5-2020

Allometric Scaling Laws Linking Biomass and Rooting Depth Vary Across Ontogeny and Functional Groups in Tropical Dry Forest Lianas and Trees

Chris M. Smith-Martin
Columbia University

Xiangtao Xu
Harvard University

David Medvigy
University of Notre Dame

Stefan A. Schnitzer
Marquette University, stefan.schnitzer@marquette.edu

Jennifer S. Powers
University of Minnesota

Allometric Scaling Laws Linking Biomass and Rooting Depth Vary Across Ontogeny and Functional Groups in Tropical Dry Forest Lianas and Trees

Chris M. Smith-Martin
Department of Ecology, Evolution, and Evolutionary Biology, Columbia University, New York, NY
Xiangtao Xu
Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA
Department of Biological Sciences, University of Notre Dame, Notre Dame, IN
David Medvigy
Department of Biological Sciences, University of Notre Dame, Notre Dame, IN
Stefan A. Schnitzer
Department of Biology, Marquette University, Milwaukee, WI
Smithsonian Tropical Research Institute, Apartado, 0843-03092 Balboa, Republic of Panama
Jennifer S. Powers

Department of Ecology, Evolution, and Evolutionary Biology, Columbia University, New York, NY
Smithsonian Tropical Research Institute, Apartado, 0843-03092 Balboa, Republic of Panama
Department of Ecology, Evolution, and Behavior, University of Minnesota, St Paul, MN

Summary

- There are two theories about how allocation of metabolic products occurs. The allometric biomass partitioning theory (APT) suggests that all plants follow common allometric scaling rules. The optimal partitioning theory (OPT) predicts that plants allocate more biomass to the organ capturing the most limiting resource.
- Whole-plant harvests of mature and juvenile tropical deciduous trees, evergreen trees, and lianas and model simulations were used to address the following knowledge gaps: (1) Do mature lianas comply with the APT scaling laws or do they invest less biomass in stems compared to trees? (2) Do juveniles follow the same allocation patterns as mature individuals? (3) Is either leaf phenology or life form a predictor of rooting depth?
- It was found that: (1) mature lianas followed the same allometric scaling laws as trees; (2) juveniles and mature individuals do not follow the same allocation patterns; and (3) mature lianas had shallowest coarse roots and evergreen trees had the deepest.
- It was demonstrated that: (1) mature lianas invested proportionally similar biomass to stems as trees and not less, as expected; (2) lianas were not deeper-rooted than trees as had been previously proposed; and (3) evergreen trees had the deepest roots, which is necessary to maintain canopy during simulated dry seasons.

Introduction

The allocation patterns of metabolic products in plants have been studied by ecologists from at least the 19th Century (Kny, **1894**) until today (Poorter *et al*., **2015**). Allocation to different organs is a zero-sum dynamic in that an increase in allocation to one organ will result in an equal decrease in allocation to another, and is thought to reflect strategies to optimize performance. Allometric biomass partitioning theory (APT) suggests that all plants follow common allometric scaling rules that constrain allocation to different plant organs (Enquist & Niklas, **2002**; Niklas & Enquist, **2002**; Niklas & Spatz, **2004**; McCarthy *et al*., **2007**). Enquist & Niklas (**2002**) proposed a universal allocation rule for nonjuvenile seed plants in which the scaling of leaf vs stem and leaf vs root (total belowground biomass) is to the ¾ power and stem vs root mass is to the 1 power (i.e. an isometric relationship). However, in the case of perennial plants, for juveniles younger than 1 yr, it was proposed that the scaling between above- and belowground biomass will have a slope of 1, possibly due to the initial growth provided by resources from the seed mass in young plants (Enquist & Niklas, **2002**; Niklas, **2005**).

An alternative perspective is the optimal partitioning theory (OPT), which allows some flexibility within fixed allocation rules. This flexibility allows plants to allocate biomass dynamically to optimize resource capture, depending on which resource most constrains productivity (Davidson, **1969**; Thornley, **1972**; Bloom *et al*., **1985**; Chave *et al*., **2014**). Thus, if water and/or nutrients are limiting, then plants should allocate more biomass to roots; if light is limiting, allocation to shoots and/or leaves should increase (Bloom *et al*., **1985**; Shipley & Meziane, **2002**; Roa-Fuentes *et al*., **2012**). In particular, the most limiting resource can vary across species and individuals and is tightly linked to specific lifeforms, ontogeny and life-history strategies (Shipley & Meziane, **2002**; Banin *et al*., **2012**; Poorter *et al*., **2012**).

In the tropics, one of the most distinctive contrasts in life forms is between lianas, which are woody vines, and trees. Lianas are thought to differ from trees in that they do not invest in stems for support, because they use trees for mechanical support (Givnish & Vermeij, **1976**; Putz, **1983**; Stevens, **1987**; Castellanos *et al*., **1989**;

Gehring *et al.*, **2004**; Selaya *et al.*, **2007**; van der Heijden *et al.*, **2013**). Thus, it is believed that lianas allocate more biomass to leaves and perhaps roots, and less to stems in comparison to trees (Putz, **1983**; Castellanos *et al.*, **1989**; van der Heijden & Phillips, **2009**; van der Heijden *et al.*, **2013**, **2015**; Schnitzer *et al.*, **2014**). For example, in a study comparing diameter growth between lianas and trees in an Amazonian forest in Peru, van der Heijden & Phillips (**2009**) found that lianas made up only one-third of the biomass that they displaced in trees due to competition, because lianas grew less in diameter than trees. In two other multiyear liana removal studies conducted in a seasonally moist lowland tropical forest in Panama, lianas were found to reduce tree stem growth in tree-fall gaps (Schnitzer *et al.*, **2014**) and in the forest (van der Heijden *et al.*, **2015**); in both experiments lianas did not make up for all the stem biomass that they displaced. However, these studies did not account for potential differences between lianas and trees in terms of stem length. Niklas (**1994**) found that temperate vines partitioned their leaf and stem biomass following similar patterns as self-supporting gymnosperms. In another study conducted in Xishuangbanna in SW China with tree and liana seedlings from a single genus, *Bauhinia*, Cai *et al.* (**2007**) found that lianas allocated more biomass to leaves and stems and less to roots than the trees.

Given a particular belowground biomass, lianas and trees may differ in their belowground architecture – that is, how belowground biomass is deployed in terms of the distribution of root length or surface area throughout the soil profile. For example, many have postulated that lianas are deeper-rooted than co-occurring trees, permitting lianas to access deeper sources of soil water than trees (Holbrook & Putz, **1996**; Andrade *et al.*, **2005**; Schnitzer, **2005**; Schnitzer *et al.*, **2005**; Toledo-Aceves & Swaine, **2008**; Schnitzer & Bongers, **2011**; Chen *et al.*, **2015**). Evidence for this idea, however, is mixed. In support of the hypothesis that lianas are relatively deep-rooted, one study showed that 15-yr-old liana saplings of one species had roots that reached depths of ≤ 10 m; however, that study focused only on one species, and co-occurring tree rooting depths were not examined (Restom & Nepstad, **2004**). By contrast, in a common garden experiment with 4-yr-old lianas and trees, rooting depths of lianas and trees were similar (Smith-Martin *et al.*, **2019**). Additionally, De Deurwaerder *et al.* (**2018**) found that in a rain forest in French Guiana, lianas used more superficial water than trees during the dry season based on stable isotopes of hydrogen and oxygen. Johnson *et al.* (**2013**) also found that two species of lianas did not have deeper roots than their host tree species in a seasonally dry tropical forest in Panama. Although these findings suggest that lianas may not be more deeply-rooted than trees, the lack of *in situ* studies investigating rooting depths of lianas and co-occurring trees is conspicuous (Powers, **2015**). Lianas are increasing in abundance in tropical forests (Schnitzer & Bongers, **2011**) and decrease forest-wide carbon sequestration (Schnitzer *et al.*, **2014**; van der Heijden *et al.*, **2015**); thus, information on biomass allocation and maximum rooting depth is essential to fully understand their roles in forest ecosystems. However, whether either APT or OPT applies to lianas is unresolved.

Furthermore, plant resource requirements may change with ontogeny. Givnish (**1988**) predicted rising costs of construction and maintenance of structural support tissues as trees become larger and several studies have found support for these predictions. For example, Sendall *et al.* (**2015**) found a decrease in net carbon gain with increases in tree size in *Acer saccharum* and Shipley & Meziane (**2002**) found that hydroponically grown herbaceous plants allocated proportionally more biomass to roots as they grew larger. Furthermore, based on a metanalysis, Poorter *et al.* (**2012**) concluded that both herbaceous and woody plants show a decrease of leaf mass fraction and an increase on stem and root mass fraction as they become larger. Also, Cavender-Bares & Bazzaz (**2000**) came to the conclusion that measurements conducted on seedlings of *Quercus rubra*, could not be extrapolated to mature individuals of *Q. rubra* as they found that the different age classes used different strategies to cope with drought. However, whether there are shifts in resource acquisition and biomass allocation patterns across ontogeny in tropical dry forest species is unknown.

Finally, in seasonal tropical forests, belowground allocation and root distribution may be linked to leaf phenology that represents water-use strategies. In a recent individual-based modeling study in a Costa Rican tropical dry forest, trees of an evergreen plant functional type (PFT) required more than doubled rooting depth compared with similar size trees of deciduous PFT in order to maintain their canopy in the dry season in the Ecosystem Demography 2 model (Xu *et al*., **2016**). In a seasonally wet forest in Panama, Markesteijn & Poorter (**2009**) found that evergreen drought-tolerant tree seedlings had high biomass investment in root systems, yet it is unknown whether adult trees follow the same allocation pattern as juveniles. In a tropical dry forest in Venezuela, Sobrado & Cuenca (**1979**) found that two evergreen woody shrubs had deeper roots than two other co-occurring deciduous species. However, due to the difficulty of excavating whole root systems, there have been few studies to determine variation in belowground allocation and rooting depths among species with distinct growth forms and/or phenology, especially for mature individuals. Because plant biomass partitioning and rooting depth play pivotal roles in both ecological theory (i.e. APT, OPT) and in ecosystem simulation models, better empirical data are needed to inform both these types of models.

In the present study, whole-plant harvests in a seasonally dry tropical forest were used to address the following three knowledge gaps: (1) Do mature lianas comply with the common scaling laws proposed by Enquist & Niklas (**2002**), or do they invest less biomass in stems compared to mature trees? (2) Do juveniles follow the same allocation patterns as mature individuals? (3) Is either leaf phenology (deciduous or evergreen) or life form (liana or tree) a predictor of rooting depth? Simulations with the Ecosystem Demography 2 model were used to explore the consequences of the empirical data herein.

Materials and Methods

Site description
This study was conducted in a tropical dry forest in Northwestern Costa Rica at Estación Experimental Forestal Horizontes (Horizontes; 10.718 N, 85.594 W), which is part of Área de Conservación Guanacaste (ACG). Mean annual precipitation is 1730 mm, mean annual temperature is 25°C, and there is a distinct 5-month-long dry season from December to May (**www.investigadoresacg.org**) during which there is little to no monthly rainfall. This experimental station was formerly a farm with mixed uses including cotton, sorghum and pasture (M. Gutierrez, pers. comm.). Current forests are *c*. 30 old and have regenerated naturally after Horizontes became a protected area (Werden *et al*., **2018**) and are taxonomically and functionally diverse with over 60 species of deciduous, evergreen and semi-deciduous trees and lianas (Waring *et al*., **2019**). Soils at Horizontes are Andic and Typic Haplustepts with a high clay content (38 ± 1%; Waring *et al*., **2019**). Soils were deep and well-drained and in no cases were rooting depths constrained by rock or hard pans.

Species selection
Two groups of plants were sampled that differed in ontonogenic stage: juveniles and adults. Phylogenetically diverse species of deciduous trees, evergreen trees and lianas were planted in a common garden to be harvested as juveniles, and mature individuals were selected in the surrounding forest for harvesting. All of the species used in the present study are common in this region (Powers *et al*., **2009**). The common garden experiment included seven species of deciduous trees (*Bauhinia ungulata*, *Dalbergia retusa*, *Gliricidia sepium*, *Luehea speciosa*, *Lysiloma divaricatum*, *Swietenia macrophylla*, *Tabebuia rosea*), two species of evergreen trees (*Crescentia alata, Simarouba glauca*) and four species of deciduous lianas (*Acacia tenuifolia*, *Amphilophium crucigerum*, *Dioclea violacea*, *Tanaecium tetragonolobum*; Table **1**). For the forest harvest of mature individuals, four species of deciduous trees (*G. sepium*, *Guazuma ulmifolia*, *L. speciose*, *T. rosea*), two species of evergreen tree (*Manilkara chicle*, *S. glauca*) and five species of deciduous lianas (*A. tenuifolia*, *A. crucigerum*, *Combretum farinosum*, *Securidaca diversifolia*, *Serjania schiedeana*; Table **1**) we selected.

Table 1. Family, species used in the study, age of individuals at the time of harvest – juveniles harvested in common garden experiment, and mature individuals harvested from secondary forest (mature) – growth form, and leaf habit.

Species	Family	Age	Growth form	Leaf habit
Acacia tenuifolia	Fabaceae	Juveniles, mature	Liana	Deciduous
Amphilophium crucigerum	Bignoniaceae	Juveniles, mature	Liana	Deciduous
Bauhinia ungulate	Fabaceae	Juveniles	Tree	Deciduous
Combretum farinosum	Combretaceae	Mature	Liana	Deciduous
Crescentia alata	Bignoniaceae	Juveniles	Tree	Evergreen
Dalbergia retusa	Fabaceae	Juveniles	Tree	Deciduous
Dioclea violacea	Fabaceae	Juveniles	Liana	Deciduous
Gliricidia sepium	Fabaceae	Juveniles, mature	Tree	Deciduous
Guazuma ulmifolia	Malvaceae	Mature	Tree	Deciduous
Luehea speciosa	Malvaceae	Juveniles, mature	Tree	Deciduous
Lysiloma divaricatum	Fabaceae	Juveniles	Tree	Deciduous
Manilkara chicle	Sapotaceae	Mature	Tree	Evergreen
Securidaca diversifolia	Polygalaceae	Mature	Liana	Deciduous
Serjania schiedeana	Sapindaceae	Mature	Liana	Deciduous
Simarouba glauca	Simaroubaceae	Juveniles, mature	Tree	Evergreen
Swietenia macrophylla	Meliaceae	Juveniles	Tree	Deciduous
Tabebuia rosea	Bignoniaceae	Juveniles, mature	Tree	Deciduous
Tanaecium tetragonolobum	Bignoniaceae	Juveniles	Liana	Deciduous

Common garden

For the common garden, seeds were collected in ACG in 2014 and in 2016 and planted in 5 × 8 cm black polyethylene bags with a 3 : 1 mix of locally collected soil and sand in May 2014 and May 2016. The seedlings were grown for three months under 90% polyethylene shade cloth and then planted in August in a 1 × 1 m grid in an open field. One month before planting the seedlings in the common garden, the shade cloth was removed to acclimate the seedlings to higher light intensity before transplanting them. Before planting, the field was cleared of all vegetation and fence posts were installed for the lianas to grow on. All individuals from the common garden planted in 2014 were harvested from June to July 2016, and the ones planted in 2016 were harvested in June 2017. Thus, they were either *c.* 12 or 24 months old at harvests, depending on planting date (2014 or 2016). All juvenile lianas were climbing except for the 12-month-old *Acacia tenuifolia* saplings, which were self-supporting; however, 24-month old saplings of *A. tenuifolia* also were harvested and at that age, they were climbing.

Mature plants

In addition to the common garden with juveniles, mature trees and lianas were harvested, which were located in the surrounding forest matrix or close to single-lane unpaved roads on the edge of the forest. All mature trees had a diameter at breast height (DBH) > 12 cm, had reached the canopy, had crowns with access to full sun, and were not over topped by other trees. Mature lianas were those that had reached the canopy and were growing across the top of host trees.

Biomass harvest

In the common garden, two to three individuals per species were harvested from June–July in 2016 and in June 2017 for a total of 47 individuals (Table **1**). Harvest of all the mature individuals occurred between August 2016 and June 2017. Three individuals per species were harvested for a total of 33 mature individuals (Table **1**). Each

individual was cut at ground level using a machete or chainsaw and aboveground liana biomass was pulled down from the canopy with a tractor (Fig. **1**a). The stem diameter was measured at 20 cm from the base and at breast height (1.3 m from the base), and then separated into stems and leaves. Following stem removal, all belowground biomass was dug up with shovels and picks; all coarse roots down to diameters of *c*. 2–5 mm (Fig. **1**b) were excavated and maximum rooting depth and the lengths of all of the excavated roots measured with a tape measure. Although fine roots can make up a large fraction of production allocation (20% or more), they represent a much smaller fraction of total biomass allocation, and are negligible for the questions addressed here.

Figure 1. Image of aboveground biomass of liana *Combretum farinosum* (a) and a root of evergreen tree *Manilkara chicle* in the process of being excavated (b).

All leaf, stem and coarse root biomass of juveniles was dried and weighed. For the mature individuals, all of the fresh biomass as weighed using a spring-loaded balance, and then between half and one-third of leaves, stems, coarse roots were dried and weighed to convert FW to oven-dried biomass estimates. All excavated belowground biomass herein constitutes coarse root biomass. Because some juveniles were < 130 cm, diameters at 20 cm above the base are reported for juveniles. The range of diameters at 20 cm from the base of juveniles was 4–83 mm for deciduous trees, 3–13 mm for evergreen trees and 4–44 mm for lianas. For mature individuals the range in stem DBH for deciduous trees was 132–307 mm and for evergreen trees 137–219 mm, and the sum of stem DBH for lianas was 19–290 mm.

Canopy leaf area

In order to determine canopy leaf area, specific leaf area (SLA, $cm^2\,g^{-1}$) including petioles on 3–6 leaves per individual was measured, and total canopy leaf area extrapolated from SLA and total leaf biomass.

Data analysis

A common framework for data analysis was employed to answer all of our questions. Linear mixed models were fitted with functional group as a categorical variable – that is, deciduous trees, evergreen trees and lianas (hereafter referred to as functional group) and species as a random effect. All continuous variables were log-transformed in all linear mixed models.

The first question to address was whether biomass allocation patterns to stems, leaves and coarse roots of juvenile and mature individuals from the different functional groups followed the same allocation patterns proposed by Enquist & Niklas (**2002**). To do this, linear mixed models were fitted with one fraction of biomass as a function of the other one, that is leaf biomass as a function of stem biomass and coarse root biomass and stem biomass as a function of coarse root biomass. Leaf mass fraction (LMF), stem mass fraction (SMF), and coarse root mass fraction (RMF) also were calculated to explore the optimal partitioning theory. Analyses were conducted separately for juvenile individuals and mature ones to address the second question of whether juveniles follow the same allocation patterns as adults. A model also was fitted with shoot biomass (leaves plus

stems) as a function of coarse root biomass for the juveniles because Enquist & Niklas (**2002**) proposed that juveniles have an isometric relationship between above- and belowground biomass.

The third question to address was whether coarse rooting depths differed predictably among functional groups of mature individuals, with respect to biomass allocation and canopy area. Linear mixed models were fitted with maximum coarse rooting depth as a function of leaf biomass, total canopy leaf area, stem biomass, coarse root biomass and total biomass, and functional group as a grouping factor. Using mixed models, it also was explored whether there was a difference among liana, deciduous tree and evergreen tree total coarse root length, and DBH, shoot biomass and total biomass. All linear mixed models (hereafter represented by chi-squared tests – χ^2) were conducted in R (v.3.5.1) using the lme4 package (R Core Development Team, Vienna, Austria). When necessary, to be able to interpret significant differences, *post hoc* Tukey's HSD tests (hereafter represented by *t*-tests – *t*) were conducted with R/emmeans package.

Ecosystem Demography 2 model

In order to better understand the implication of the observed allometric relationships and illustrate the importance of rooting depth as an evolutionary consequence of phenology, the Ecosystem Demography model 2 (ED2) described by Xu *et al*. (**2016**) was used as a case study. ED2 is an individual-based terrestrial biosphere model that has been well-evaluated in tropical dry forests (Xu *et al*., **2016**; Medvigy *et al*., **2019**). In the model, plant height, leaf biomass, stem biomass and rooting depth change directly or indirectly with DBH following power-law allometric relationships. PFT-specific parameters of these relationships were calibrated from literature values or field observations in tropical dry forests (See table S3 in Xu *et al*., **2016**, for details). Meanwhile, ED2 assumes constant ratios (1) between leaf biomass and fine root biomass and (2) between below ground coarse root and aboveground stem biomass. For tropical dry forest simulations, these two ratios are set to be 1.0 and 0.25, respectively. There is no difference in allometric relationships between juveniles and mature individuals in ED2.

First, a comparison was made between the default biomass allocation and rooting depth relationships in ED2 and the relationships acquired from the observations in the present study. Of interest was which allometric relationship in ED2 had the largest biases from the observation. Second, to evaluate the importance of rooting depth allometry for canopy phenology, simulations were conducted for six 0.1-ha plots in a Costa Rican tropical dry forest that differed in parameterizations of rooting depth. In the default ('Default') simulation herein, the same rooting depth parameters were used as Xu *et al*. (**2016**). Specifically, a maximum rooting depth was assigned to the evergreen plant functional type (PFT E) that was about twice the rooting depth of the deciduous plant functional type (PFT D). In the 'Observation' simulation herein, rooting depth parameters were assigned to the model's PFT E and PFT D based on the present study's measurements. Because there are only five evergreen individuals tall enough to measure DBH for which maximum rooting depth was measured, the root depth allometry was construct based on stem height and the height-based relationship implemented in ED2. In the 'Switch' simulation herein, the measured PFT D rooting depth was assigned to the model's PFT E, and *vice versa*. In the 'Same' simulation herein, PFT E and PFT D were both assigned the same rooting depth parameter, calculated as the mean value of the OBSERVATION PFT E and PFT D parameters. The differences between deciduous and evergreen trees were focused on, because lianas are currently not represented in ED2 or any other ecosystem models.

Results

Biomass allocation patterns in juvenile lianas, deciduous trees, and evergreen trees

In the whole-plant harvests of trees and lianas herein, allocation patterns differed among functional group (lianas, evergreen trees, deciduous trees) in juvenile plants. In general lianas allocated more biomass to leaves

and stems, and the deciduous and evergreen trees allocated more to coarse roots. When comparing the allocation to leaves vs allocation to stems, lianas allocated proportionally more to leaves and deciduous trees to stems (Fig **2**a; Supporting Information **Table S1**; χ^2 = 10.07, P = 0.007; t = −2.95, P = 0.045). Furthermore, in the trade-off between the allocation to leaves vs coarse roots, lianas also allocated more to leaves and deciduous and evergreen trees to coarse roots (Fig **2**b; **Table S1**; χ^2 = 15.15, P < 0.001; deciduous–liana t = −3.64, P = 0.010; evergreen–liana t = −2.49, P = 0.051). Finally, when comparing allocation to stem vs allocation to coarse roots, lianas allocated more biomass to stems and deciduous and evergreen trees to coarse roots (Fig **2**c; **Table S1**; χ^2 = 13.39, P = 0.001; deciduous–liana t = −2.90, P = 0.036; evergreen–liana t = −2.65, P = 0.036). It also was found that juveniles did not scale isometrically between shoot and coarse root biomass. Instead, as they became larger, lianas allocated more biomass to shoots and deciduous and evergreen trees to coarse roots (**Fig. S1**; χ^2 = 16.80, P < 0.001; deciduous–liana t = −3.60, P = 0.011; evergreen–liana t = −2.96, P = 0.018).
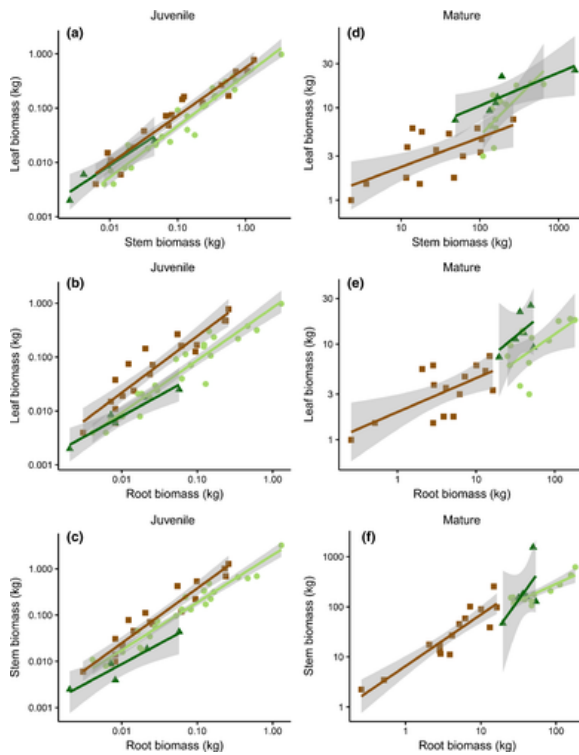

Figure 2. Relationship between leaf and stem biomass, leaf and coarse root biomass, and stem and coarse root biomass of juvenile (a–c), and mature (d–f) deciduous trees (light green circles), evergreen trees (dark green triangles), and lianas (brown squares). Juvenile lianas allocated proportionally more biomass to leaves, deciduous trees to stems (a; χ^2 = 10.07, P = 0.007; deciduous–liana t = −2.95, P = 0.045), and deciduous and evergreen trees to coarse roots (b; χ^2 = 15.15, P ≤ 0.001; deciduous–liana t = −3.64, P = 0.010; evergreen–liana t = −2.49, P = 0.051). Juvenile lianas also allocated more biomass to stems and deciduous and evergreen trees to coarse roots (c; χ^2 = 13.39, P = 0.001; deciduous–liana t = −2.90, P = 0.036; evergreen–liana t = −2.65, P = 0.036). Mature individuals allocated similar proportions of biomass to leaves and stem (d; χ^2 = 5.26, P = 0.072), leaves and coarse roots (e; χ^2 = 4.21, P = 0.122), and stems and coarse roots (f; χ^2 = 2.89, P = 0.236). Shaded areas represent 95% confidence intervals and all variables have been log-transformed.

In terms of mass fractions, in general lianas allocated more biomass to leaves and less to coarse roots, deciduous trees allocated less biomass to leaves and more to stems and coarse roots, and evergreen trees allocated less biomass to stems and more biomass to coarse roots (Fig **3**a–c). Specifically, lianas had greater LMFs than deciduous trees (Fig. **3**a; χ^2 = 12.03, P = 0.002; deciduous–liana t = −3.45, P = 0.019), deciduous trees

had greater SMFs than evergreen trees (Fig **3**b; χ^2 = 9.28, P = 0.010; deciduous–evergreen t = −2.53, P = 0.027), and deciduous and evergreen trees had greater RMFs than lianas (Fig **3**c; χ^2=16.89, P < 0.001; deciduous–liana t = 2.72, P = 0.054; evergreen–liana t = 3.95, P = 0.006).
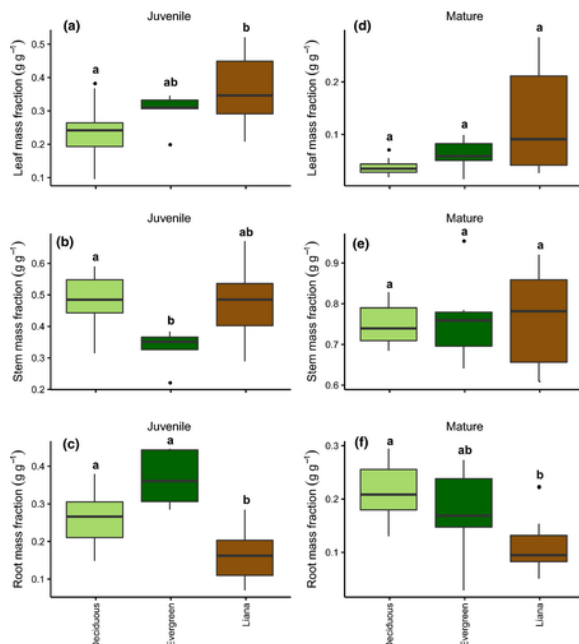

Figure 3. Leaf (LMF), stem (SMF) and coarse root mass fraction (RMF) of juvenile (a–c) and mature (d–f) deciduous trees (light green), evergreen trees (dark green) and lianas (brown). Box plot midlines are medians, box edges are first and third quartiles, whiskers are the minimums and maximums, and points are outliers. Letters at the top of box plots indicate significant (P < 0.05) differences among groups based on Tukey's HSD tests.

Biomass allocation patterns in mature lianas, deciduous and evergreen trees

Mature lianas, deciduous trees and evergreen trees all followed the same allocation patterns to leaves, stems and coarse roots. These patterns were consistent when comparing allocation to leaves vs stems (Fig **2**d; **Table S1**; χ^2 = 5.26, P = 0.0720), leaves vs coarse roots (Fig **2**e; **Table S1**; χ^2 = 4.21, P = 0.122), and stems vs coarse roots (Fig **2**f; **Table S1**; χ^2 = 2.89, P = 0.236). In terms of mass fractions, all individuals had similar LMFs (Fig **3**d; χ^2 = 4.43, P = 0.109) and SMFs (Fig **3**e; χ^2 = 0.07, P = 0.964); however, deciduous trees had greater RMFs than lianas (Fig **3**f; χ^2 = 10.46, P < 0.005; deciduous–liana t = 3.20, P = 0.030).

Trends in maximum rooting depth in relation to biomass and canopy area in mature individuals

Overall, it was found that contrary to expected lianas had the shallowest coarse roots followed by deciduous trees, and as expected evergreen trees had the deepest coarse roots (Fig. **4**; χ^2 = 34.33, P < 0.001; deciduous–evergreen t = −3.205, P = 0.026; deciduous–liana t = 3.14, P = 0.034; evergreen–liana t = 5.70, P < 0.001). Deciduous and evergreen trees had deeper roots than lianas independent of leaf biomass (Fig. **5**a; **Table S1**; χ^2 = 13.70, P < 0.001; deciduous–liana t = 2.77, P = 0.042; evergreen–liana t = 3.47, P = 0.011) and total leaf canopy leaf area (Fig. **5**b; **Table S1**; χ^2 = 21.45, P < 0.001; deciduous–liana t = 3.36, P = 0.019; evergreen–liana t = 4.24, P = 0.005). Evergreen trees had deeper roots than deciduous trees and also lianas, when stem biomass was controlled for (Fig. **5**c; **Table S1**; χ^2 = 16.81, P < 0.001; evergreen–deciduous t = −3.11, P = 0.033; evergreen–liana t = 3.88, P = 0.008), coarse root biomass (Fig. **5**d; **Table S1**; χ^2 = 10.50, P = 0.005; evergreen–deciduous t = −2.78, P = 0.054; evergreen–liana t = 2.62, P = 0.055), and total biomass (Fig. **5**e; **Table S1**;

$\chi^2 = 15.18$, $P < 0.001$; evergreen–deciduous $t = -3.09$, $P = 0.034$; evergreen–liana $t = 3.58$, $P = 0.012$). When DBH was taken into account as a covariate, evergreen trees still had deeper roots than lianas (Fig. **5**f; **Table S1**; $\chi^2 = 11.05$, $P = 0.004$; $t = 3.23$, $P = 0.019$).
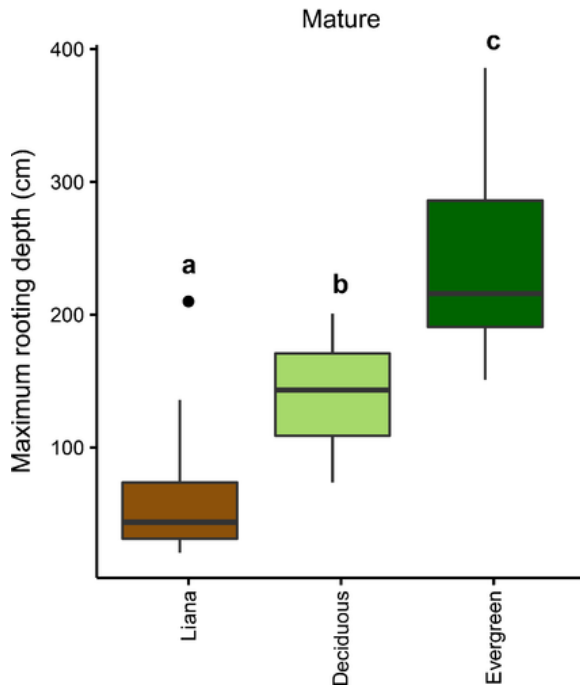

Figure 4. Maximum depth of coarse roots of mature deciduous trees (light green), evergreen trees (dark green), and lianas (brown). Box plot midlines are medians, box edges are first and third quartiles, whiskers are the minimums and maximums, and points are outliers. Letters at the top of box plots indicate significant ($P < 0.05$) differences among groups based on Tukey's HSD tests.
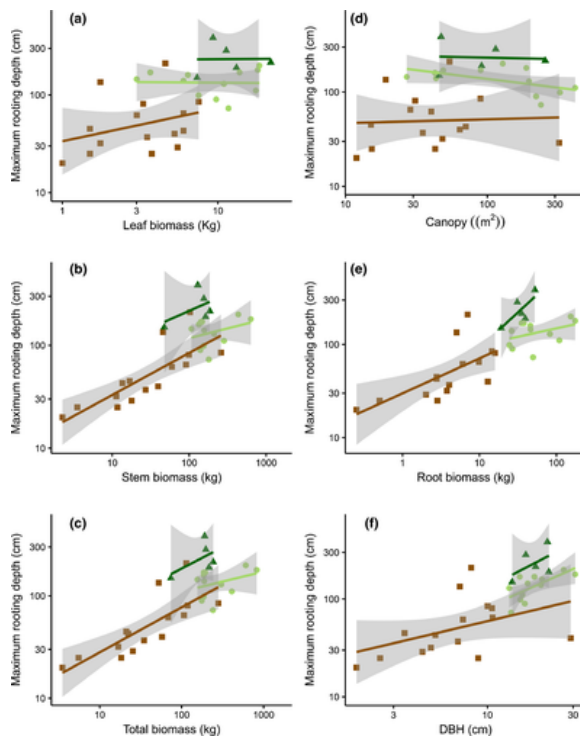

Figure 5. Relationship between maximum depth of coarse roots and leaf biomass (a), total canopy area (b), stem biomass (c), coarse root biomass (d), total biomass (e) and diameter at breast height (DBH) (f) of mature

deciduous trees (light green circles), evergreen trees (dark green triangles) and lianas (brown squares). Deciduous and evergreen trees had deeper roots than lianas independent of leaf biomass (a; χ^2 = 13.70, P < 0.001; deciduous–liana t = 2.77, P = 0.042 evergreen–liana t = 3.47, P = 0.011) and total leaf canopy area (b; χ^2 = 21.45, P > 0.001; deciduous–liana t = 3.36, P = 0.019; evergreen–liana t = 4.24, P = 0.005). Evergreen trees had deeper roots than deciduous trees and lianas independent of stem biomass (c; χ^2 = 16.81, P < 0.001; evergreen–deciduous t = −3.11, P = 0.033; evergreen–liana t = 3.88, P = 0.008), root biomass (d; χ^2 = 10.50, P = 0.005; evergreen – deciduous t = −2.78, P = 0.054; evergreen – liana t = 2.62, P = 0.055) and total biomass (e; χ^2 = 15.18, P < 0.001; evergreen – deciduous t = −3.09, P = 0.034; evergreen – liana t = 3.58, P = 0.012). Evergreen trees still had deeper roots than lianas independent of DBH (f; χ^2 = 11.05, P = 0.004; t = 3.23, P = 0.019). Shaded areas represent 95% confidence intervals and all variables have been log-transformed.

Differences in total root length among functional group

No difference was found among total coarse root length of deciduous trees, evergreen trees and lianas when accounting for DBH (**Fig. S2**a; χ^2 = 2.81, P = 0.246), shoot biomass (**Fig. S2**a; χ^2 = 2.71, P = 0.259) and total biomass (**Fig. S2**a; χ^2 = 0.267, P = 0.263). However, in general the total coarse root length in lianas increased as they became larger, whereas the patterns in trees were more variable.

Comparison of observed and ED2 allometry

Key biomass-size allometry assumptions in ED2 are generally consistent with the observed values (Fig. **6**a–d). In ED2, the evergreen PFT is featured with higher wood density and has 50–100% higher biomass than the deciduous PFT at a given size. Such difference is loosely supported by the observations in leaf biomass allometry. However, with limited data points in evergreen plants and large variations within each PFT, it is hard to evaluate the significance of the difference. The height and DBH relationship in ED2 clearly captured the difference between juvenile and mature plants in the observations but underestimates the stem height in juveniles for deciduous PFT (Fig. **6**e). The largest mismatch between ED2 and the observation is the rooting depth allometry (Fig. **6**f). Although the ED2 allometry allows evergreen PFT to have deeper roots than deciduous PFT, the rooting depth for both PFTs are underestimated compared with the observations. However, the absolute difference in rooting depth for mature individuals (> 10 cm DBH) is similar in the model and the observations (*c.* 100 cm).
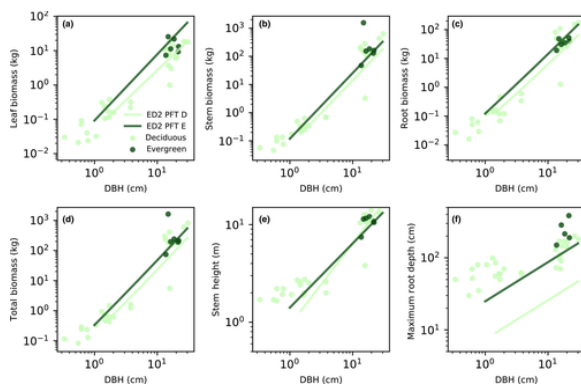

Figure 6. Key allometric relationships from this study (dots) compared with the default tropical dry forest relationships in Ecosystem Demography model 2 (ED2; lines) based on Xu *et al*. (2016). Parameters shown are (a) leaf biomass, (b) aboveground stem biomass, (c) belowground coarse root biomass, (d) total biomass, (e) stem Height and (f) maximum coarse root depth (depth above which 99% of fine root biomass is found in ED2) as a function of diameter at breast height (DBH). The allometry is plotted only for individuals taller than 1.3 m for both the observations and the ED2 relationships.

Subsequent numerical simulations herein demonstrated that evergreen tree species only maintained a high percentage of dry season canopy cover when the simulations were conducted with evergreen species having double the rooting depth of deciduous ones ('Default'); and when the species were assigned the maximum rooting depths obtained from this study ('Observation'), in which cases evergreen trees had deeper roots than the deciduous ones (Figs **7**, **S3**). When the rooting depths of evergreen and deciduous species were switched ('Switch') in the simulation, then deciduous species maintained a higher percentage of cover than the evergreen species (Fig. **7**). When all of the species were assigned the same rooting depth ('Same'), they all maintained a low percentage of leaf cover during the simulated dry season (Fig. **7**). In general, this result holds despite the fact that the evergreen plant functional type was parameterized to have the most drought-resistant aboveground traits (e.g. water potential at which 50% of hydraulic conductivity has been lost and turgor loss point) of any plant functional type.
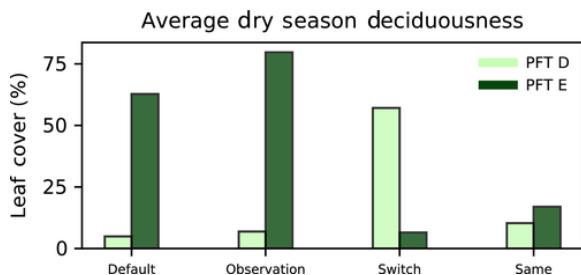

Figure 7. Ecosystem Demography model 2 (ED2) simulated dry season deciduousness (from 2009 to 2014) for coexisting deciduous (PFT D) and evergreen (PFT E) plant functional types in a Costa Rican tropical dry forest under different parameterization for rooting depth allometry based on Xu *et al*. (2016). The dry season deciduousness is defined as the average ratio of active leaf area over maximum leaf area in April, the peak of dry season. Higher leaf cover means more evergreenness. In the 'Default' simulation, maximum rooting depth of PFT E was about twice the rooting depth of the PFT D. In the 'Observation' simulation, rooting depth parameters were assigned to the model's PFT E and PFT D based on the present study's measurements. In the 'Switch' simulation, the measured PFT D rooting depth was assigned to the model's PFT E, and *vice versa*. In the 'Same' simulation, PFT E and PFT D were both assigned the same rooting depth parameter, calculated as the mean value of the observation PFT E and PFT D parameters.

Discussion

This is one of the first studies to use whole-plant harvest of juveniles and mature individuals to address allometric scaling laws in deciduous trees, evergreen trees and lianas, and to explore maximum rooting depth of these groups. Using the simple technology of shovels and chainsaws, four key discoveries were made. First, contrary to expectations, mature lianas did not allocate less biomass to stems than trees, but instead followed the same allometric scaling laws. Second, juveniles and mature individuals did not follow the same allocation patterns. The third discovery, also opposite to the general belief, was that lianas have shallower roots than trees. Fourth, evergreen trees had maximum rooting depth double that of deciduous trees, supporting the assumptions in previous modeling analyses.

Allocation patterns of mature individuals of lianas and trees

It was found that in general mature lianas followed the allocation patterns predicted by the allometric biomass partitioning theory (APT). Moreover, by excavating whole coarse root systems and harvesting all aboveground biomass of mature lianas and trees, it was found that lianas allocated more biomass to stems than expected. It has long been thought that lianas do not invest as much biomass in stems relative to trees, because lianas use the stem architecture of trees to reach the forest canopy (Givnish & Vermeij, **1976**; Putz, **1983**; Castellanos *et al*., **1989**; van der Heijden & Phillips, **2009**; van der Heijden *et al*., **2013**). The results herein show,

at least for the individuals harvested, that lianas followed the same allocation patterns as mature co-occurring evergreen and deciduous trees. Stem length helps to explain this finding. Lianas and trees have similar biomass allocation patterns for stems, because even though lianas have smaller stem DBH than trees, they very long stems and many small branches in the canopy of the host trees. Cumulatively, when expressed as a proportion of total biomass, the 'longer, skinnier' liana stems compare favorably with the 'shorter, fatter' tree stems. This pattern also was observed by Niklas (**1994**) for aboveground biomass (leaves and stems) of temperate vines and gymnosperms; however, that study did not harvest roots.

The only difference found herein among the growth forms was that the deciduous trees had larger coarse root mass fractions than the lianas. A potential explanation for this difference, is that trees require coarse roots, not only for water and nutrient transport, but also to prevent them from toppling over –that is, for mechanical support (Coutts *et al*., **1999**; Ennos, **2000**; Soethe *et al*., **2006**). Because lianas do not support themselves, they only need to prevent themselves from being uprooted vertically (Ennos, **2000**), which potentially requires less investment in coarse roots. Although evergreen trees had similar coarse root mass fractions as the deciduous trees and lianas, in general the evergreen trees harvested herein were smaller than the deciduous trees, which could explain why they needed fewer coarse roots for support. These findings suggest that when it comes to root mass fractions, mature individuals also may follow patterns associated with the optimal partitioning theory (OPT); in this, trees, by contrast to lianas, need to 'optimize' over a greater suite of pressures – nutrient and water acquisition plus support – whereas lianas only have to optimize for nutrient and water acquisition. It is acknowledged that forest age may affect allometry (Waring & Powers, **2017**); however, as secondary forest now comprises the majority of all tropical forest, especially dry forest, results are likely to be broadly applicable.

Juvenile vs adult biomass allocation patterns

Juveniles and adults did not follow the same allocation patterns. The adult individuals in the present study all followed the same global allocation rules proposed by Enquist & Niklas (**2002**) in their biomass APT. However, the juveniles had biomass allocation patterns that complied better with the OPT. Perhaps although juvenile individuals are smaller, they optimize resource acquisition to survive and grow; however, as individuals become larger, they become constrained by maximum resource harvesting capacity and transport forcing them to follow the same allocation rules (Enquist & Niklas, **2002**; Niklas & Enquist, **2002**). Consistent with the findings of Cai *et al*. (**2008**) in *Bauhinia* liana and tree seedlings, it was found herein that juvenile lianas allocated more biomass to leaves and stems and less to roots than trees. In a shade house experiment conducted in the same region and with some of the same species, Smith-Martin *et al*. (**2017**) found that under lower light intensities seedlings allocated more biomass to leaves, whereas under higher light intensities they allocated more to roots. Thus, juveniles may need to be more flexible in their allocation patterns to be able to respond to the environment and dynamically allocate more biomass depending on whether above- vs belowground resource availability is scarcest. Irrespective of the causes of different allocation patterns between juveniles and adults, these results imply that allocation in mature plants cannot be inferred by studying juvenile plants. Nevertheless, such ontogenetic differences in allometry are not represented in individual-based models such as ED2 (Fig. **6**), which can lead to biases in biomass accumulation and seedling survivals in model simulations.

Rooting depths of adult lianas and trees

In the seasonally dry tropical forest studied herein, lianas had the shallowest maximum rooting depths, followed by deciduous trees, and evergreen trees tended to have the deepest maximum rooting depths. This overall pattern was consistent, even after taking into account total biomass, DBH, allocation to leaves, stems and roots, and total canopy area. Whether these patterns hold in other types of tropical forests is not known. The present findings that lianas do not have deeper roots than co-occurring trees are consistent with harvests of 4-yr-old lianas and trees in a common garden in Panama (Smith-Martin *et al*., **2019**). Furthermore, a recent study using indirect methods to assess this question for wet forest in French Guiana showed that lianas do not use deeper

sources of water than trees, even during the dry season (De Deurwaerder *et al.*, **2018**). As all of the species of lianas studied herein are deciduous, it would be logical to expect that deciduous trees and lianas would have had similar rooting depth. One potential explanation for the shallower rooting depth found in the lianas is that lianas only need their roots for resource uptake, whereas trees also need their roots for support, potentially explaining why deciduous trees had deeper roots despite having the same leaf phenology.

The findings herein are contrary to the hypothesis that lianas are deep-rooted (Holbrook & Putz, **1996**; Andrade *et al.*, **2005**; Schnitzer, **2005**; Schnitzer *et al.*, **2005**; Toledo-Aceves & Swaine, **2008**; Schnitzer & Bongers, **2011**; Chen *et al.*, **2015**). The limitations of the present study are evident: it is difficult to harvest entire rooting systems of mature plants, the study of coarse roots does not allow us to distinguish roots designed for anchoring and support vs those designed for water uptake, and there was a limited sample size from only one location where lianas were deciduous and thus there may not have been the need for exceptionally deep roots. Nevertheless, the data herein do suggest no evidence that lianas have deeper rooting depths than co-occurring trees in this dry forest, consistent with findings from another common garden study (Smith-Martin *et al.*, **2019**), and thus the assumption of deeper liana rooting depths is not supported.

The present findings leave many important questions unresolved. Lianas are increasing in many forests (Schnitzer & Bongers, **2011**) and liana competition with trees has been shown to reduce net forest carbon storage (van der Heijden *et al.*, **2015**). This increase in lianas had been attributed to their better performance than trees during seasonal drought; part of the explanation for this pattern is the assumption that lianas have deeper roots than co-occurring tree, and thus can access deeper sources of water. However, based on the present study in Costa Rican dry forest and a previous study in moist forest in Panama (Smith-Martin *et al.*, **2019**), direct evidence from harvests is accumulating and is overturning the common assumption that lianas are deeper-rooted than trees. How lianas maintain similar or better water status during seasonal drought (Smith-Martin *et al.*, **2019**) and are able to grow more during the dry season whereas co-occurring trees grow more during the wet season in semi-moist forest still remains unknown (Schnitzer & van der Heijden, **2019**). Smith-Martin *et al.* (**2019**) found that lianas appeared to explore more soil volume per stem diameter than did co-occurring trees, yet the present study did not find that lianas had greater root extensions per stem diameter, shoot biomass, or total biomass. Moreover, the measurements herein did not quantify fine root biomass (typically defined as roots < 2 mm diameter), which may play a role in differentiating trees and lianas, if lianas have more fine root mass. Clearly, there is more to be learnt about the comparative morphology and physiology of trees and lianas, and their implications for forest carbon cycling and storage.

Coordination between rooting depth and canopy phenology

It is not surprising that the largest mismatch between the observed and ED2 default allometry was found in the rooting depth, which was the least-constrained relationship in Xu *et al.* (**2016**). However, the belowground excavation herein validates the assumption of the coordination between rooting depth and canopy phenology. Evergreen trees had the deepest coarse roots of all the individuals harvested. One explanation for this pattern is that plants coordinate their belowground allocation with their aboveground water demand. Although there is limited previous information on dry forest rooting depth, there seems to be a tendency for dry forest species to deploy a greater proportion of their roots deeper in the soil than wet forest species (Holbrook *et al.*, **1995**). Thus, to sustain leaves during the extended dry seasons, evergreen species are most likely deeper-rooted to access deeper sources of water during times when this resource is limited. Furthermore, the degree of deciduousness simulated by the ecosystem demography model indicates that evergreen plant functional types can retain sufficiently high water potential in the dry season and remain evergreen only by developing deeper rooting profiles relative to other plant functional types. Thus, the simulations suggest that the differences between evergreen and deciduous trees might result from an ecological coordination between above- and belowground processes. Moreover, the lianas measured in Costa Rica are deciduous in the dry season, which is

again consistent with their observed shallow rooting depths. The present results provide evidence for such ecological coordination as well as valuable datasets for terrestrial biosphere models that consider vegetation demography (Fisher *et al.*, **2018**).

Conclusion

It is demonstrated that mature lianas follow the same biomass allocation patterns as co-occurring trees, and invest proportionally similar biomass to stems. The findings herein indicate that juvenile lianas, deciduous trees and evergreen trees differ in allocation patterns, potentially consistent with the optimal partitioning theory, whereas mature individuals show allocation patterns that follow allometric biomass partitioning theory. Thus, as proposed previously (Bazzaz *et al.*, **1987**; Cavender-Bares & Bazzaz, **2000**), it is not possible to infer the allometry and allocation patterns of mature plants from studies of seedlings and/or saplings. Last, the results herein also show that lianas, which are deciduous at this site, had the shallowest rooting depths and evergreen tropical trees have the deepest roots, which are most likely needed to sustain their leaves during the extended periods of seasonal drought, as shown with the model simulation. There is an acute need to better understand how increasing liana abundances are impacting carbon storage and cycling in tropical forests (van der Heijden *et al.*, **2015**). Studies such as the present one that clarify the structure and implications of belowground biomass patterns in tropical forests are needed to inform both conceptual and simulation models of tropical forest dynamics and quantify the implications of global environmental change.

Author contributions

CMSM and JSP designed the research; CMSM collected and analyzed data and wrote a draft of the manuscript with substantial input from XX, DM, SAS and JSP; and XX and DM ran Ecosystem Demography model 2.

References

Andrade JL, Meinzer FC, Goldstein G, Schnitzer SA. 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* **19**: 282– 289.

Banin L, Feldpausch TR, Phillips OL, Baker TR, Lloyd J, Affum-Baffoe K, Arets EJMM, Berry NJ, Bradford M, Brienen RJW *et al.* 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography* **21**: 1179– 1190.

Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. 1987. Allocating resources to reproduction and defense. *BioScience* **37**: 58– 67.

Bloom AJ, Chapin FS, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics* **16**: 363– 392.

Cai ZQ, Poorter L, Cao KF, Bongers FJJM. 2007. Seedling growth strategies in *Bauhinia* species: comparing lianas and trees. *Annals of Botany* **100**: 831– 7364.

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

Castellanos AE, Mooney HA, Bullock SH, Jones C, Robichaux R. 1989. Leaf, stem, and metamer characteristics of vines in a tropical deciduous forest in Jalisco, Mexico. *Biotropica* **21**: 41– 49.

Cavender-Bares J, Bazzaz FA. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* **124**: 8– 18.

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman RC *et al*. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* **20**: 3177– 3190.

Chen Y-J, Cao K-F, Schnitzer SA, Fan Z-X, Zhang J-L, Bongers F. 2015. Water-use advantage for lianas over trees in tropical seasonal forests. *New Phytologist* **205**: 128– 136.

Coutts MP, Nielsen CCN, Nicoll BC. 1999. The development of symmetry, rigidity and anchorage in the structural root system of conifers. *Plant and Soil* **217**: 1– 15.

Davidson RL. 1969. Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Annals of Botany* **33**: 561– 569.

De Deurwaerder H, Hervé-Fernández P, Stahl C, Burban B, Petronelli P, Hoffman B, Bonal D, Boeckx P, Verbeeck H. 2018. Liana and tree below-ground water competition – evidence for water resource partitioning during the dry season. *Tree Physiology* **38**: 1071– 1083.

Ennos AR. 2000. The mechanics of root anchorage. *Advances in Botanical Research* **33**: 133– 157.

Enquist BJ, Niklas KJ. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* **295**: 1517– 1520.

Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ *et al*. 2018. Vegetation demographics in earth system models: a review of progress and priorities. *Global Change Biology* **24**: 35– 54.

Gehring C, Park S, Denich M. 2004. Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management* **195**: 69– 83.

Givnish T. 1988. Adaptation to sun and shade: a whole-plant perspective. *Functional Plant Biology* **15**: 63– 92.

Givnish TJ, Vermeij GJ. 1976. Sizes and shapes of liane leaves. *The American Naturalist* **110**: 743– 778.

van der Heijden GMF, Phillips OL. 2009. Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences* **6**: 2217– 2226.

van der Heijden GMF, Powers JS, Schnitzer SA. 2015. Lianas reduce carbon accumulation and storage in tropical forests. *Proceedings of the National Academy of Sciences, USA* **112**: 13267– 13271.

van der Heijden GM, Schnitzer SA, Powers JS, Phillips OL. 2013. Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica* **45**: 682– 692.

Holbrook NM, Putz FE. 1996. Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down. In: SS Mulkey, RL Chazdon, AP Smith, eds. *Tropical forest plant ecophysiology*. Boston, MA, USA: Springer US, 363– 394.

Holbrook NM, Whitbeck JL, Mooney HA. 1995. Drought responses of neotropical dry forest trees. In: E Medina, HA Mooney, SH Bullock, eds. *Seasonally dry tropical forests*. Cambridge, UK: Cambridge University Press, 243– 276.

Johnson DM, Domec JC, Woodruff DR, McCulloh KA, Meinzer FC. 2013. Contrasting hydraulic strategies in two tropical lianas and their host trees. *American Journal of Botany* **100**: 374– 383.

Kny L. 1894. On correlation in the growth of roots and shoots. *Annals of Botany* **8**: 265– 280.

Markesteijn L, Poorter L. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* **97**: 311– 325.

McCarthy MC, Enquist BJ, Kerkhoff AJ. 2007. Organ partitioning and distribution across the seed plants: assessing the relative importance of phylogeny and function. *International Journal of Plant Sciences* **168**: 751– 761.

Medvigy D, Wang G, Zhu Q, Riley WJ, Trierweiler AM, Waring Bonnie G, Xu X, Powers JS. 2019. Observed variation in soil properties can drive large variation in modelled forest functioning and composition during tropical forest secondary succession. *New Phytologist* **223**: 1820– 1833.

Niklas KJ. 1994. Comparisons among biomass allocation and spatial distribution patterns of some vine, pteridophyte, andgymnosperm shoots. *American Journal of Botany* **81**: 1416– 1421.

Niklas KJ. 2005. Modelling below- and above-ground biomass for non-woody and woody plants. *Annals of Botany* **95**: 315– 321.

Niklas KJ, Enquist BJ. 2002. Canonical rules for plant organ biomass partitioning and annual allocation. *American Journal of Botany* **89**: 812– 819.

Niklas KJ, Spatz H-C. 2004. Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proceedings of the National Academy of Sciences, USA* **101**: 15661– 15663.

Poorter H, Jagodzinski AM, Oleksyn J, Ruiz-Peinado R, Kuyah S, Luo Y, Reich PB, Usoltsev VA, Buckley TN, Sack L. 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytologist* **208**: 736– 749.

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* **193**: 30– 50.

Powers JS. 2015. Reciprocal interactions between lianas and forest soil. In: SA Schnitzer, F Bongers, RJ Burnham, FE Putz, eds. *Ecology of lianas*. Chichester, UK: John Wiley & Sons, 175– 187.

Powers JS, Becknell JM, Irving J, Pèrez-Aviles D. 2009. Diversity and structure of regenerating tropical dry forests in Costa Rica: geographic patterns and environmental drivers. *Forest Ecology and Management* **258**: 959– 970.

Putz FE. 1983. Liana biomass and leaf area of a "*Tierra Firme*" forest in the Rio Negro Basin, Venezuela. *Biotropica* **15**: 185– 189.

Restom TG, Nepstad DC. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management* **190**: 109– 118.

Roa-Fuentes LL, Campo J, Parra-Tabla V. 2012. Plant biomass allocation across a precipitation gradient: an approach to seasonally dry tropical forest at Yucatán, Mexico. *Ecosystems* **15**: 1234– 1244.

Schnitzer SA. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist* **166**: 262– 276.

Schnitzer SA, Bongers F. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* **14**: 397– 406.

Schnitzer SA, Kuzee ME, Bongers F. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology* **93**: 1115– 1125.

Schnitzer SA, van der Heijden GMF. 2019. Lianas have a seasonal growth advantage over cooccurring trees. *Ecology* **100**: e02655.

Schnitzer SA, van der Heijden GMF, Mascaro J, Carson WP. 2014. Lianas in gaps reduce carbon accumulation in a tropical forest. *Ecology* **95**: 3008– 3017.

Selaya NG, Anten NPR, Oomen RJ, Matthies M, Werger MJA. 2007. Above-ground biomass investments and light interception of tropical forest trees and lianas early in succession. *Annals of Botany* **99**: 141– 151.

Sendall KM, Lusk CH, Reich PB. 2015. Becoming less tolerant with age: sugar maple, shade, and ontogeny. *Oecologia* **179**: 1011– 1021.

Shipley B, Meziane D. 2002. The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology* **16**: 326– 331.

Smith-Martin CM, Bastos CL, Lopez OR, Powers JS, Schnitzer SA. 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. *Ecology* **100**: e02827.

Smith-Martin CM, Gei MG, Bergstrom E, Becklund KK, Becknell JM, Waring BG, Werden LK, Powers JS. 2017. Effects of soil type and light on height growth, biomass partitioning, and nitrogen dynamics on 22 species of tropical dry forest tree seedlings: comparisons between legumes and nonlegumes. *American Journal of Botany* **104**: 399– 410.

Sobrado M, Cuenca G. 1979. Aspectos del uso de agua de especies deciduas y siempreverdes en un bosque seco tropical de Venezuela. *Ada Cientifica Venezolana* **30**: 302– 308.

Soethe N, Lehmann J, Engels C. 2006. Root morphology and anchorage of six native tree species from a tropical montane forest and an elfin forest in Ecuador. *Plant and Soil* **279**: 173– 185.

Stevens GC. 1987. Lianas as structural parasites: the *Bursera Simaruba* example. *Ecology* **68**: 77– 81.

Thornley JHM. 1972. A balanced quantitative model for root: shoot ratios in vegetative plants. *Annals of Botany* **36**: 431– 441.

Toledo-Aceves T, Swaine MD. 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecology* **196**: 233– 244.

Waring BG, Pérez-Aviles D, Murray JG, Powers JS. 2019. Plant community responses to stand-level nutrient fertilization in a secondary tropical dry forest. *Ecology* **100**: e02691.

Waring BG, Powers JS. 2017. Overlooking what is underground: root:shoot ratios and coarse root allometric equations for tropical forests. *Forest Ecology and Management* **385**: 10– 15.

Werden LK, Alvarado JP, Zarges S, Calderón ME, Schilling EM, Gutiérrez LM, Powers JS. 2018. Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. *Journal of Applied Ecology* **55**: 1019– 1028.

Xu X, Medvigy D, Powers JS, Becknell JM, Guan K. 2016. Diversity in plant hydraulic traits explains seasonal and inter- annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80– 95.