtii),PH_Bischofia_javanica),((PH_Actephila_lindleyi,PH_Phyllanthus_flexuosus),(PH_Cleistanthus_schlechteri,(PH_Bridelia_insulana,PH_Bridelia_retusa))))PHYLLANHACEAE),(((EU_Alchornea_costaricensis,EU_Discoglypremna_caloneura),((EU_Ptychopyxis_caputmedusae,(((EU_Macaranga_heynei,(EU_Macaranga_hypoleuca,EU_Macaranga_triloba)),EU_Macaranga_lowii),(EU_Mallotus_nesophilus,(EU_Mallotus_paniculatus,EU_Mallotus_philippensis)))),(EU_Dalechampia_scandens,(EU_Acalypha_skutchii,EU_Claoxylon_indicum)))),((EU_Suregada_zanzibariensis,(((EU_Micrandra_sprucei,EU_Manihot_chlorosticta),EU_Elateriospermum_tapos),(EU_Dodecastigma_uleanum,(((EU_Croton_billbergianus,EU_Croton_schiedeanus),EU_Croton_steenkampianus),EU_Croton_draco)))),(EU_Omphalea_oleifera,((EU_Dichostemma_glaucenscens,EU_Euphorbia_colletioides),(EU_Sapium_glandulosum,(EU_Triadica_cochinchinensis,EU_Homalanthus_novoguineensis))))))EUPHORBIACEAE),((((MP_Cottsia_scandens,MP_Cottsia_linearis),MP_Gaudichaudia_macvaughii),MP_Stigmaphyllon_lindenianum),(((MP_Heteropterys_palmeri,MP_Heteropteris_sp.),MP_Tetrapterys_sp.),MP_Mascagnia_macroptera))MALPIGHIACEAE),(HU_Humiria_balsamifera,(AH_Kiggelaria_africana,(((GO_Goupia_glabra,GO_Iryanthera_sagotiana)GOUPIACEAE,(VI_Rinorea_neglecta,(VI_Rinoreocarpus_ulei,(VI_Amphirrhox_longifolia,VI_Orthion_oblanceolatum)))VIOLACEAE),((PA_Barteria_fistulosa,(PA_Efulensia_clematoides,(((PA_Passiflora_edulis,PA_Passiflora_subpeltata),PA_Passiflora_foetida),PA_Passiflora_juliana)))PASSIFLORACEAE,(((SA_Casearia_arborea,SA_Casearia_sylvestris),(((SA_Scolopia_mundii,SA_Scolopia_zeyheri),(SA_Pleuranthodendron_lindenii,SA_Dovyalis_longispina)),(((((SA_Populus_maximowiczii,(SA_Populus_balsamifera,(SA_Populus_heterophylla,SA_Populus_sieboldii))),SA_Populus_deltoides),SA_Populus_fremontii),(SA_Populus_alba,(SA_Populus_tremuloides,SA_Populus_tremula))),((SA_Salix_glauca,(SA_Salix_caprea,SA_Salix_planifolia)),(SA_Salix_laevigata,(SA_Salix_pentandra,(SA_Salix_fragilis,SA_Salix_alba))))))),(SA_Zuelania_guidonia,SA_Lunania_mexicana))SALICACEAE))))),((((OC_Lophira_alata,OC_Ochna_natalitia)OCHNACEAE,((((CB_Hirtella_punctillata,CB_Hirtella_triandra),(CB_Licania_arborea,CB_Licania_heteromorpha)),CB_Parinari_excelsa)CHRYSOBALANACEAE,(PU_Drypetes_arguta,PU_Drypetes_natalensis)PUTRANJIVACEAE)),(CY_Caryocar_brasiliense,((((CI_Garcinia_ovalifolia,CI_Garcinia_intermedia),(CI_Garcinia_mannii,(CI_Garcinia_bancana,CI_Garcinia_malaccensis))),(CI_Clusia_elliptica,CI_Clusia_multiflora))CLUCIACEAE,((((CL_Caraipa_heterocarpa,CL_Kielmeyera_coriacea),(CL_Calophyllum_polyanthum,CL_Calophyllum_longifolium)),CL_Mammea_africana)CALOPHYLLACEAE,(HP_Vismia_japurensis,HP_Vismia_lauriformis)HYPERICACEAE)))),((EY_Erythroxylum_densum,EY_Erythroxylum_cumanense,EY_Erythroxylum_orinocense)ERYTHROXYLACEAE,(RZ_Cassipourea_ruwensore

```
nsis,(RZ_Carallia_brachiata,(RZ_Bruguiera_cylindrica,(RZ_Ceriops_tagal,(RZ_Rhizophora_apicu
lata,RZ_Rhizophora_mucronata)))))RHIZOPHORACEAE))),(C1_Connarus_suberosus,((C4_Pse
udoweinmannia_lachnocarpa,(C4_Eucryphia_cordifolia,(C4_Cunonia_capensis,(C4_Weinmannia
_sp.,C4_Weinmannia_trichosperma))))CUNONIACEAE,((EA_Elaeocarpus_angustifolius,EA_Ela
eocarpus_sylvestris),EA_Sloanea_woollsii)ELAEOCARPACEAE))),(((((CE_Celastrus_orbiculatus
,CE_Celastrus_paniculatus),(CE_Cassine_schinoides,CE_Euonymus_europaeus)),CE_Maytenu
s_magellanica),(CE_Maytenus_acuminata,CE_Maytenus_oleoides)),(CE_Prionostemma_aspera,
(CE_Tontelea_ovalifolia,(CE_Salacia_leptoclada,CE_Salacia_cordata))))CELASTRACEAE))),(VT
_Leea_asiatica,((((VT_Cissus_antarctica,VT_Cissus_hypoglauca),VT_Vitis_vinifera),(VT_Rhoicis
sus_tomentosa,(((VT_Cayratia_clematidea,VT_Cayratia_eurynema),(VT_Tetrastigma_nitens,VT
_Tetrastigma_planicaule)),(VT_Cissus_verticillata,VT_Cissus_producta)))),VT_Nothocissus_sterc
uliifolia))VITACEAE),((AL_Liquidambar_styraciflua,(HA_Trichocladus_crinitus,HA_Trichocladus_
ellipticus)HAMAMELIDACEAE),CC_Cercidiphyllum_japonicum))),BX_Buxus_macowanii),(PL_Pla
tanus_occidentalis,((PC_Persoonia_linearis,PC_Faurea_macnaughtonii),((PC_Brabejum_stellatif
olium,PC_Gevuina_avellana),((PC_Banksia_attenuata,PC_Banksia_menziesii),((PC_Xylomelum
_pyriforme,PC_Helicia_glabriflora),(PC_Embothrium_coccineum,((PC_Hakea_arborescens,PC_
Hakea_leucoptera),PC_Lomatia_hirsuta))))))PROTEACEAE)PROTEACEAE),(((BE_Berberis_ilici
folia,((RA_Clematis_vitalba,RA_Clematis_lasiantha),RA_Clematis_glycinoides)RANUNCULACE
AE),(((MN_Stephania_japonica,MN_Cissampelos_pareira),(((MN_Anomospermum_reticulatum,(
MN_Abuta_rufescens,MN_Abuta_panamensis)),MN_Cocculus_moorei),MN_Sarcopetalum_harv
eyanum)),(MN_Tinospora_sp.,MN_Tinomiscium_tonkinense))MENISPERMACECAE),LR_Akebia
_trifoliata)),(AR_Pothos_longipes,(DO_Dioscorea_transversa,(((RI_Rhipogonum_elseyanum,RI_
Rhipogonum_album)RHIPOGONACEAE,(SM_Smilax_australis,(SM_Smilax_aspera,(SM_Smilax
_microphylla,(SM_Smilax_corbularia,SM_Smilax_hypoglauca))))SMILACACEAE),(XA_Geitonopl
esium_cymosum,((AE_Calamus_muelleri,(AE_Livistona_humilis,((AE_Socratea_exorrhiza,AE_Di
ctyocaryum_sp.),(((AE_Archontophoenix_cunninghamiana,AE_Oenocarpus_mapora),AE_Astroc
aryum_mexicanum),(AE_Chamaedorea_alternans,AE_Chamaedorea_pinnatifrons)))))ARECACE
AE,(FL_Flagellaria_indica,PO_Bambusa_bambos))))))),(CH_Hedyosmum_mexicanum,(((((((((A
O_Polyalthia_longifolia,(AO_Guamia_sp.,AO_Desmopsis_panamensis)),(AO_Polyalthia_pendula
,AO_Miliusa_tomentosa)),AO_Monocarpia_marginalis),((AO_Fissistigma_polyanthoides,AO_Fiss
istigma_polyanthum),AO_Melodorum_leichhardtii)),((((AO_Annona_spraguei,(AO_Annona_coria
cea,AO_Annona_squamosa)),AO_Monanthotaxis_caffra),(AO_Cymbopetalum_baillonii,(AO_Dug
uetia_furfuracea,AO_Duguetia_cadaverica))),(AO_Guatteria_dumentorum,AO_Artabotrys_honko
ngensis)))ANNONACEAE,EP_Eupomatia_laurina),(MA_Liriodendron_tulipifera,((MA_Magnolia_fr
aseri,(MA_Magnolia_grandiflora,MA_Magnolia_schiedeana)),(MA_Magnolia_obovata,(MA_Magn
olia_nilagirica,MA_Magnolia_floribunda))))MAGNOLIACEAE),(MI_Horsfieldia_sp.,((MI_Virola_se
bifera,MI_Virola_elongata),MI_Virola_surinamensis))MYRICACEAE),((AM_Daphnandra_micranth
a,AM_Laureliopsis_philippiana)ATHEROSPERMATACEAE,((((LU_Cryptocarya_alba,LU_Cryptoc
arya_erythroxylon,LU_Cryptocarya_densiflora),(LU_Beilschmiedia_obtusifolia,LU_Endiandra_mu
elleri)),((((LU_Apollonias_barbujana,LU_Alseodaphne_petiolaris),LU_Machilus_thunbergii),(LU_P
ersea_lingue,LU_Persea_indica)),((LU_Laurus_azorica,(LU_Litsea_panamanja,(LU_Actinodaphn
e_ambigua,(LU_Neolitsea_dealbata,LU_Neolitsea_sericea)))),(((LU_Cinnamomum_oliveri,LU_Ci
nnamomum_tenuifolium),LU_Cinnamomum_barbeyanum),(((LU_Ocotea_esmeraldana,(LU_Nect
andra_ambigens,LU_Nectandra_purpurea)),(LU_Licaria_brasiliensis,LU_Ocotea_aciphylla)),(LU_
Ocotea_bullata,LU_Agathophyllum_persoonianum))))))LAURACEAE,(MO_Palmeria_scandens,(
MO_Xymalos_monospora,MO_Kibara_macrophylla))MONIMIACEAE))),(((PP_Piper_amalago,PP
_Piper_novaehollandiae)PIPERACEAE,A3_Aristolochia_taliscana),WI_Drimys_winteri)))),(SC_Illi
cium_anisatum,SC_Schisandra_repanda)SCHISANDRACEAE),(((GN_Gnetum_costatum,GN_G
netum_gnemon),((GN_Gnetum_latifolium,GN_Gnetum_pendulum),GN_Gnetum_parvifolium))GN
ETACEAE,((((PI_Abies_alba,PI_Abies_lasiocarpa),PI_Tsuga_canadensis),((PI_Pseudotsuga_me
nziesii,(PI_Larix_decidua,PI_Larix_laricina)),((PI_Picea_sitchensis,((PI_Picea_glauca,PI_Picea_e
ngelmannii),(PI_Picea_abies,PI_Picea_mariana))),(((((PI_Pinus_nigra,PI_Pinus_resinosa),PI_Pin
us_sylvestris),((PI_Pinus_pinaster,PI_Pinus_canariensis),PI_Pinus_halepensis)),(PI_Pinus_bank
```

siana,((PI_Pinus_ponderosa,PI_Pinus_jeffreyi),(PI_Pinus_palustris,(PI_Pinus_rigida,PI_Pinus_serotina))))),((PI_Pinus_monophylla,PI_Pinus_edulis),(PI_Pinus_flexilis,PI_Pinus_strobus))))))PINACEAE,((AU_Araucaria_araucana,(PD_Saxegothaea_conspicua,(PD_Prumnopitys_andina,(PD_Dacrydium_beccarii,(PD_Afrocarpus_falcatus,((PD_Podocarpus_neriifolius,PD_Podocarpus_elatus),(PD_Podocarpus_salignus,(PD_Podocarpus_nubigenus,(PD_Podocarpus_latifolius,PD_Podocarpus_elongatus))))))))PODOCARPACEAE),(TA_Taxus_baccata,((((C5_Juniperus_communis,(C5_Juniperus_phoenicea,(C5_Juniperus_virginiana,(C5_Juniperus_osteosperma,C5_Juniperus_monosperma)))),C5_Thuja_occidentalis),(C5_Callitris_columellaris,C5_Austrocedrus_chilensis)),C5_Taxodium_distichum)CUPRESSACEAE))))));

Appendix H: Model comparisons for phylogenetic analyses

Table H1. All models for ordinary least squares (OLS), phylogenetic generalized least squares (PGLS) and Ornstein-Uhlenbeck (OU) for leaf and photosynthetic traits comparisons between trees and lianas for maximally resolved (Max) and conservatively resolved (Con) tree with branch lengths of 1 and with arbitrary branch lengths (Arb).

Trait	Tree	Branch	Model	Slope	Slope SE	*T*-Statistic	df	*P*-Value	r^2 for Model
A_{area}	N/A	N/A	OLS	-0.0108	0.0946	-0.1143	437	0.9091	0.0000
A_{area}	Max	1	PGLS	0.1247	0.1004	1.2422	437	0.2148	0.0035
A_{area}	Max	1	OU	0.0232	0.0961	0.2411	437	0.8096	0.0001
A_{area}	Max	Arb	PGLS	0.2222	0.0953	2.3325	437	0.0201	0.0123
A_{area}	Max	Arb	OU	0.0277	0.0946	0.2933	437	0.7694	0.0002
A_{area}	Con	1	PGLS	0.0897	0.1021	0.8782	437	0.3803	0.0018
A_{area}	Con	1	OU	0.0205	0.0957	0.2139	437	0.8307	0.0001
A_{area}	Con	Arb	PGLS	0.1690	0.0991	1.7054	437	0.0888	0.0066
A_{area}	Con	Arb	OU	0.0116	0.0948	0.1227	437	0.9024	0.0000
A_{mass}	N/A	N/A	OLS	1.7275	0.4197	4.1166	406	<0.0000	0.0401
A_{mass}	Max	1	PGLS	2.3587	0.4446	5.3054	406	<0.0000	0.0648
A_{mass}	Max	1	OU	1.9227	0.4273	4.4993	406	<0.0000	0.0475
A_{mass}	Max	Arb	PGLS	2.4603	0.4086	6.0217	406	<0.0000	0.0820
A_{mass}	Max	Arb	OU	2.0344	0.4175	4.8728	406	<0.0000	0.0553
A_{mass}	Con	1	PGLS	2.1234	0.4400	4.8263	406	<0.0000	0.0543
A_{mass}	Con	1	OU	1.9123	0.4253	4.4962	406	<0.0000	0.0474
A_{mass}	Con	Arb	PGLS	2.2311	0.4191	5.3231	406	<0.0000	0.0652
A_{mass}	Con	Arb	OU	1.9362	0.4206	4.6029	406	<0.0000	0.0496
c_a-c_i	N/A	N/A	OLS	-4.3450	0.8808	-4.9331	164	<0.0000	0.1292
c_a-c_i	Max	1	PGLS	-4.5815	0.7729	-5.9274	164	<0.0000	0.1764
c_a-c_i	Max	1	OU	-4.4517	8.3792	5.3128	164	<0.0000	0.1468

Table H1 (continued).

Trait	Tree	Branch	Model	Slope	Slope SE	*T*-Statistic	df	*P*-Value	r^2 for Model
c_a-c_i	Max	Arb	PGLS	-4.9500	0.6447	-7.6775	164	<0.0000	0.2644
c_a-c_i	Max	Arb	OU	-4.5989	0.7848	5.8601	164	<0.0000	0.1731
c_a-c_i	Con	1	PGLS	-4.6731	0.7918	-5.9018	164	<0.0000	0.1752
c_a-c_i	Con	1	OU	-4.4958	0.8438	5.3280	164	<0.0000	0.1476
c_a-c_i	Con	Arb	PGLS	-4.9490	0.7542	-6.5620	164	<0.0000	0.2080
c_a-c_i	Con	Arb	OU	-4.4815	0.8573	5.2274	164	<0.0000	0.1428
g_s	N/A	N/A	OLS	-0.0909	0.0676	-1.3457	220	0.1798	0.0082
g_s	Max	1	PGLS	0.0038	0.0756	0.0503	220	0.9599	0.0000
g_s	Max	1	OU	-0.0675	0.0712	0.9482	220	0.3441	0.0041
g_s	Max	Arb	PGLS	-0.1027	0.0713	-1.4398	220	0.1513	0.0093
g_s	Max	Arb	OU	-0.0894	0.0686	1.3036	220	0.1937	0.0077
g_s	Con	1	PGLS	-0.1033	0.0792	-1.3044	220	0.1935	0.0077
g_s	Con	1	OU	-0.0807	0.0691	1.1675	220	0.2443	0.0062
g_s	Con	Arb	PGLS	-0.1025	0.0819	-1.2514	220	0.2121	0.0071
g_s	Con	Arb	OU	-0.0820	0.0684	1.1986	220	0.2320	0.0065
LL	N/A	N/A	OLS	-0.2202	0.0947	-2.3263	332	0.0206	0.0160
LL	Max	1	PGLS	-0.2426	0.0945	-2.5663	332	0.0107	0.0195
LL	Max	1	OU	-0.2288	0.0953	2.4018	332	0.0169	0.0171
LL	Max	Arb	PGLS	-0.2368	0.0887	-2.6709	332	0.0079	0.0210
LL	Max	Arb	OU	-0.2486	0.0952	2.6104	332	0.0095	0.0201
LL	Con	1	PGLS	-0.2281	0.0980	-2.3276	332	0.0205	0.0161
LL	Con	1	OU	-0.2364	0.0966	2.4469	332	0.0149	0.0177
LL	Con	Arb	PGLS	-0.2371	0.0943	-2.5150	332	0.0124	0.0187
LL	Con	Arb	OU	-0.2514	0.0962	2.6144	332	0.0093	0.0202
LMA	N/A	N/A	OLS	-0.2204	0.0202	-10.8958	996	<0.0000	0.1065
LMA	Max	1	PGLS	-0.2083	0.0204	-10.2038	996	<0.0000	0.0946
LMA	Max	1	OU	-0.2103	0.0203	10.3645	996	<0.0000	0.0974

Table H1 (continued).

Trait	Tree	Branch	Model	Slope	Slope SE	*T*-Statistic	df	*P*-Value	r^2 for Model
LMA	Max	Arb	PGLS	-0.2059	0.0203	-10.1397	996	<0.0000	0.0936
LMA	Max	Arb	OU	-0.2150	0.0203	10.6005	996	<0.0000	0.1014
LMA	Con	1	PGLS	-0.2007	0.0205	-9.7701	996	<0.0000	0.0875
LMA	Con	1	OU	-0.2100	0.0203	10.3201	996	<0.0000	0.0966
LMA	Con	Arb	PGLS	-0.1991	0.0205	-9.7072	996	<0.0000	0.0864
LMA	Con	Arb	OU	-0.2132	0.0203	10.4810	996	<0.0000	0.0993
N_{area}	N/A	N/A	OLS	-0.0449	0.0197	-2.2768	836	0.0231	0.0062
N_{area}	Max	1	PGLS	-0.0417	0.0203	-2.0562	836	0.0401	0.0050
N_{area}	Max	1	OU	-0.0418	0.0199	2.1032	836	0.0357	0.0053
N_{area}	Max	Arb	PGLS	-0.0289	0.0201	-1.4371	836	0.1511	0.0025
N_{area}	Max	Arb	OU	-0.0435	0.0197	2.2058	836	0.0277	0.0058
N_{area}	Con	1	PGLS	-0.0382	0.0203	-1.8833	836	0.0600	0.0042
N_{area}	Con	1	OU	-0.0446	0.0198	2.2501	836	0.0247	0.0060
N_{area}	Con	Arb	PGLS	-0.0280	0.0204	-1.3744	836	0.1697	0.0023
N_{area}	Con	Arb	OU	-0.0451	0.0197	2.2831	836	0.0227	0.0062
N_{mass}	N/A	N/A	OLS	0.2768	0.0288	9.5819	895	<0.0000	0.0930
N_{mass}	Max	1	PGLS	0.2587	0.0274	9.4339	895	<0.0000	0.0904
N_{mass}	Max	1	OU	0.2663	0.0281	9.4783	895	<0.0000	0.0912
N_{mass}	Max	Arb	PGLS	0.2646	0.0264	10.0344	895	<0.0000	0.1011
N_{mass}	Max	Arb	OU	0.2694	0.0277	9.7349	895	<0.0000	0.0957
N_{mass}	Con	1	PGLS	0.2607	0.0274	9.5162	895	<0.0000	0.0919
N_{mass}	Con	1	OU	0.2649	0.0279	9.5008	895	<0.0000	0.0916
N_{mass}	Con	Arb	PGLS	0.2634	0.0269	9.7753	895	<0.0000	0.0965
N_{mass}	Con	Arb	OU	0.2689	0.0279	9.6459	895	<0.0000	0.0942
P_{area}	N/A	N/A	OLS	-0.1283	0.0353	-3.6396	449	0.0003	0.0287
P_{area}	Max	1	PGLS	-0.0830	0.0355	-2.3363	449	0.0199	0.0120
P_{area}	Max	1	OU	-0.1105	0.0355	3.1155	449	0.0020	0.0212

Table H1 (continued).

Trait	Tree	Branch	Model	Slope	Slope SE	*T*-Statistic	df	*P*-Value	r^2 for Model
P_{area}	Max	Arb	PGLS	-0.0689	0.0353	-1.9520	449	0.0516	0.0084
P_{area}	Max	Arb	OU	-0.1140	0.0352	3.2358	449	0.0013	0.0228
P_{area}	Con	1	PGLS	-0.0796	0.0359	-2.2140	449	0.0273	0.0108
P_{area}	Con	1	OU	-0.1149	0.0354	3.2490	449	0.0012	0.0230
P_{area}	Con	Arb	PGLS	-0.0696	0.0367	-1.8955	449	0.0587	0.0079
P_{area}	Con	Arb	OU	-0.1203	0.0354	3.3940	449	0.0007	0.0250
P_{mass}	N/A	N/A	OLS	0.0488	0.0359	1.3586	446	0.1750	0.0041
P_{mass}	Max	1	PGLS	0.0526	0.0333	1.5770	446	0.1155	0.0055
P_{mass}	Max	1	OU	0.0525	0.0349	1.5034	446	0.1335	0.0050
P_{mass}	Max	Arb	PGLS	0.0537	0.0317	1.6909	446	0.0916	0.0064
P_{mass}	Max	Arb	OU	0.0476	0.0338	1.4111	446	0.1589	0.0044
P_{mass}	Con	1	PGLS	0.0514	0.0352	1.4573	446	0.1458	0.0047
P_{mass}	Con	1	OU	0.0429	0.0353	1.2172	446	0.2242	0.0033
P_{mass}	Con	Arb	PGLS	0.0533	0.0355	1.5038	446	0.1333	0.0050
P_{mass}	Con	Arb	OU	0.0442	0.0356	1.2415	446	0.2151	0.0034
PNUE	N/A	N/A	OLS	0.0522	0.3412	0.1529	365	0.8785	0.0001
PNUE	Max	1	PGLS	0.8311	0.3675	2.2612	365	0.0243	0.0138
PNUE	Max	1	OU	0.2333	0.3509	0.6649	365	0.5065	0.0012
PNUE	Max	Arb	PGLS	1.2890	0.3622	3.5588	365	0.0004	0.0335
PNUE	Max	Arb	OU	0.1733	0.3446	0.5029	365	0.6154	0.0007
PNUE	Con	1	PGLS	0.8663	0.3786	2.2883	365	0.0227	0.0141
PNUE	Con	1	OU	0.2786	0.3504	0.7952	365	0.4270	0.0017
PNUE	Con	Arb	PGLS	1.2900	0.3728	3.4608	365	0.0006	0.0318
PNUE	Con	Arb	OU	0.2779	0.3479	0.7987	365	0.4250	0.0017
PPUE	N/A	N/A	OLS	0.1662	0.1017	1.6347	171	0.1040	0.0154
PPUE	Max	1	PGLS	0.0368	0.1079	0.3405	171	0.7339	0.0007
PPUE	Max	1	OU	0.1354	0.1305	1.3089	171	0.1923	0.0099

Table H1 (continued).

Trait	Tree	Branch	Model	Slope	Slope SE	*T*-Statistic	df	*P*-Value	r^2 for Model
PPUE	Max	Arb	PGLS	0.0513	0.1044	0.4911	171	0.6240	0.0014
PPUE	Max	Arb	OU	0.1428	0.1014	1.4079	171	0.1610	0.0115
PPUE	Con	1	PGLS	0.0221	0.1075	0.2053	171	0.8376	0.0002
PPUE	Con	1	OU	0.1407	0.1029	1.3674	171	0.1733	0.0108
PPUE	Con	Arb	PGLS	0.0503	0.1063	0.4727	171	0.6371	0.0013
PPUE	Con	Arb	OU	0.1431	0.1018	1.4048	171	0.1619	0.0114
R_{area}	N/A	N/A	OLS	0.6280	0.0994	6.3189	162	<0.0000	0.1977
R_{area}	Max	1	PGLS	0.4319	0.1093	3.9511	162	0.0001	0.0879
R_{area}	Max	1	OU	0.6280	0.0994	6.3189	162	<0.0000	0.1977
R_{area}	Max	Arb	PGLS	0.2233	0.1067	2.0919	162	0.0380	0.0263
R_{area}	Max	Arb	OU	0.6280	0.0994	6.3189	162	<0.0000	0.1977
R_{area}	Con	1	PGLS	0.4332	0.1137	3.8096	162	0.0002	0.0822
R_{area}	Con	1	OU	0.6280	0.0994	6.3189	162	<0.0000	0.1977
R_{area}	Con	Arb	PGLS	0.2231	0.1165	1.9148	162	0.0573	0.0221
R_{area}	Con	Arb	OU	0.6280	0.0994	6.3189	162	<0.0000	0.1977
R_{mass}	N/A	N/A	OLS	0.1788	0.0525	3.4038	158	0.0008	0.0683
R_{mass}	Max	1	PGLS	0.1335	0.0559	2.3891	158	0.0181	0.0349
R_{mass}	Max	1	OU	0.1665	0.0530	3.1406	158	0.0020	0.0588
R_{mass}	Max	Arb	PGLS	0.0868	0.0450	1.9282	158	0.0556	0.0230
R_{mass}	Max	Arb	OU	0.1354	0.0494	2.7428	158	0.0068	0.0454
R_{mass}	Con	1	PGLS	0.0971	0.0503	1.9328	158	0.0551	0.0231
R_{mass}	Con	1	OU	0.1535	0.0512	2.9986	158	0.0032	0.0538
R_{mass}	Con	Arb	PGLS	0.0874	0.0478	1.8293	158	0.0692	0.0207
R_{mass}	Con	Arb	OU	0.1412	0.0505	2.7975	158	0.0058	0.0472

Table H1 (continued).

Trait	Tree	Branch	Model	d REML	d ML	ln REML	ln ML Like	AIC (ML)	AICc (ML)	MSE	SE of Est
A_{area}	N/A	N/A	OLS				-440.1130	886.2260	886.2820	0.4368	0.6609
A_{area}	Max	1	PGLS				-514.0820	1034.160	1034.220	0.4433	0.6658
A_{area}	Max	1	OU	0.2276	0.2235	-431.1340	-432.3250	872.6500	872.7420	0.4216	0.6493
A_{area}	Max	Arb	PGLS				-546.0740	1098.150	1098.200	0.4544	0.6741
A_{area}	Max	Arb	OU	0.1201	0.1172	-434.7060	-435.7950	879.5900	879.6820	0.4283	0.6545
A_{area}	Con	1	PGLS				-513.5810	1033.160	1033.220	0.4349	0.6595
A_{area}	Con	1	OU	0.2373	0.2328	-432.7430	-433.9250	875.8500	875.9420	0.4247	0.6517
A_{area}	Con	Arb	PGLS				-556.4700	1118.940	1119.000	0.4876	0.6983
A_{area}	Con	Arb	OU	0.0937	0.0912	-434.9830	-436.0780	880.1570	880.2490	0.4289	0.6549
A_{mass}	N/A	N/A	OLS				-1005.2000	2016.400	2016.460	8.1213	2.8498
A_{mass}	Max	1	PGLS				-1061.0200	2128.050	2128.100	7.5937	2.7557
A_{mass}	Max	1	OU	0.2964	0.2910	-989.9940	-994.1780	1996.360	1996.450	7.6943	2.7739
A_{mass}	Max	Arb	PGLS				-1072.4100	2150.810	2150.870	7.0152	2.6486
A_{mass}	Max	Arb	OU	0.3048	0.2998	-990.6680	-994.7890	1997.580	1997.680	7.7173	2.7780
A_{mass}	Con	1	PGLS				-1050.9100	2107.830	2107.890	7.0799	2.6608
A_{mass}	Con	1	OU	0.3489	0.3423	-991.0240	-995.2550	1998.510	1998.610	7.7351	2.7812
A_{mass}	Con	Arb	PGLS				-1078.5800	2163.160	2163.220	7.3953	2.7194
A_{mass}	Con	Arb	OU	0.2866	0.2818	-991.4940	-995.6240	1999.250	1999.350	7.7490	2.7837
c_a-c_i	N/A	N/A	OLS				-406.7970	819.5950	819.7430	7.9679	2.8227
c_a-c_i	Max	1	PGLS				-429.9110	865.8220	865.9700	5.4911	2.3433
c_a-c_i	Max	1	OU	0.4131	0.4006	-400.2710	-404.3680	816.7360	816.9840	7.7387	2.7819
c_a-c_i	Max	Arb	PGLS				-432.3730	870.7460	870.8940	4.5463	2.1322
c_a-c_i	Max	Arb	OU	0.4570	0.4488	-399.2270	-403.2170	814.4330	814.6820	7.6318	2.7626
c_a-c_i	Con	1	PGLS				-431.3750	868.7500	868.8980	5.3406	2.3110
c_a-c_i	Con	1	OU	0.3905	0.3784	-399.2540	-403.2980	814.5950	814.8440	7.6394	2.7640
c_a-c_i	Con	Arb	PGLS				-450.0880	906.1770	906.3250	5.8336	2.4153
c_a-c_i	Con	Arb	OU	0.1536	0.1481	-401.0760	-405.0160	818.0330	818.2810	7.7988	2.7926

Table H1 (continued).

Trait	Tree	Branch	Model	d REML	d ML	ln REML	ln ML	AIC (ML)	AICc (ML)	MSE	SE of Est
g_s	N/A	N/A	OLS				-55.9204	117.8410	117.9510	0.0978	0.3127
g_s	Max	1	PGLS				-95.9066	197.8130	197.9230	0.0821	0.2866
g_s	Max	1	OU	0.2741	0.2638	-54.1871	-53.8919	115.7840	115.9680	0.0960	0.3099
g_s	Max	Arb	PGLS				-120.1290	246.2580	246.3680	0.0830	0.2881
g_s	Max	Arb	OU	0.0272	0.0227	-56.1968	-55.7358	119.4720	119.6560	0.0976	0.3124
g_s	Con	1	PGLS				-103.7250	213.4510	213.5610	0.0840	0.2898
g_s	Con	1	OU	0.1986	0.1919	-53.2153	-52.8189	113.6380	113.8220	0.0951	0.3084
g_s	Con	Arb	PGLS				-138.6680	283.3370	283.4470	0.1027	0.3204
g_s	Con	Arb	OU	0.0412	0.0397	-54.2489	-53.8001	115.6000	115.7850	0.0959	0.3097
LL	N/A	N/A	OLS				-130.1000	266.2000	266.2730	0.1284	0.3583
LL	Max	1	PGLS				-195.7390	397.4780	397.5500	0.1266	0.3557
LL	Max	1	OU	0.1767	0.1645	-130.0120	-129.9090	267.8190	267.9400	0.1282	0.3581
LL	Max	Arb	PGLS				-194.8150	395.6290	395.7020	0.1082	0.3290
LL	Max	Arb	OU	0.2591	0.2530	-125.7730	-125.7060	259.4130	259.5340	0.1250	0.3536
LL	Con	1	PGLS				-166.9310	339.8610	339.9340	0.1041	0.3226
LL	Con	1	OU	0.3801	0.3713	-122.2570	-122.3600	252.7200	252.8410	0.1226	0.3501
LL	Con	Arb	PGLS				-201.3720	408.7430	408.8160	0.1148	0.3388
LL	Con	Arb	OU	0.2103	0.2042	-125.5110	-125.4410	258.8820	259.0040	0.1248	0.3533
LMA	N/A	N/A	OLS				75.8393	-145.6790	-145.6540	0.0504	0.2245
LMA	Max	1	PGLS				-67.3031	140.6060	140.6300	0.0643	0.2535
LMA	Max	1	OU	0.2089	0.2070	96.3382	97.2152	-186.4300	-186.3900	0.0483	0.2197
LMA	Max	Arb	PGLS				-126.4850	258.9700	258.9940	0.0717	0.2677
LMA	Max	Arb	OU	0.1381	0.1368	94.6139	95.5792	-183.1580	-183.1180	0.0484	0.2201
LMA	Con	1	PGLS				-24.5431	55.0861	55.1102	0.0591	0.2432
LMA	Con	1	OU	0.2680	0.2656	101.2990	102.0900	-196.1800	-196.1400	0.0478	0.2187
LMA	Con	Arb	PGLS				-128.2140	262.4290	262.4530	0.0721	0.2685
LMA	Con	Arb	OU	0.1398	0.1384	93.3324	94.2811	-180.5620	-180.5220	0.0486	0.2204

Table H1 (continued).

Trait	Tree	Branch	Model	d REML	d ML	ln REML	ln ML	AIC (ML)	AICc (ML)	MSE	SE of Est
N_{area}	N/A	N/A	OLS				233.4930	-460.9850	-46.9560	0.0336	0.1833
N_{area}	Max	1	PGLS				69.2673	-132.5350	-132.5060	0.0447	0.2113
N_{area}	Max	1	OU	0.1097	0.1039	236.3770	237.8080	-467.6170	-467.5690	0.0333	0.1824
N_{area}	Max	Arb	PGLS				4.5948	-3.1895	-3.1607	0.0502	0.2241
N_{area}	Max	Arb	OU	0.0378	0.0371	236.1310	237.6220	-467.2430	-467.1950	0.0333	0.1824
N_{area}	Con	1	PGLS				109.0850	-212.1710	-212.1420	0.0406	0.2015
N_{area}	Con	1	OU	0.1764	0.1739	240.9510	242.3230	-476.6470	-476.5990	0.0329	0.1814
N_{area}	Con	Arb	PGLS				14.4326	-22.8651	-22.8364	0.0493	0.2220
N_{area}	Con	Arb	OU	0.0568	0.0558	238.3270	239.7850	-471.5700	-471.5220	0.0331	0.1820
N_{mass}	N/A	N/A	OLS				-93.9470	193.8940	193.9210	0.0724	0.2690
N_{mass}	Max	1	PGLS				-197.1590	400.3170	400.3440	0.0840	0.2898
N_{mass}	Max	1	OU	0.2786	0.2765	-61.5971	-61.1381	130.2760	130.3210	0.0673	0.2593
N_{mass}	Max	Arb	PGLS				-240.5540	487.1090	487.1360	0.0894	0.2990
N_{mass}	Max	Arb	OU	0.2296	0.2276	-67.9423	-67.3714	142.7430	142.7880	0.0682	0.2611
N_{mass}	Con	1	PGLS				-155.6510	317.3020	317.3290	0.0766	0.2768
N_{mass}	Con	1	OU	0.3354	0.3326	-54.1138	-53.7418	115.4840	115.5280	0.0662	0.2572
N_{mass}	Con	Arb	PGLS				-237.9690	481.9370	481.9640	0.0895	0.2992
N_{mass}	Con	Arb	OU	0.2274	0.2254	-64.2460	-63.6842	135.3680	135.4130	0.0676	0.2601
P_{area}	N/A	N/A	OLS				-11.5766	29.1531	29.2068	0.0619	0.2488
P_{area}	Max	1	PGLS				-98.8931	203.7860	203.8400	0.0656	0.2560
P_{area}	Max	1	OU	0.1779	0.1732	-9.1790	-8.3553	24.7306	24.8202	0.0610	0.2471
P_{area}	Max	Arb	PGLS				-121.9390	249.8770	249.9310	0.0664	0.2578
P_{area}	Max	Arb	OU	0.1139	0.1107	-9.8657	-9.0064	26.0128	26.1025	0.0612	0.2474
P_{area}	Con	1	PGLS				-83.3356	172.6710	172.7250	0.0601	0.2451
P_{area}	Con	1	OU	0.2442	0.2387	-9.1365	-8.3648	24.7297	24.8194	0.0610	0.2471
P_{area}	Con	Arb	PGLS				-132.7010	271.4020	271.4550	0.0692	0.2631
P_{area}	Con	Arb	OU	0.0654	0.0623	-11.3300	-10.4564	28.9129	29.0026	0.0616	0.2482

Table H1 (continued).

Trait	Tree	Branch	Model	d REML	d ML	ln REML	ln ML	AIC (ML)	AICc (ML)	MSE	SE of Est
P_{mass}	N/A	N/A	OLS				0.1974	45.4728	45.5269	0.0642	0.2534
P_{mass}	Max	1	PGLS				-67.7884	141.5770	141.6310	0.0575	0.2397
P_{mass}	Max	1	OU	0.3588	0.3541	-4.2101	-3.6016	15.2032	15.2935	0.0598	0.2445
P_{mass}	Max	Arb	PGLS				-74.8046	155.6090	155.6630	0.0535	0.2312
P_{mass}	Max	Arb	OU	0.3920	0.3879	0.7039	1.3741	5.2518	5.3421	0.0585	0.2418
P_{mass}	Con	1	PGLS				-72.7899	151.5800	151.6340	0.0574	0.2397
P_{mass}	Con	1	OU	0.3484	0.3434	-7.7263	-7.0904	22.1808	22.2711	0.0607	0.2464
P_{mass}	Con	Arb	PGLS				-117.5100	241.0200	241.0740	0.0643	0.2535
P_{mass}	Con	Arb	OU	0.2140	0.2103	-12.9280	-12.1593	32.3186	32.4089	0.0621	0.2492
PNUE	N/A	N/A	OLS				-803.0700	1612.140	1612.210	4.6832	2.1641
PNUE	Max	1	PGLS				-862.1610	1730.320	1730.390	4.3974	2.0970
PNUE	Max	1	OU	0.2352	0.2279	-795.2050	-798.7710	1605.540	1605.650	4.5749	2.1389
PNUE	Max	Arb	PGLS				-902.8500	1811.700	1811.770	4.7730	2.1847
PNUE	Max	Arb	OU	0.0472	0.0447	-798.8180	-802.2440	1612.490	1612.600	4.6622	2.1592
PNUE	Con	1	PGLS				-862.0870	1730.170	1730.240	4.3386	2.0829
PNUE	Con	1	OU	0.2377	0.2304	-796.7840	-800.3390	1608.680	1608.790	4.6142	2.1481
PNUE	Con	Arb	PGLS				-896.4900	1798.980	1799.050	4.7392	2.1770
PNUE	Con	Arb	OU	0.1160	0.1112	-797.7470	-801.2380	1610.480	1610.590	4.6368	2.1533
PPUE	N/A	N/A	OLS				-140.5610	287.1220	287.2650	0.3008	0.5485
PPUE	Max	1	PGLS				-165.9760	337.9530	338.0950	0.2057	0.4535
PPUE	Max	1	OU	0.2950	0.2774	-137.8980	-138.6390	285.2780	285.5160	0.2942	0.5424
PPUE	Max	Arb	PGLS				-173.9070	353.8140	353.9560	0.1877	0.4332
PPUE	Max	Arb	OU	0.2779	0.2680	-137.3660	-138.0680	284.1360	284.3740	0.2923	0.5406
PPUE	Con	1	PGLS				-163.7720	333.5430	333.6850	0.1905	0.4364
PPUE	Con	1	OU	0.3375	0.3212	-137.6740	-138.4350	284.8700	285.1090	0.2935	0.5418
PPUE	Con	Arb	PGLS				-173.9080	353.8160	353.9580	0.1824	0.4271
PPUE	Con	Arb	OU	0.3332	0.3230	-136.9430	-137.6740	283.3480	283.5860	0.2909	0.5394

Table H1 (continued).

Trait	Tree	Branch	Model	d REML	d ML	ln REML	ln ML	AIC (ML)	AICc (ML)	MSE	SE of Est
R_{area}	N/A	N/A	OLS				-108.5830	223.1660	223.3160	0.2228	0.4720
R_{area}	Max	1	PGLS				-143.4260	292.8530	293.0030	0.1658	0.4072
R_{area}	Max	1	OU	0.0000	0.0000	-108.2530	-108.5830	225.1660	225.4170	0.2228	0.4720
R_{area}	Max	Arb	PGLS				-159.5720	325.1440	325.2940	0.1652	0.4065
R_{area}	Max	Arb	OU	0.0000	0.0000	-108.2530	-108.5830	225.1660	225.4170	0.2228	0.4720
R_{area}	Con	1	PGLS				-149.2650	304.5310	304.6810	0.1750	0.4183
R_{area}	Con	1	OU	0.0000	0.0000	-108.2530	-108.5830	225.1660	225.4170	0.2228	0.4720
R_{area}	Con	Arb	PGLS				-167.2090	340.4180	340.5680	0.1846	0.4296
R_{area}	Con	Arb	OU	0.0000	0.0000	-108.2530	-108.5830	225.1660	225.4170	0.2228	0.4720
R_{mass}	N/A	N/A	OLS				-1.0504	8.1008	8.2546	0.0601	0.2451
R_{mass}	Max	1	PGLS				-32.5329	71.0659	71.2197	0.0429	0.2072
R_{mass}	Max	1	OU	0.3216	0.3068	-0.7832	0.0639	7.8721	8.1302	0.0592	0.2434
R_{mass}	Max	Arb	PGLS				-17.3954	40.7907	40.9446	0.0292	0.1709
R_{mass}	Max	Arb	OU	0.5271	0.5143	3.4162	4.1938	-0.3875	-0.1294	0.0563	0.2372
R_{mass}	Con	1	PGLS				-14.7795	35.5590	35.7128	0.0339	0.1841
R_{mass}	Con	1	OU	0.4975	0.4824	4.0562	4.7655	-1.5309	-1.2728	0.0559	0.2364
R_{mass}	Con	Arb	PGLS				-20.1442	46.2884	46.4422	0.0308	0.1756
R_{mass}	Con	Arb	OU	0.4992	0.4879	4.4519	5.2586	-2.5171	-2.2591	0.0555	0.2356

Photosynthesis per mass (A_{mass}, nmol g^{-1} s^{-1}), photosynthesis per area (A_{area}, μmol m^{-2} s^{-1}), partial pressure CO_2 between atmosphere and intercellular space (c_a-c_i, ppm), stomatal conductance (g_s, mmol m^{-2} s^{-1}), leaf mass area (LMA, g/m^2), leaf lifespan (LL, mo^{-1}), leaf nitrogen per mass (N_{mass}, %), leaf nitrogen per area (N_{area}, g/m^2), leaf phosphorus per mass (P_{mass}, %), leaf phosphorus per area (P_{area}, g/m^2), photosynthetic nitrogen use efficiency (PNUE, μmol mol N^{-1} s^{-1}), photosynthetic phosphorus use efficiency (PPUE, nmol mol P^{-1} s^{-1}), respiration per mass (R_{mass}, nmol g^{-1} s^{-1}) and respiration per area (R_{area}, μmol m^{-2} s^{-1}).

Appendix I: Model comparisons for phylogenetic signal

Table I1. All models for phylogenetic signal using phylogenetic generalized least squares (PGLS) model for leaf and photosynthetic traits comparisons between trees and lianas for maximally resolved (Max) and conservatively resolved (Con) tree with branch lengths of 1 and with arbitrary branch lengths (Arb).

Trait	Tree	Branch	*N*	*K*-statistic	*K*-star	ln Like	ln Like Star	*P*-value
A_{area}	Con	1	439	0.1257	0.1839	-513.9680	-440.1200	0.0015
A_{area}	Con	Arb	439	0.1255	0.1427	-557.9260	-440.1200	0.0035
A_{area}	Max	1	439	0.1289	0.1926	-514.8550	-440.1200	0.0010
A_{area}	Max	Arb	439	0.1427	0.1622	-548.7900	-440.1200	0.0015
A_{mass}	Con	1	408	0.1420	0.2085	-1062.2900	-1013.5400	<0.0000
A_{mass}	Con	Arb	408	0.1512	0.1725	-1092.3400	-1013.5400	<0.0000
A_{mass}	Max	1	408	0.1390	0.2057	-1074.7000	-1013.5400	<0.0000
A_{mass}	Max	Arb	408	0.1670	0.1903	-1089.8600	-1013.5400	<0.0000
c_a-c_i	Con	1	166	0.1883	0.2627	-447.3600	-418.2810	0.0275
c_a-c_i	Con	Arb	166	0.1759	0.2018	-469.4390	-418.2810	0.1145
c_a-c_i	Max	1	166	0.1996	0.2735	-446.0220	-418.2810	0.0075
c_a-c_i	Max	Arb	166	0.2236	0.2563	-457.8580	-418.2810	0.0725
g_s	Con	1	222	0.1502	0.2175	-104.5800	-56.8303	0.1025
g_s	Con	Arb	222	0.1362	0.1549	-139.4560	-56.8303	0.3855
g_s	Max	1	222	0.1581	0.2397	-95.9079	-56.8303	0.0080
g_s	Max	Arb	222	0.1791	0.2036	-121.1700	-56.8303	0.1940
LL	Con	1	334	0.1587	0.2275	-169.6340	-132.8000	<0.0000
LL	Con	Arb	334	0.1587	0.1796	-204.5230	-132.8000	0.0005
LL	Max	1	334	0.1330	0.1330	-199.0190	-132.8000	0.0205
LL	Max	Arb	334	0.1792	0.2025	-198.3650	-132.8000	0.0010
LMA	Con	1	998	0.1069	0.1615	-70.2117	19.6204	<0.0000
LMA	Con	Arb	998	0.0989	0.1159	-173.3220	19.6204	<0.0000

Table I1 (continued).

Trait	Tree	Branch	*N*	*K*-statistic	*K*-star	ln Like	ln Like Star	*P*-value
LMA	Max	1	998	0.1020	0.1585	-116.9160	19.6204	<0.0000
LMA	Max	Arb	998	0.1052	0.1232	-175.5060	19.6204	<0.0000
N_{area}	Con	1	838	0.1023	0.1537	107.3110	230.9020	<0.0000
N_{area}	Con	Arb	838	0.0949	0.1105	13.4869	230.9020	0.0040
N_{area}	Max	1	838	0.0962	0.1486	67.1535	230.9020	0.0260
N_{area}	Max	Arb	838	0.0993	0.1156	3.5609	230.9020	0.0210
N_{mass}	Con	1	897	0.1168	0.1758	-198.8790	-137.7460	<0.0000
N_{mass}	Con	Arb	897	0.1147	0.1307	-283.4660	-137.7460	<0.0000
N_{mass}	Max	1	897	0.1103	0.1710	-239.6770	-137.7460	<0.0000
N_{mass}	Max	Arb	897	0.1218	0.1387	-288.3690	-137.7460	<0.0000
P_{area}	Con	1	451	0.2019	0.1920	-85.7840	-18.1332	<0.0000
P_{area}	Con	Arb	451	0.1430	0.1461	-134.4980	-18.1332	0.0020
P_{area}	Max	1	451	0.2100	0.1865	-101.6180	-18.1332	0.0080
P_{area}	Max	Arb	451	0.1589	0.1621	-123.8440	-18.1332	0.0025
P_{mass}	Con	1	448	0.1933	0.2054	-73.8540	-20.6616	<0.0000
P_{mass}	Con	Arb	448	0.1469	0.1606	-118.6430	-20.6616	<0.0000
P_{mass}	Max	1	448	0.1967	0.2182	-69.0339	-20.6616	<0.0000
P_{mass}	Max	Arb	448	0.1880	0.2054	-76.2360	-20.6616	<0.0000
PNUE	Con	1	367	0.1378	0.1960	-864.7000	-803.0810	0.0075
PNUE	Con	Arb	367	0.1349	0.1539	-902.4150	-803.0810	0.0100
PNUE	Max	1	367	0.1374	0.2048	-864.7140	-803.0810	0.0005
PNUE	Max	Arb	367	0.1426	0.1625	-909.1100	-803.0810	0.0880
PPUE	Con	1	173	0.2378	0.2957	-163.7930	-141.9030	0.0085
PPUE	Con	Arb	173	0.2386	0.2616	-174.0210	-141.9030	0.0060
PPUE	Max	1	173	0.2261	0.2891	-166.0350	-141.9030	0.0080
PPUE	Max	Arb	173	0.2473	0.2710	-174.0290	-141.9030	0.0150

Table I1 (continued).

Trait	Tree	Branch	*N*	*K*-statistic	*K*-star	In Like	In Like Star	*P*-value
R_{area}	Con	1	164	0.1874	0.2760	-156.3010	-126.6490	0.0690
R_{area}	Con	Arb	164	0.2085	0.2430	-169.0440	-126.6490	0.0630
R_{area}	Max	1	164	0.2024	0.3081	-150.9700	-126.6490	0.0145
R_{area}	Max	Arb	164	0.2473	0.2881	-161.7580	-126.6490	0.0535
R_{mass}	Con	1	160	0.2557	0.3517	-16.6489	-6.7114	<0.0000
R_{mass}	Con	Arb	160	0.3015	0.3386	-21.8209	-6.7114	<0.0000
R_{mass}	Max	1	160	0.2084	0.2912	-35.3720	-6.7114	0.0435
R_{mass}	Max	Arb	160	0.3386	0.3800	-19.2561	-6.7114	<0.0000

Photosynthesis per mass (A_{mass}, nmol g^{-1} s^{-1}), photosynthesis per area (A_{area}, μmol m^{-2} s^{-1}), partial pressure CO_2 between atmosphere and intercellular space (c_a-c_i, ppm), stomatal conductance (g_s, mmol m^{-2} s^{-1}), leaf mass area (LMA, g/m^2), leaf lifespan (LL, mo^{-1}), leaf nitrogen per mass (N_{mass}, %), leaf nitrogen per area (N_{area}, g/m^2), leaf phosphorus per mass (P_{mass}, %), leaf phosphorus per area (P_{area}, g/m^2), photosynthetic nitrogen use efficiency (PNUE, μmol mol N^{-1} s^{-1}), photosynthetic phosphorus use efficiency (PPUE, nmol mol P^{-1} s^{-1}), respiration per mass (R_{mass}, nmol g^{-1} s^{-1}) and respiration per area (R_{area}, μmol m^{-2} s^{-1}).