

Ontogenetic modulation of branch size, shape, and biomechanics produces diversity across habitats in the *Bursera simaruba* clade of tropical trees

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SUMMARY Organismal size and shape inseparably interact with tissue biomechanical properties. It is therefore essential to understand how size, shape, and biomechanics interact in ontogeny to produce morphological diversity. We estimated within species branch length-diameter allometries and reconstructed the rates of ontogenetic change along the stem in mechanical properties across the *simaruba* clade in the tropical tree genus *Bursera*, measuring 376 segments from 97 branches in nine species in neotropical dry to rain forest. In general, species with stiffer materials had longer, thinner branches, which became stiffer more quickly in ontogeny than their counterparts with more flexible materials.

We found a trend from short stature and flexible tissues to tall statures and stiff tissues across an environmental gradient of increasing water availability, likely reflecting a water storage–mechanical support tradeoff. Ontogenetic variation in size, shape, and mechanics results in diversity of habits, for example, rapid length extension, sluggish diameter expansion, and flexible tissues results in a liana, as in *Bursera instabilis*. Even species of similar habit exhibited notable changes in tissue mechanical properties with increasing size, illustrating the inseparable relationship between organismal proportions and their tissue mechanics in the ontogeny and evolution of morphological diversity.

INTRODUCTION

Size and shape are enshrined in the canon of developmental evolutionary biology (Thompson 1924; Atchley and Rutledge 1980). Conceptual frameworks such as those of Alberch (1989) and Alberch et al. (1979) endeavored to describe the evolution of organismal form, understood as modulation of size and shape in development. More recently, evo-devo has coalesced around questions of form (Laubichler and Maienschein 2009; Klingenberg 2010). The study of size and shape is so deeply seated in developmentalist evolutionary biology that it needs no apologetics.

Less discussed but just as important is that size and shape are but two members of a developmental trinity that also includes biomechanical properties (Alfaro et al. 2004; Salazar-Ciudad and Jernvall 2010). There can be no change in size or shape without changes in the emergent mechanical behavior of a structure as a whole. This can be readily understood

based on common experience. A thin filament of steel will behave very differently from a thick rod or a block. Similarly, different materials will be associated with different mechanical behaviors. A rod made out of steel will sustain its own weight whereas an identical one of gelatin will not. Organismal structures obey the same principles. Ontogenetic differences in size, shape, or tissue mechanical characteristics will inevitably cause a difference in a structure's performance, whether it be a cell membrane, a crab claw, or a tree trunk (Niklas 1992; Vogel 2003). Morphological diversity across species can thus be viewed as the result of ontogenetic variation in the members of the size–shape–biomechanics trinity.

Despite the crucial role of ontogenetic modulation of the size–shape–biomechanics trinity in the production of morphological diversity, much information is lacking (Jaffe 1973; Chehab et al. 2009; Gallenmüller et al. 2001; Lahaye et al. 2005; Rowe and Speck 2005; Speck and Rowe 1999). Particularly crucial is that there is little information regarding

how size and shape vary with biomechanical behavior across clades across habitats. Yet because ultimately morphological and functional diversity both within and between species emerge from the interplay among size, shape, and biomechanics in ontogeny, it is essential to document how ontogenetic modulation within the trinity is associated with diversity across species.

Tree stems provide a convenient study system for testing hypotheses concerning the ways that organismal proportions should vary with mechanics through ontogeny and across sizes and habits (Niklas 1992; Sterck et al. 2006). Trees are ideal for ontogenetic study because they trace a record of their own ontogeny in space (Olson and Rosell 2006; Olson 2007). From the youngest part of the branch tip toward the base, we can reconstruct the ontogenetic “decisions” that a branch has taken (Rosell and Olson 2007). How mechanical contributions vary in ontogeny should in turn be reflected in diversity of sizes and habits. We provide detailed documentation of ontogenetic trajectories in mechanical parameters across species that range from 5- to 30-m tall in a small clade of tropical trees.

To examine how ontogenetic differences underlie interspecific diversity, we examine the way that mechanical properties are reflected in organismal size and shape by testing the expectation, analogous to the gelatin-steel example above, that stiffer stem materials should be associated with longer branches for a given diameter across species. This expectation can be expressed in terms of the modulus of elasticity E and the second moment of area I . The modulus of elasticity describes how resistant a given material is to bending, and refers to a material in the abstract, so hard-to-bend “steel” has high

E whereas squishy “gelatin” has low E (Gere 2002). The second moment of area I describes the size and shape of a beam in cross-section in terms of how well placed its material is to resist bending (Niklas 1992). The product EI expresses the resistance to bending of a particular beam. How much a beam attached at one end bends (its deflection δ) can be approximated as $qL^4/8EI$, where q is a weight distributed along the beam, such as the weight of the beam itself, and L is its length (Gere 2002). Thinking of unbranched stems as beams, this equation illustrates how evolutionary changes in E should affect stem proportions. In self-supporting trees, natural selection should favor individuals with branches that maintain their position in the canopy without excessive support costs (Niklas 1993). Assuming for the moment that this means that δ will remain constant between species, then two trees that differ only in E will necessarily have different branch proportions: either stems must become thicker, increasing their I , or decrease in length. Without these changes in organ proportionality, δ will increase, meaning floppier branches that might not maintain their position in the canopy. These interactions among length, I , and E underlie our central prediction that branches made up of higher wood and whole-branch E should be longer and thinner than those with low E .

We focus on the members of the *simaruba* clade in the genus *Bursera* (Burseraceae; Rosell et al. 2010), a group of rich diversity in size, habit, and habitats (Fig. 1). The namesake species *Bursera simaruba* is an unmistakable tree to 30-m tall in virtually all lowland forests from Florida to northern South America (Fig. 1A). The other species in the clade range from *B. simaruba*-like subdeciduous forest trees (*B. attenuata* and *B. roseana*; Fig. 1B) to tropical deciduous forest trees

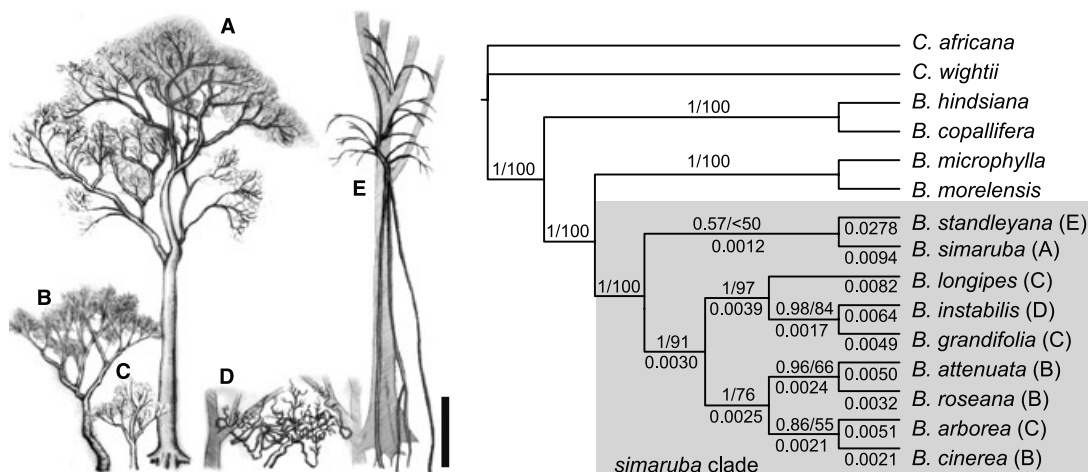


Fig. 1. Diversity in shape, size, and habit in the *Bursera simaruba* clade, and phylogenetic relationships of sampled species. The clade includes “conventional” trees such as (A) *Bursera simaruba*, the largest species, (B) intermediate (<20 m), and (C) small (<10 m) species, (D) *B. instabilis*, a tree with lianescent branches, and (E) *B. standleyana*, a hemiepiphyte (support plants in gray). Scale bar = 5 m. To the right, Bayesian 50% majority rule consensus with posterior probabilities/bootstrap values above branches and branch lengths below. *C.* = *Commiphora*; letters in parentheses refer to the habit categories at left.

averaging a scant 5-m tall (*B. grandifolia*, *B. longipes*; Fig. 1C). Mexican dry forest endemic *B. instabilis* is unusual in that its stems are lianescent (Fig. 1D) whereas Costa Rican endemic *B. standleyana* is a hemiepiphyte that grows high in rainforest trees (Fig. 1E). To our knowledge, this is the first study to survey stem biomechanical evolution in the members of a clade across habitats (see Sterck et al. 2006; Jacobsen et al. 2007).

We used the descendants of a common ancestor to examine the ways that ontogenetic modulation of branch proportions and mechanical characteristics produces the diversity observed across species. Most members of the *simaruba* clade are self-supporting trees of more or less conventional tree habit, and on first glance appear to differ mainly in size. We show that these size differences, possibly related to moisture availability across habitats, are associated with marked differences in stem mechanical properties and length-diameter ontogenies. In addition, we use *B. standleyana* and *B. instabilis*, the two species of divergent habit, to illustrate the ways that ontogenetic variation in the relationship between stem proportions and biomechanics should lead to the evolution of morphological and functional diversity across plants at large. We conclude by underscoring the importance of mechanics as a central member of the study of organismal form.

MATERIALS AND METHODS

Our central objective was to examine the way that ontogenetic variation in size, proportions, and tissue biomechanics is associated with morphological diversity in the *simaruba* clade. To do so, it was first necessary to document differences in branch size and shape. Accordingly, we examined variation in branch length-diameter proportions across species (section “Variation in branch length-diameter scaling exponent α across species”). It was then necessary to explore the patterns of variation in mechanical properties along ontogeny across species (section “Ontogenetic change in mechanics, and mechanical differences between species”). We could then assess our main prediction regarding the degree to which ontogenetic changes in branch mechanical properties predict proportions across species. Specifically, we tested the expectation that self-supporting branches made up of stiffer tissues (E_{wood} and E_{struct}) should be longer and thinner, and explored associations between interspecific ontogenetic diversity and environmental variation (section “Association between size, shape, and biomechanics across environmental gradients”).

Variation in branch length-diameter scaling exponent α across species

Differences in branch length-diameter proportions were evaluated through comparisons of allometric parameters. We

measured diameter (D) and length (L) of an average of 12 branches for each of nine species (Table 1). We measured only six branches of *B. standleyana* because of limited availability. We used the Huxley equation $\log_{10}L = \log_{10}\gamma + \alpha\log_{10}D$, where α is the allometric slope compared across species (Niklas 1994). We estimated α , and the intercept $\beta(\log_{10}\gamma)$ via reduced major axis regression (RMA, Warton et al. 2006) using the package *smatr* (Warton and Ormerod 2007) in R version 2.14.1 (<http://www.R-project.org>).

Ontogenetic change in mechanics, and mechanical differences between species

Trees modify branch mechanical behavior via ontogenetic modulation of wood and bark mechanical properties and quantities. It is possible to trace biomechanical ontogenetic trajectories by measuring mechanical properties along branches. We collected healthy, leading, straight branches with few side branches from two to four trees per species. Each branch was divided into segments with 1:20 span:length ratios to perform three-point bending tests using a digital micrometer (Rosell and Olson 2007). We tested segments in such a way to avoid rotation about their longitudinal axis. EI_{struct} (“struct” denoting the whole-branch or “structural” stiffness) and EI_{wood} were measured from intact and debarked segments, respectively. We computed second moments of area for the whole branch (I_{struct}), and the wood (I_{wood}) with formulas for circular or elliptical hollow cylinders (Niklas 1992), subtracting the pith and averaging apical and basal segment diameters. Computation of elastic moduli (E_{struct} , E_{wood}) was straightforward after measuring EI and I . I and EI are structure-level properties whereas E describes the tendency for a given material to resist deformation. In organisms, the materials are biological tissues, so we refer to E_{wood} and E_{struct} as “tissue” mechanical properties. E_{wood} reflects the stiffness of wood, and E_{struct} reflects the stiffness of the wood and the bark combined (Rosell and Olson 2007). We used the distance from the midpoint of each segment to the tip of the branch as a standard against which to compare ontogenies across species (Rosell and Olson 2007). The average number of branches per species was 11, ranging from 7 to 14, depending on the availability of material (Table 1). Branch length averaged 1.92 m (Table 1), ranging from 0.5 to approximately 4 m. Branches were divided into an average of four segments each, for a mean of 42 segments per species (no. of segments/species in Table 1). All 376 segments tested bore secondary xylem.

To test how ontogenetic modulation of stems was associated with changes in mechanical parameters, it was first necessary to map ontogenetic changes in E_{struct} and E_{wood} within species (Rosell and Olson 2007), and second to compare these traits between species. We addressed these aspects simultaneously using multiple linear models. Fitting a global

Table 1. Branch allometric models, sampling for biomechanical tests, and maximum tree height for the species of the *simaruba* clade

Species	Allometric models				Branch sampling for biomechanics			
	<i>n</i>	<i>R</i> ²	α (95% CI)	β (95% CI)	<i>n</i>	Mean length (m)	Total segments	Maximum height (m)
<i>B. arborea</i>	10	0.63	1.308 (0.811–2.111)	1.664 (1.276–2.051)	11	1.95	50	10.44
<i>B. attenuata</i>	8	0.88	0.891 (0.630–1.260)	1.880 (1.620–2.140)	14	1.98	51	10.5
<i>B. cinerea</i>	11	0.69	0.790 (0.526–1.187)	1.907 (1.627–2.187)	12	1.60	42	14.58
<i>B. grandifolia</i>	12	0.68	0.794 (0.536–1.174)	1.972 (1.783–2.162)	7	0.76	13	9.28
<i>B. instabilis</i>	18	0.23	1.640 (1.045–2.572)	1.673 (1.175–2.172)	9	3.12	47	9.75
<i>B. longipes</i>	11	0.87	0.752 (0.576–0.982)	1.903 (1.820–1.986)	11	0.77	29	8.69
<i>B. roseana</i>	13	0.86	1.047 (0.816–1.344)	1.815 (1.618–2.012)	11	2.04	49	16.85
<i>B. simaruba</i>	10	0.76	1.416 (0.957–2.093)	1.479 (0.996–1.963)	13	2.44	53	25.15
<i>B. standleyana</i>	6	0.98	0.964 (0.812–1.145)	2.121 (2.051–2.191)	7	2.71	42	5.36

α = scaling exponent, β = $\log_{10}\gamma$, following the \log_{10} transformation of the Huxley allometric equation $L = \gamma D^\alpha$, CI = confidence intervals

model to all of the data is preferable to the alternative of fitting numerous individual regression models per species. It avoids the need to test for different intercepts and slopes between all possible pairwise combinations of species, estimates parameters common to all models only once using all of the data, and is associated with lower Type I error rates (Kutner et al. 2005). The fitting of our multiple models involved a multistep procedure summarized in Fig. 2. This figure shows the steps followed to fit the model on which inferences regarding E_{struct} are based, the main biological questions addressed through each step, and how the questions were translated into statistical terms. The steps to build the model predicting E_{wood} were identical to those involved in the model predicting E_{struct} , except for the final step, as explained below.

We started the process by fitting a model predicting E_{struct} based on distance from the segment midpoint to the branch tip (distance) and species (Sp) as independent variables (model 1, Fig. 2A). The variable Sp was represented by seven dummy variables accounting for the eight species in the dataset. Models for lianescent *B. instabilis* were fitted separately given that its branches do not become stiffer in ontogeny (see Results). The violation of homoscedasticity and residual normality of the preliminary model was alleviated by \log_{10} transforming E_{struct} and distance (Quinn and Keough 2002). Branches may vary in their characteristics depending on the vagaries of their history, with segments from the same branch potentially resembling one another closely. To assess this potential violation of independence, we tested the significance of a random effect for branch membership (Zuur et al. 2009) using the R package nlme (Pinheiro et al. 2009). We found that branch membership of a segment did not provide additional explanatory power to models according to likelihood ratio tests and Akaike and Bayesian Information

Criteria, and that segment data could therefore be pooled by species.

Once we determined that E_{struct} increased in ontogeny, we needed to ask whether the rate of increase differed between species (Fig. 2B). To this end, we added a distance \times Sp interaction term, which would indicate whether species differed in their E_{struct} –distance slope, that is, in their rate of ontogenetic change in E_{struct} (model 2, Fig. 2B). The interaction was significant, indicating that at least one species differed in rate when compared to the species used as a reference category when fitting the model (*B. roseana*). Species with different rates were detected through the significance of their associated interaction terms.

In addition to comparing ontogenetic rates, we also needed to assess how ontogenetic modulation results in differences in mean mechanical performance across species (Fig. 2C). Using a model with heterogeneous slopes such as model 2 for comparisons between species would be very difficult, given that comparisons would only be valid in the range of distance from the tip where the fitted lines do not cross. These comparisons would need to be performed by species pairs (Quinn and Keough 2002), making general inferences unfeasible. Instead, we followed standard statistical procedure in fitting more parsimonious models with fewer terms and more straightforward interpretation (Kutner et al. 2005). Fewer terms implied grouping species based on model 1 as having statistically indistinguishable mean E_{struct} (Fig. 2C). As discussed in Results, three groups emerged: species with higher, equivalent, or lower values of E_{struct} compared to *B. roseana*, the reference category. These groups had a statistical origin, but were biologically meaningful because they coincided with environmental conditions (see Results). Model 3, with species group instead of species, had fewer parameters,

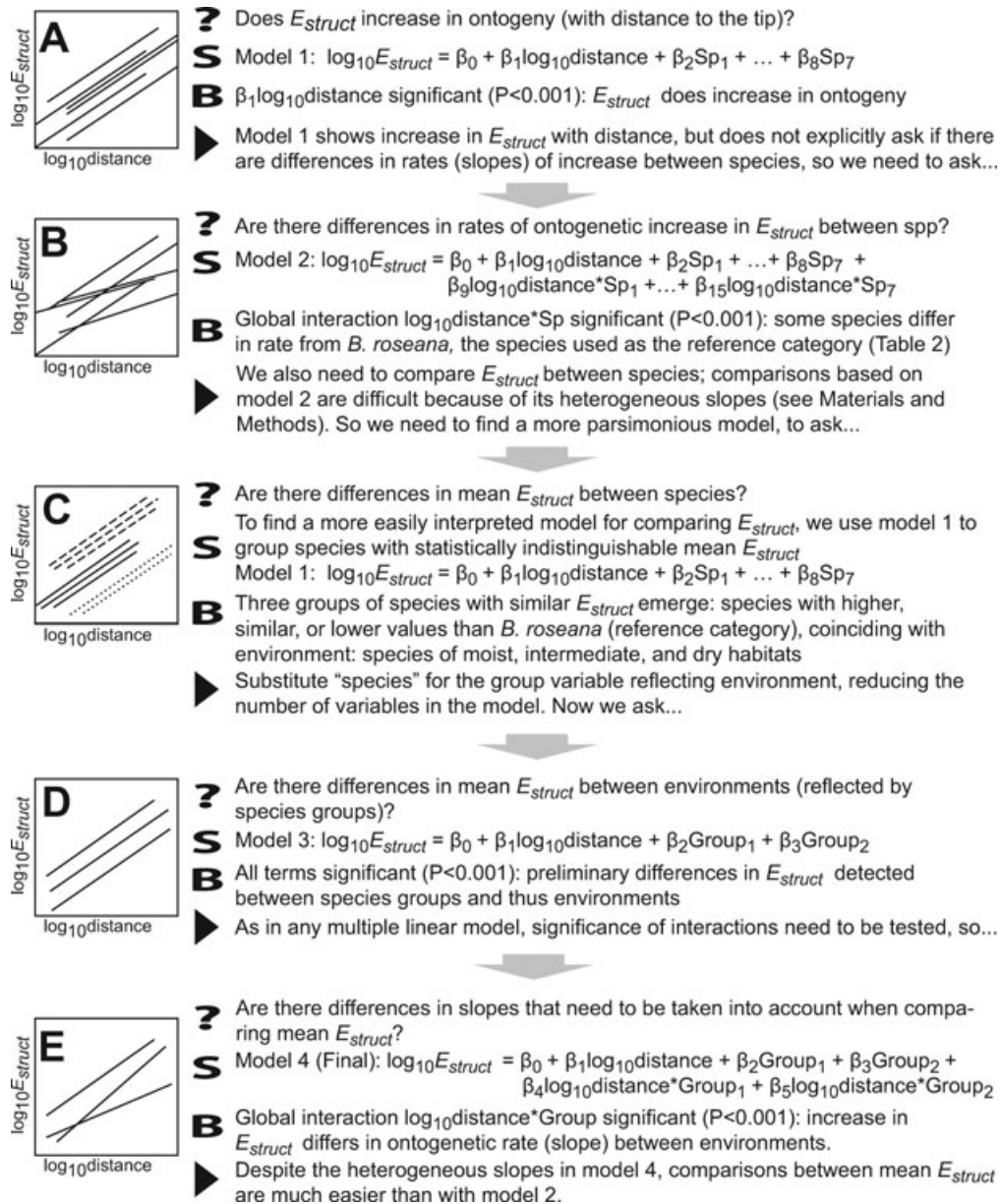


Fig. 2. Schematic diagram illustrating the fitting of the multiple linear models predicting E_{struct} used to test hypotheses of ontogenetic modulation in stems. The procedure for fitting the models predicting E_{wood} was identical, except for the last step (see Materials and Methods and Results). At left are graphical interpretations of the fitted models, ? = biological question, S = statistical translation of the biological question in terms of the fitted model, B = biological conclusion from the fitted model, triangle = general conclusion and justification for next step.

more degrees of freedom, and was much easier to interpret (Kutner et al. 2005, Fig. 2D).

Following standard model fitting practice, we tested the significance of the distance \times Sp group interaction (model 4, Fig. 2E) before comparing mean E_{struct} . The significance of this term indicated slope differences between species groups, and thus between environments. Even in the presence of het-

erogeneous slopes, model 4 (Fig. 2E) was easier to interpret than model 2 (Fig. 2B), and is thus the final model for comparing mean E_{struct} . The fitting of models predicting E_{wood} was identical to that for E_{struct} , except for the final step. Fitting of model 4 for E_{wood} resulted in a nonsignificant distance \times Sp group interaction, meaning that E_{wood} could be readily compared through the intercepts of model 3 (Fig. 2D,

substituting E_{wood} as the predicted variable), as in any analysis of covariance (Quinn and Keough 2002).

Association between size, shape, and biomechanics across environmental gradients

To test our central prediction that branch tissue mechanical parameters should predict stem proportions, we calculated correlations between E_{struct} , E_{wood} , and α (see supporting information Table S1 for data). Given that mechanical properties varied with ontogeny, we used the mean value of E_{struct} and E_{wood} of segments between 100 and 140 cm from the tip. Correlations including α were based on “conventional” trees, that is they excluded *B. standleyana* and *B. instabilis*. To assess how ontogenetic modulation in stem proportions and mechanics changed across environments, we also calculated correlations between E_{struct} , E_{wood} , α , height, and environmental variables. Correlations involving height did not include *B. standleyana*, because its hemiepiphytic habit made height not comparable with terrestrial species (Fig. 1). All correlations were calculated based on raw data and also taking into account phylogenetic relationships within the clade.

Environmental information was extracted from WorldClim version 1.4 (Hijmans et al. 2005; see Appendix S1) for each species. Many of the 19 environmental variables were markedly associated with one another. Therefore, we built environmental indices based on variables strongly correlated ($|R| > 0.75$) with elastic moduli. We generated a precipitation and a temperature seasonality index performing principal component analyses (PCA) on the standardized dataset, and using the first PC of each PCA. Precipitation variables were \log_{10} transformed before PCA, given their curvilinear relationship with elastic moduli. We measured tree height with rappelling gear.

To provide a framework for phylogenetic comparative analyses, we reconstructed the phylogeny of the sampled species using five nuclear and chloroplast markers drawn from Rosell et al. (2010). Details on the reconstruction can be found in Appendix S2 (in supporting information). We tested for phylogenetic signal on residuals of regressions predicting α based on E_{struct} , E_{wood} , or environmental indices, and also of regressions predicting E_{struct} , E_{wood} , or height based on environmental indices, through a randomization procedure using phylogenetically independent contrasts (PICs, Revell 2010) and the K statistic of Blomberg et al. (2003). When necessary, we reestimated correlations using PICs. We performed these analyses in the R packages picante (Kembel et al. 2010) and ape (Paradis et al. 2004). We treated polytomies as soft (Garland and Díaz-Uriarte 1999) and used raw branch lengths assuming an anagenetic mode of evolution, and also unity branch lengths, assuming a cladogenetic mode.

RESULTS

Variation in branch length-diameter scaling exponent α across species

Allometric models revealed marked variation between species, ranging from the stubby, fat-twigged *B. longipes* with $\alpha = 0.752$ (Fig. 3A) to the long, slender-twigged *B. simaruba* with $\alpha = 1.416$. Fits ranged from $R^2 = 0.63$ to $R^2 = 0.98$ (Table 1), except for *B. instabilis* ($R^2 = 0.23$, Fig. 3B), revealing the high length-diameter variation in its lianescent branches.

Ontogenetic change in mechanics, and mechanical differences between species

We observed marked variation in mechanical parameters (Fig. 3C and D). For distal segments between 0 and 50 cm from the tip, E_{struct} varied from 0.15 to 2.64 GN/m² and E_{wood} from 0.68 to 4.55 GN/m², with standard errors of 0.05 and 0.10, respectively. Older segments between 150 and 200 cm had E_{struct} values ranging from 0.48 to 3.51 GN/m², whereas E_{wood} ranged from 0.81 to 6.18 GN/m². Variation in older segments was larger, with standard errors of 0.78 for E_{struct} and 1.29 for E_{wood} .

We used linear models to test for differences in rates of ontogenetic change and in mean values of E_{struct} or E_{wood} between species. The models predicting E_{struct} or E_{wood} based on distance from the tip, species, and a distance \times Sp interaction term (model 2, Fig. 2B) fit well (68 and 52% of explained variance), indicating that E increased with ontogeny (Table 2), but at different rates across species, as suggested by the significant distance \times Sp interaction ($P < 0.001$, Fig. 2B). Slopes (rates) per species are reported in Table 2, and suggest two groups of species: those with rates similar to *B. roseana* (nonsignificant slope), and those with lower rates (significant slope). Species of dry environments, such as *B. cinerea* and *B. longipes*, tended to have lower rates of change in E_{struct} than those of moister environments (Table 2). The same applied to E_{wood} , which changed less along branches of the dry habitat species *B. grandifolia* and the intermediate habitat species *B. arborea*. The only exception to this general trend was the rainforest *B. standleyana*, which showed rates comparable to dry forest species. The parameters of the full model 2 for E_{struct} and E_{wood} are shown in supporting information Table S2, which also explains how slopes in Table 2 were computed based on the full model. The separate models for lianescent *B. instabilis* had a nonsignificant slope suggesting no change in E_{struct} or E_{wood} with ontogeny (supporting information Table S3).

To compare mean E_{struct} and E_{wood} between species, we fitted more parsimonious models using species groups (model 3, Fig. 2D). The groupings for E_{struct} , based on mean values as suggested by model 1, coincided with broad habitat

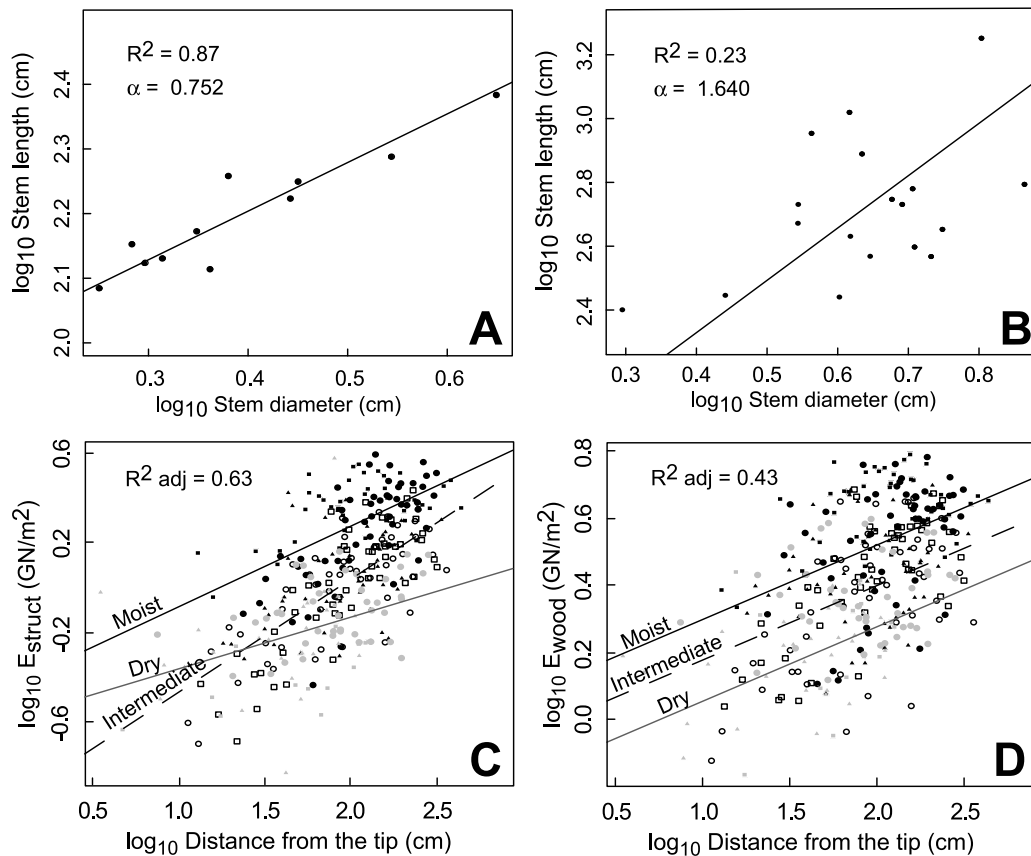


Fig. 3. Models of branch length-diameter allometry and of ontogenetic change in mechanical properties. (A) Allometric models for *B. longipes* and (B) for lianescent *B. instabilis*; (C) E_{struct} (model 4; see Materials and Methods), and (D) E_{wood} (see model 3) increased with distance from the tip and were higher in species of moister locales. Species groupings for E_{struct} were: moist, *B. simaruba* (●) and *B. standleyana* (■); intermediate, *B. arborea* (▲), *B. attenuata* (□), and *B. roseana* (○); dry, *B. cinerea* (◊), *B. grandifolia* (■), and *B. longipes* (▲). For the model predicting E_{wood} , *B. cinerea* fell in the intermediate group, whereas *B. arborea* fell in the moist group.

classes: 1. *B. cinerea*, *B. grandifolia*, and *B. longipes*, species of dry habitats; 2. *B. arborea*, *B. attenuata*, and *B. roseana* of intermediate habitats; and 3. *B. simaruba* and *B. standleyana*, species of moist forests. The model predicting E_{struct} based on distance, species group, and the distance \times Sp group interaction (model 4, Fig. 2E) explained 63% of the variation in E_{struct} (Table 3). The interaction was significant ($P < 0.001$), but only the dry species group differed markedly in its lower slope. Even in the presence of heterogeneous slopes, model 4 (Fig. 2E) was of easier interpretation than model 2 (Fig. 2B). This is because over the span of the fitted line, only the dry and intermediate slopes cross, and even then only at the range of values corresponding to the young branch tips (Fig. 3C). According to model 4 (Table 3), species of dry environments had lower values of E_{struct} , followed by species of intermediate and moist sites. Species of dry locales also increase in E_{struct} in ontogeny at a slower pace (Table 3, Fig. 3C).

Species groups for E_{wood} based on model 1 were very similar to those of E_{struct} , with the exception of *B. cinerea*, which

fell with species of intermediate habitats, and *B. arborea*, which moved to the group of moist environments. Model 4 for E_{wood} did not have a significant interaction term ($P = 0.061$), so it could be reduced to model 3 (Fig. 2D). This model explained 43% of the variation in E_{wood} , and with its homogeneous slopes, mean E_{wood} could be compared between species through intercepts (Table 3). Again, species of moist environments had higher E_{wood} , followed by species of intermediate and dry environments (Table 3, Fig. 3D).

Association between size, shape, and biomechanics across environmental gradients

In agreement with our hypothesis that variation in E should be associated with interspecific differences in branch length-diameter proportions, we found E_{struct} and E_{wood} to be strongly and positively associated with α (Table 4, Fig. 4). Biomechanical variables were strongly correlated with environmental indices (Table 4, Fig. 5). The scaling exponent

Table 2. Models for comparing ontogenetic change in E_{struct} and E_{wood} between species (model 2, Fig. 2B)

	$\log_{10} E_{struct}$	$\log_{10} E_{wood}$
R^2_{adj}	0.68	0.52
Model ANOVA	$F_{(15,313)} = 46.6^{***}$	$F_{(15,313)} = 24.22^{***}$
\log_{10} distance	0.49 ^{***}	0.33 ^{***}
Slope for <i>B. arborea</i>	0.31	0.08 ^{**}
Slope for <i>B. attenuata</i>	0.66	0.39
Slope for <i>B. cinerea</i>	0.18 ^{**}	0.06 ^{**}
Slope for <i>B. grandifolia</i>	0.25	0.10 [*]
Slope for <i>B. longipes</i>	0.15 ^{**}	0.14 [*]
Slope for <i>B. roseana</i>	0.49	0.33
Slope for <i>B. simaruba</i>	0.57	0.29
Slope for <i>B. standleyana</i>	0.21 ^{**}	0.15 [*]

Only the coefficient for distance and the slopes per species are shown. Full models and how slopes were calculated can be found in supporting information Table S2. The level of significance for slopes indicates whether each species has a rate of ontogenetic change differing from *B. roseana*, the species used as the reference category when fitting the model.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. R^2_{adj} = adjusted R^2

Table 3. Models for comparing mean E_{struct} (model 4, Fig. 2E) and E_{wood} (model 3, Fig. 2D)

	$\log_{10} E_{struct}$	$\log_{10} E_{wood}$
R^2_{adj}	0.63	0.43
Model ANOVA	$F_{(5,323)} = 111.6^{***}$	$F_{(3,325)} = 84.67^{***}$
Intercept	-0.97 (0.08) ^{***}	-0.05 (0.05)
\log_{10} distance	0.50 (0.04) ^{***}	0.22 (0.03) ^{***}
Dry	0.38 (0.12) ^{**}	-0.12 (0.03) ^{***}
Moist	0.53 (0.15) ^{***}	0.12 (0.02) ^{***}
\log_{10} distance \times Dry	-0.27 (0.06) ^{***}	Interaction term nonsignificant
\log_{10} distance \times Moist	-0.14 (0.07) [*]	

Species falling in the dry, moist, and intermediate (the reference category) groups can be found in the Materials and Methods section. Standard errors of estimates are given in parentheses. Significance notation and abbreviations as in Table 2. Slopes for the model predicting $\log_{10} E_{struct}$ are 0.23^{***} for the dry species group, 0.36^{*} for the moist species group, and 0.50 for that inhabiting intermediate locales. See supporting information Table S2 for the calculation of these slopes.

α was positively correlated with seasonality in temperature, whereas maximum height was associated with precipitation, as well as with mechanical parameters (Table 4). Correlations imply that longer branches for a given diameter are found in more mechanically resistant species in wetter and more even climates.

Environmental variables reflected the habitat diversity of the *simaruba* clade, with annual precipitation ranging from

Table 4. Correlations between elastic moduli, environmental indices, branch length-diameter scaling exponent (α), and maximum tree height

	E_{struct}	E_{wood}	α	Height
E_{struct}	–	–	0.81 [*]	0.84 ^{**}
E_{wood}	0.95 ^{***}	–	0.75 [*]	0.76 [*]
Precipitation index	0.96 ^{***} (0.95 ^{***})	0.88 ^{**} (0.85 ^{**})	0.7	0.77 [*]
Seasonality index	-0.84 ^{**}	-0.69 [*]	-0.79 [*]	-0.55

Correlations involving height excluded *B. standleyana*, whereas those involving α also excluded *B. instabilis*. Correlations between E_{struct} -Ppt and E_{wood} -Ppt needed to be recalculated using PICs in the context of original branch lengths (in parentheses).
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

680 to more than 3600 mm. Differences in temperature seasonality were also marked with annual temperature swings from 25°C to only 14°C (supporting information Table S1). Of the 19 environmental variables (see Appendix S2), six precipitation and three temperature seasonality variables were correlated with structural variables and are the basis for the precipitation and seasonality indices. The first principal components of these indices explained $\geq 87\%$ of the variability. Variables had similar loading magnitudes within each index (supporting information Table S4).

To assess whether phylogeny needed to be taken into account in calculating correlations, we tested for phylogenetic signal (Revell 2010). Signal in residuals was only present in regressions of E_{struct} or E_{wood} on the precipitation index, and only with raw branch lengths (supporting information Table S5). Correlations for these two cases with PICs were very similar to those with raw data (Table 4, Fig. 4A and C).

DISCUSSION

In trees, the relationship between stem length and diameter is the result of continual developmental interplay between apical and lateral growth (e.g., Plomion et al. 2001; Rowe and Speck 2005; Telewski 2006). Roughly, initial twig diameter and the diameter of the pith are determined at and immediately adjacent to the apical meristem, whereas the lateral meristems determine the rate of thickening along the length of the stem. Thickening rate is crucially related to extension growth, because elongation increases the mechanical load experienced by a given stem segment. Different relationships in development between lateral and apical growth result in much of the diversity in habit observed across plant stems (Table 5). Here, we documented how different

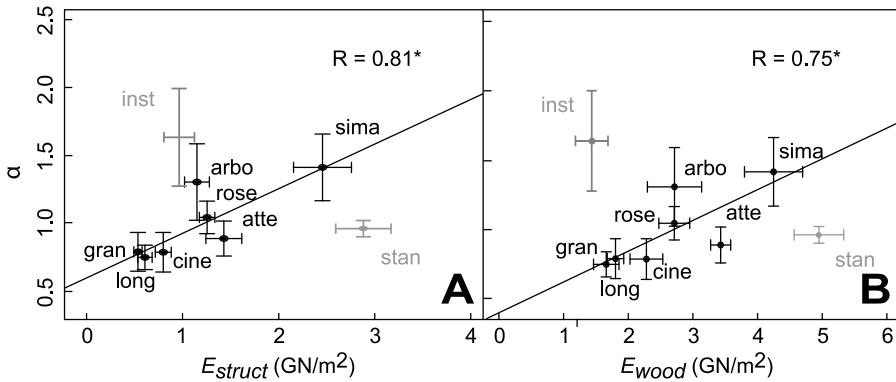


Fig. 4. Correlations between the scaling exponent α and (A) E_{struct} , and (B) E_{wood} . Lianescent *B. instabilis* and hemiepiphytic *B. standleyana* are displaced from the “conventional” tree axis. Fit and correlation calculated based only on conventional trees. Abbreviations are as follows: arbo: *B. arborea*, atte: *B. attenuata*, cine: *B. cinerea*, gran: *B. grandifolia*, inst: *B. instabilis*, long: *B. longipes*, sima: *B. simaruba*, rose: *B. roseana*, stan: *B. standleyana*. Bars represent standard errors of sample means or of the slope estimate in the case of α .

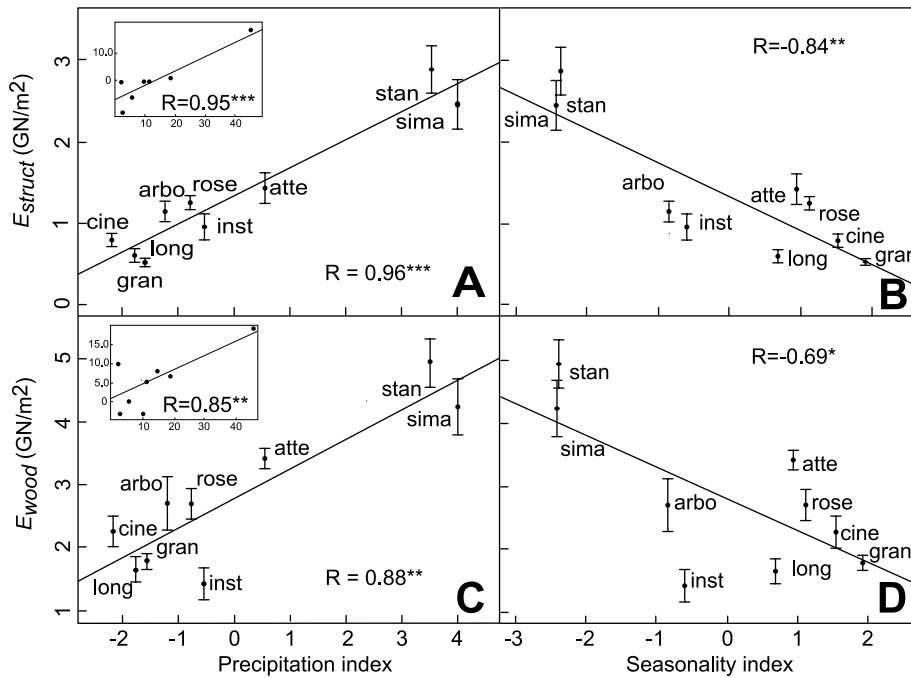


Fig. 5. Correlations between elastic moduli and environmental indices. (A) E_{struct} versus precipitation and (B) temperature seasonality; (C) E_{wood} versus precipitation and (D) temperature seasonality. Insets are with phylogenetically independent contrasts (PICs). Abbreviations as in Fig. 3. Bars represent standard errors of sample means.

length-diameter ontogenies interact with tissue mechanical properties in the diversification of a clade of tropical trees.

Our results across the “conventional” trees illustrate the intimate relationship between organ proportions and tissue mechanical properties. Across these species, E_{struct} and E_{wood} strongly predicted the stem length-diameter scaling exponent α (Table 4, Fig. 4). In other words, species with higher E_{struct} and E_{wood} had branches that were longer for their diameters than species with more flexible wood. The gross similarity in habit between “conventional” trees of the *simaruba* clade (Fig. 1A–C) hides marked differences between species in mean values of tissue stiffness and its rates of change in ontogeny. For example, for a given distance from the tip, the smaller species of drier areas invariably had lower E_{struct} and E_{wood} than the large species of moister sites. At 300 cm from the tip, model 4 indicated that E_{wood} would be 2.37, 3.13,

and 4.12 GN/m² for species of dry, intermediate, and moist environments, respectively. Moreover, although in all species E_{struct} and E_{wood} become higher with ontogeny, this increase is proportionately less in species of dry environments (Table 2, Fig. 3C). Taken together, our results show that even though most species of the *simaruba* clade share an outwardly similar self-supporting conventional tree habit, their diversification in size is associated with pronounced differences in the ontogeny of their tissue mechanical properties.

Displacement along the stem proportionality–mechanics slope is associated with broadly similar habits (Fig. 4). Shifts perpendicular to this slope inevitably produce a change in habit. Table 5 shows that sluggish lateral meristem activity in combination with rapid stem elongation is associated with the liana habit. Returning to the formula $\delta = qL^4/8EI$, when I fails to keep pace with the increase in L , stem deflection

Table 5. Interaction between lateral and apical growth and stem habitat diversity; rapid or slow can be absolute or relative to the other type of growth

		Axial (elongation) growth	
		Rapid	Slow
Lateral meristem growth	Rapid	Thick trunks and twigs of moderate E , relatively high I Fast absolute rates, self-supporting proportions For example, early successional trees, water storing trees	Very thick stems with low E , very high I Slow absolute rates, fast relative lateral growth For example, Succulents, <i>Welwitschia</i> , <i>Adenia pechuelii</i>
	Slow	Very long, slender stems with low E , low I Fast absolute and relative extension rate For example, Vines, lianas	Slender trunks and twigs with high E , low I Slow absolute rates, self-supporting proportions For example, Dryland trees and shrubs

will increase. In these terms, lianas are plants that have narrow diameters (reflected in the formula by I) for their length. In Fig. 4A and B, the space above the “conventional,” self-supporting line is associated with branches that are longer and thinner for their tissue mechanical properties, making the extreme upper left the liana corner (Rowe et al. 2004). Basal diameter predicts length well in self-supporting trees, length being related to the moment that the base of a given branch is subject to. In lianas, the bulk of the stem is supported on other plants. As a result, diameter predicts stem length less effectively than in self-supporting plants, as in *B. instabilis* (Fig. 3B, e.g., Gallenmüller et al. 2001). These habit differences therefore reflect ontogenetic variation in proportions and mechanics, with different combinations of ontogenetic increase in length, diameter, and mechanics seeming to be favored in different selective situations.

Variation across environments

It is often asked whether trends in comparative data reflect “fixed” (or “genetic”) versus “plastic” differences. This distinction hinges on two aspects, one being the amplitude of the plastic range (narrow ranges being considered “fixed” within species) and, perhaps more surprisingly, the phylogenetic level at which a given plastic response can be considered synapomorphic (e.g., Herron and Doebli 2011; see also Jamniczky 2008). Taking as an example the *simaruba* clade, suppose that the same plastic response machinery governing stem allometry was present in the ancestor of the clade and was inherited intact by all descendants. Then, the entire range of sizes and proportions in the clade would simply represent different expressions of the same developmental response. Such a situation does not affect study of how ontogenetic modulation produces morphological differences, our main goal here. For inferences of adaptation it would, however, affect the inferences made, because nine independent

events of convergent evolution provide more evidence than just a single one. In our case, the range of sizes and habits is so wide, and costs of plasticity seem generally sufficiently high, that it is unlikely that, say, dryland *B. longipes* would grow as a rainforest emergent if only it were grown in a *B. simaruba* rainforest. In addition, that *B. instabilis* and *B. standleyana* showed such marked differences from other species also argues against the “single plastic response” interpretation. Regardless of the ranges of intraspecific variation in the clade, the patterns observed seem congruent with the adaptive responses that might be expected given competition for light and other resources, and we turn to these now.

The *simaruba* clade spans an environmental range from warm rainforest to seasonal dry tropical forest. Total plant size and branch stiffness track this range in water availability and temperature evenness. Taller trees with stiffer and more slender branches are found in moister sites with more even temperatures, whereas shorter trees with more flexible and stubbier branches inhabit dry, seasonal environments (Table 4, Fig. 5). The association between height and water availability we found for the *simaruba* clade ($R = 0.77$, Table 4) parallels global tendencies for trees to be taller in moister environments (Moles et al. 2009). There are many reasons to expect trees to be taller in moister areas, including selection favoring light capture in plants taller than their neighbors, increased root reach associated with larger overall size, and more distant dispersal of propagules that are located higher (Mäkelä 1985; Waller and Steingraber 1995; Clark and Clark 2001). Tree height in the *simaruba* clade closely parallels or exceeds average vegetation height. *Simaruba* clade habitats are dense and small-statured individuals are severely shaded, at least in the rainy season. Selection should favor individuals with statures that allow light access greater or at least similar to neighbors. Across the environmental gradients we studied, greater water availability implies taller forest, and selection favoring greater stature. This increase is accompanied

by an increase in E_{struct} and E_{wood} and branches with greater reach for a given diameter. Although we measured branches, stature is an aspect that includes the main trunk. We found a strong correlation between branch mechanical parameters and total tree height (Table 4). This association could suggest that the ranking of species based on branch mechanical performance in the *simaruba* clade is similar to the ranking based on main trunks. This observation suggests that differences observed across species at the level of branches might be proportional to those observed at the level of main stems (Swenson and Enquist 2008).

Finding stiff stem tissues and tall trees in moist areas and flexible tissues and short trees in dry areas is congruent with the hypothesis of a tradeoff between support and storage in the stems of these trees (Zanne and Falster 2010). A higher level of stem water storage would be associated with greater allocation of space to cell lumen and less to the cell walls that offer mechanical stiffness. As a result, the species of dry areas would be expected to have lower E_{struct} and E_{wood} (see Chapotin et al. 2006; Méndez-Alonzo et al. in press). More flexible tissues limit critical tree buckling height (Niklas 1992). In turn, the association between mechanical properties and α across conventional trees (Table 4, Fig. 4) presumably results from selection acting against variants that cannot support their branches or that overinvest in support to the detriment of other traits, such as reproduction or crown expansion (see Niklas and Spatz 1999).

Selection favoring different wood densities may also explain contrasting patterns between the *simaruba* clade and a recent study of Australian woody plants. In one of the few studies to examine variation in stem biomechanics with environment in multiple species, Onoda et al. (2010) documented much higher values of E_{wood} and E_{struct} than we did for similar stem sizes. Even the most flexible stems that Onoda et al. tested were much stiffer than the stiffest ones in the *simaruba* clade. Our E_{wood} (the highest being 6.2 GN/m²) values may seem low (e.g., Cannell and Morgan 1987), but many other water-storing trees of the tropics appear to have wood with elasticity comparable to our values, for example, *Plumeria rubra* or *Cochlospermum vitifolium* (Méndez-Alonzo et al. in press). In the mostly sclerophyllous temperate evergreen species Onoda et al. examined, higher wood density and thus higher E_{wood} is probably favored in cavitation resistance, important in plants bearing leaves even through extended drought (Maherali et al. 2004; Bonser 2006). In contrast, many dry tropical trees have low-density wood that stores abundant water and starch. These trees have wide vessels that sustain high conductive rates in the rainy season. In the dry season, the trees escape highly negative xylem pressures by dropping their leaves and surviving on water stored in stems (Olson and Carlquist 2001; Méndez-Alonzo et al. in press). As a result, in deciduous tropical trees such as *Bursera*, selection favoring stem water storage in drier areas

would lead to stem tissues of lower density of cell wall per unit volume (Choat et al. 2005), and thus lower E , leading to a positive relationship between E and water availability. The evolution of functional syndromes depends directly on the morphologies that can be produced in plant ontogeny and exposed to selection (see, e.g., Körner 1991), highlighting the need for a concerted effort to explore the extent to which plants occupy functionally relevant morphospace and where and why empty areas occur (Donovan et al. 2011).

Conclusion: ontogenetic potential, constraint, and morphological diversity

The relationship between ontogenetic potential and inter-specific diversity can be generalized to a hypothetical three-dimensional space defined by stem diameter, length, and E_{struct} (Fig. 6). The majority of plants likely lie near the axis along which diameter and length scale predictably with each other and with E_{struct} . If stems lengthen markedly for their diameter, with no change in E , a liana will result as stems can no longer support their own weight, as in *B. instabilis* (Fig. 6; Lahaye et al. 2005). At another extreme, succulents are plants with squat stems with tissues of low E . In turn, small, self-supporting stems with very high E are found in desert shrubs, which have dense, cavitation-resistant xylem (Hacke and Sperry 2001). Some plants trace less-common arcs through developmental space as they change habits throughout their lives. Many lianas begin life as self-supporting treelets, whereas strangler figs become self-supporting only with age. For their part, semi-self-supporting species maintain more or less constant E and, though not climbing, remain erect by leaning on neighbors, often members of their own species (Spatz et al. 1998; Speck and Rowe 1999, 2001).

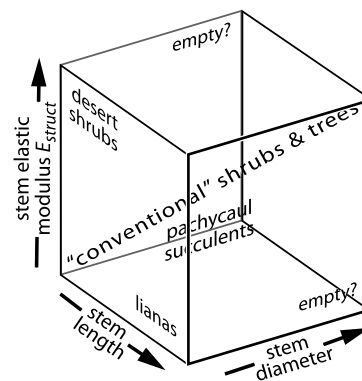


Fig. 6. Heuristic morphospace defined by E_{struct} , stem length, and stem diameter. Most woody plants likely describe a “conventional” axis with length, diameter, and tissue stiffness increasing more or less predictably. Displacement from this relationship should result in lianas, succulents, and cavitation-resistant shrubs with dense wood. Empty areas seem ontogenetically accessible but maladaptive.

Just as important as the areas of the length–diameter–mechanics morphospace that are filled are the areas that are not. If these areas are inaccessible ontogenetically then they may result from some sort of developmental constraint (Olson 2012). However, there would seem to be no reason that many of these morphologies could not be produced by plant meristems; they simply seem to be maladaptive (see the plant morphospaces of Niklas 1997, 2009, or Prusinkiewicz et al. 2007). For example, a tall tree with low E_{struct} could certainly be produced by plant developmental systems, but in the earth's gravity it would buckle. This is not a “constraint” in the sense of an area of morphospace that is inaccessible as the result of internal factors that are arbitrary with regard to function (Alberch 1989). Instead, it seems an example of natural selection eliminating morphologies that do not meet their mechanical needs (e.g., Jaouen et al. 2010). By the same token, plants with wide, short stems and high E_{struct} seem ontogenetically possible, with stumpy *Welwitschia* of the Namib Desert a possible step in this direction. The *simaruba* clade illustrates how diversification in organismal form emerges from ontogenetic modulation in the holy trinity of morphological evolution, size, shape, and biomechanics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Data per species. α = stem length-diameter scaling exponent; height = maximum tree height; precipitation and evenness indices were derived from PCAs based on the climatic variables included in this table (see Materials and Methods).

Table S2. Complete models for comparing ontogenetic change in mechanical parameters between species (models 3 and 4, see Materials and Methods).

Table S3. Univariate regression models predicting $\log_{10} E_{struct}$ and $\log_{10} E_{wood}$ for *B. instabilis*.

Table S4. Variables and loadings of the first PC axes of the two PCAs used to construct the precipitation (Ppt) and temperature (T) seasonality indices.

Table S5. Phylogenetic signal in the residual deviation of regression models.

Appendix S1. Environmental variables extracted from WorldClim version 1.4 (Hijmans et al. 2005).

Appendix S2. Phylogenetic reconstruction of the sampled species in the *simaruba* clade, including locality, voucher information, and Genbank accession numbers.

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