Received: 31 October 2023 | Revised: 31 January 2024 | Accepted: 12 February 2024

DOI: 10.1002/ecs2.4835

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ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Flow similarity model predicts allometric size dependence, curvature, and covariation of 285 North American tree species

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Handling Editor: Keirith Snyder

Abstract

Scaling patterns in plants have long interested biologists, particularly whether different species share similar patterns of growth, and whether differences in growth trajectories depend on plant size. Using 8,794,737 measurements for 285 species from the U.S. Forest Inventory and Analysis database, we test several predictions emerging from a recently published "flow similarity" model for plant growth and allometry. We show that the model's predicted curvature for intraspecific relationships between height, dbh, and biomass is found in 88.1% of examined cases, and empirical slopes fall as predicted between the elastic similarity and flow similarity predictions in 71.1% of cases. We also find a strong size dependence in observed intraspecific allometric exponents, with large species, particularly gymnosperms, converging near the expectation for elastic similarity and the central tendency among small species approaching the expectations for flow similarity in most cases. Our results support the idea that differences in growth patterns across plant species depend on plant size and their attendant hydraulic and/or biomechanical demands and helps to delineate the bounds of the theoretical morphospace in which they occur.

KEYWORDS
allometry, biomass, elastic similarity, flow similarity, tree diameter at breast height, tree height

INTRODUCTION

Of all the ways one can measure variability across life, perhaps no single trait can explain more variability in other traits, than organism size. Size has been linked to a suite of life history trade-offs and strategies and variability due to size is well documented in all clades (Brown & West, 2000; Calder, 1984; Charnov, 1993; Niklas, 1994; Peters, 1983; Schmidt-Nielsen, 1984; Sibly et al., 2012). However, all large organisms start small and need to grow to attain their large sizes, and thus, organism growth and development has also garnered considerable attention (Hulshof et al., 2015; Niklas, 1994; Shipley & Meziane, 2002; West et al., 2001). Tree species are among the largest organisms on earth, and there has been considerable interest in uncovering and modeling the physical principles governing tree growth and form for decades (Hulshof et al., 2015; Koch et al., 2004; McMahon & Kronauer, 1976; Niklas & Spatz, 2004; Ryan & Yoder, 1997; Shinozaki et al., 1964; West et al., 1999).

Models linking tree growth and some proxy for size (mass, volume, height, dbh) have typically invoked hydraulic principles, biomechanical principles, or both. A prominent early approach is the elastic similarity biomechanical model which utilizes the Euler buckling formula to predict how maximum height scales with diameter in idealized cylindrical columns (McMahon & Kronauer, 1976; Niklas, 1994). Another recent model (West et al., 1999; West, Brown and Enquist [WBE]) has invoked a fractal structure to predict numerous aspects of tree form and physiology (West et al., 1999). Because the WBE model assumes elastic similarity, it predicts the same numerical exponents for the allometric slopes describing the relationships between tree height, basal stem diameter, and mass as the original elastic similarity model (Table 1). However, WBE goes on to make additional assumptions about branching architecture to predict physiological features that we do not consider here (number of leaves, xylem tapering, etc.), which distinguishes it from the elastic similarity model by itself. These models have been thoroughly tested with mixed results (see reviews in Price et al., 2012; Savage et al., 2008). A balanced view suggests that our understanding of the constraints governing macroscopic plant growth and form is incomplete.

A more recent modeling attempt has departed from a "one size fits all" approach and suggests that different parts of a tree's branching structure may be adapted to perform different functions, with the allometry terminal stems of woody plants more in line with predictions derived from hydraulic principles, and the allometry of basal boles and branches more consistent with biomechanical principles, particularly as trees increase in size (Price, 2023; Price et al., 2022). Clearly both tree trunks and terminal branches serve both biomechanical and hydraulic functions; however, the Price et al. model simply argues that the geometry of branching structures approach scaling relationships more consistent with biomechanical or hydraulic principles at either end of the branching structure, that is, from trunk to tips within a single tree, or ontogenetically, as saplings become trees (Figure 1).

The model is derived by examining the consequences of fluid flow in bifurcating networks with flow dynamics described by the Hagen–Poiseuille model for laminar flow in cylindrical tubes (Lewis & Boose, 1995; Venturas et al., 2017). The model posits that similarity in volumetric flow and velocity across branching generations (flow similarity) leads to length (L) to diameter (D) allometric relationships in terminal stems and saplings close to L vs. D^2, but as trees become large, with increases in both static and dynamic loads, biomechanical demands drive the basal branches of trees (boles) toward L vs. $D^{2/3}$ scaling, as described by the Euler buckling model (McMahon & Kronauer, 1976; Niklas, 1994) and the same value assumed by WBE (Price et al., 2012). Similar relationships are derived for how branch length, diameter, surface area, and volume all scale with one another within and across trees (Price et al., 2022). Because different parts of trees perform different functions and thus may align with different scaling principles, allometric data spanning large size ranges are predicted to follow specific curvilinearity (Figure 1) and that regression slopes fit to curvilinear data will often fall between the elastic similarity and flow similarity model predictions for terminal branches (Table 1). Thus, the flow similarity approach predicts that relationships between tree height, dbh, and mass will be non-linear on log–log axes, follow a specific curvature, and have slopes that fall within certain bounds (Figure 1, Table 1). In contrast, the elastic similarity model (which WBE assumes) predicts these scaling relationships will be linear on log–log axes, with a single value for the exponent and makes no prediction about interspecific variability.

The flow similarity model is best evaluated by examining the dimensions, topology, conduit anatomy, fluid dynamics, and biomechanics of branches, within and across trees. For example, Price et al. (2022) examined

TABLE 1 Predicted relationships for the flow similarity and elastic similarity models between length (L), diameter (D), and volume (V).

			α value by model			
***Y* variable**	***X* variable**	**Expression**	**Flow**	**Elastic**	**Curvature**	**Range**
Length	Diameter	$L \propto D^{\alpha}$	2	2/3	Concave, 2 to 2/3	4/3
Diameter	Volume	$D \propto V^{1/(\alpha+2)}$	1/4	3/8	Convex, 1/4 to 3/8	1/8
Length	Volume	$L \propto V^{\alpha/(\alpha+2)}$	1/2	1/4	Concave, 1/2 to 1/4	1/4

Note: Predicted functions for the relationships between length, diameter, and volume under the flow and elastic similarity models. The flow similarity model predicts relationships for the dimensions of tree networks, particularly length and volume (not height and mass). Elastic similarity similarly predicts a relationship between the length and volume of an idealized column. Both models can be interpreted within the context of plant height and mass under the assumption that there is a correlation between plant height and path length (flow similarity) and plant height and column length (elastic similarity). Similarly, the models can be interpreted using mass ($M = V\rho$) provided there is no systematic trend in density (ρ) with size, which is likely a more valid simplifying assumption intraspecifically than interspecifically.

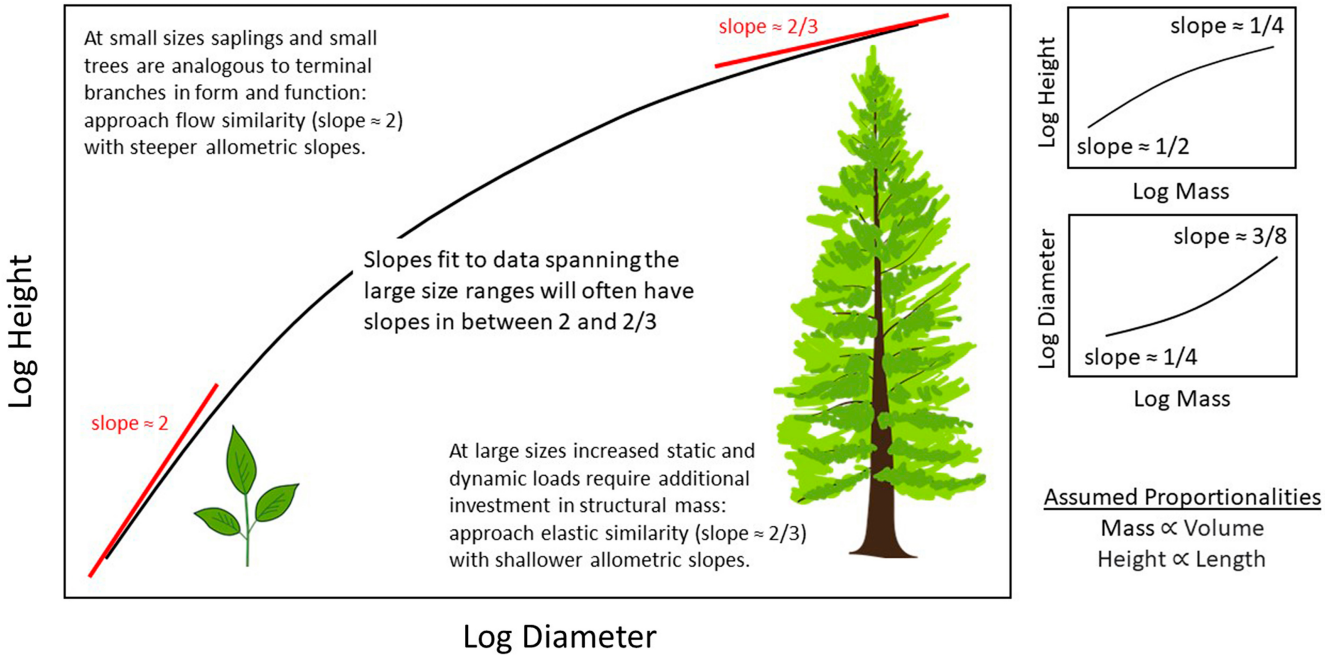

FIGURE 1 Flow similarity model allometric expectations. Graphical representation of the allometric expectations described by the flow similarity model. The model posits that terminal branches and saplings are more closely aligned with the expectations derived from hydraulic considerations, whereas tall trees, particularly those exhibiting strong apical dominance, will align with the expectations from the elastic similarity model. Intraspecific data spanning large size ranges will thus exhibit specific curvatures going from small to large sizes. The graphic here is not to scale and the curvature exaggerated for instructive purposes. Both models predict relationships between length (L) and volume (V) in idealized cylinders. Empirical data are typically for tree height (H) and mass (M); thus, both models assume a proportionality between idealized cylinder length and tree height, and cylinder volume and tree mass (see *Materials and methods* and *Discussion*).

the dimensions and topology of saplings, terminal branches, and petioles in support of the paper introducing the model. However, due to the time, effort, and expertise required, such data are rarely collected. In contrast, data on the coarse dimensions of trees, their height, and dbh, are routinely measured (which yield estimates of tree mass), particularly as part of national forest inventories whose aims are to monitor timber volume, forest health, structure, and carbon dynamics at large spatial and temporal scales.

Such data allow for important tests of some of the coarse scale predictions emerging from the flow similarity and elastic similarity models. Here, we utilize data from one of the largest collections of woody plant allometric data, the United States Forest Service's Forest Inventory and Analysis (FIA) dataset, which contains millions of measurements of woody plant height, dbh, and estimates of above ground mass, to evaluate several key predictions emerging from the flow similarity model:

1. Slopes fit to intraspecific data will often fall between elastic and flow similarity predictions (Table 1).
2. Intraspecific allometric data will exhibit specific curvilinearity (Figure 1):
   a. Log–log plots of tree height (y-axis) vs. dbh (x-axis) will be concave.
   b. Log–log plots of dbh (y-axis) vs. mass (x-axis) will be convex.
   c. Log–log plots of tree height (y-axis) vs. mass (x-axis) will be concave.
3. Interspecific covariation among intraspecific allometric slopes will fall along predicted covariation functions (Table 2).
4. Slopes fit to intraspecific data will trend toward elastic similarity at large plant sizes and flow similarity at small sizes.

MATERIALS AND METHODS

FIA data

All woody plant (tree) data are from the United States Department of Agriculture, FIA program (Burrill et al., 2021). The FIA program maintains a national network of field plots at a density of roughly one plot per 2428 ha in the lower 48 states. The 1998 Agriculture Research, Extension and Education Reform Act (1998 Farm Bill) called for the adoption of national measurement standards with annual resampling of all plots every 5–7 years in the east and

TABLE 2 Predicted covariation functions for the relationships between allometric exponents.

Allometric covariation			
***Y* variable**	***X* variable**	**Covariation expression**	**Figure 3**
$L \propto V^{\alpha/(\alpha+2)}$	$D \propto V^{1/(\alpha+2)}$	$\alpha/(\alpha+2) = 1 - (2/(\alpha+2))$	Panel A: (*H* vs. *M*)–(*D* vs. *M*)
$L \propto V^{\alpha/(\alpha+2)}$	$L \propto D^{\alpha}$	$\alpha/(\alpha+2) = \alpha/(\alpha+2)$	Panel B: (*H* vs. *M*)–(*H* vs. *D*)
$D \propto V^{1/(\alpha+2)}$	$L \propto D^{\alpha}$	$1/(\alpha+2) = 1/(\alpha+2)$	Panel C: (*D* vs. *M*)–(*H* vs. *D*)

Note: Similar to Price et al. (2007), the flow similarity model (Price et al., 2022) predicts allometric covariation functions for the relationships between each pairwise combination of exponents. The flow similarity model uses a single parameter (α) to do this, whereas Price et al. (2007) use two parameters following West et al. (1999). Each function is drawn as a black line in the indicated panels of Figure 3.

every 10 years in the west (Tinkham et al., 2018); thus, we restricted our analysis to all records post 1998.

Each FIA plot consists of four circular subplots each with a 7.31-m (24-foot) radius in which all trees with dbh ≥ 5 in are measured. Within each subplot, there is a 2.07-m (6.8-foot) radius microplot within which all trees <5 in and ≥1 in dbh are measured. The height of all measured trees is either directly measured or estimated in the field using clinometers, hypsometers, or tape measures for small trees (reported in feet).

Note that both the elastic similarity and flow similarity models predict the length (*L*), diameter (*D*), and volume (*V*) of idealized cylinders. Our empirical data are for the height (*H*), dbh or root collar (which we refer collectively to as *D*), or mass (*M*) of trees. We use the abbreviations *L* and *V* when referring to the theoretical predictions (Tables 1 and 2), and *H* and *M* when referring to empirical data. *D* applies to both because it refers to analogous structures in either context. Equating mass (*M*) with volume (*V*) requires that density is constant. Wood density varies considerably between species (Chave et al., 2009) but is much less variable within species; thus, we have only performed allometric regressions on intraspecific data.

We limited our analyses to live individuals (FIA status code = 1) and also individuals that had heights that were "field measured" (FIA height code = 1) (STATUSCD and HTCD, respectively, in the FIA database), where height is the length from the ground to the tip of the apical meristem (highest branch). Diameter is measured at breast height (reported in inches) or the root collar for multistemmed plants that lack sizeable boles. Biomass estimates (reported in pounds) for trees with dbh greater than or equal to 5 inches (12.7 cm) in the FIA database are based on the component ratio method (CRM; Heath et al., 2009). The CRM estimates the oven-dry biomass of tree bole, bark, tree tops, limbs, and stumps using measured dimensions (height, dbh, canopy, and trunk) to calculate the volume of each respective component and then utilizing known specific gravities to convert volume to biomass estimates (Heath et al., 2009; Jenkins et al., 2003; Raile, 1982). Thus, each individual woody plant has its own biomass estimate based on the observed dimensions of these components. Biomass estimates for trees smaller than 5 inches basal diameter (from microplots) are based solely on diameter and thus were not included in our analysis.

Variable names for the parameters contained within the FIA database are as follows in parentheses (Burrill et al., 2021): height (HT), diameter (DIA), bole dry biomass (DRYBIO_BOLE, which includes bark), dry biomass in the top and limbs of the tree (DRYBIO_TOP), dry biomass in the tree stump (DRYBIO_STUMP). The biomass estimates for the top, limbs, bole and trunk were summed to give a total mass estimate for above ground portions of the tree (*M* = DRYBIO_BOLE + DRYBIO_TOP + DRYBIO_STUMP).

Statistical model fitting

For each species, we first examined the relationship between *H* and *D*. If the number of individuals for a species was greater than 20 individuals, allometric analysis was performed on the relationships between plant *H*, *D*, and *M* by fitting standard major axis (SMA, aka reduced major axis regression [RMA]) regression slopes (Warton et al., 2006) to log-transformed bivariate relationships and recording the fitted slopes, intercepts, and R^2 values. We also recorded the largest and smallest measurements for each attribute (*H*, *D*, *M*), for each species, irrespective of whether each of those measures came from the same individual or not.

In a handful of instances, recorded *H* or *D* values for trees of a given species seemed larger than expected, likely due to errors in data entry or transfer. To test whether the maximum *H* or *D* recorded for a given species was within a reasonable range, when possible, we compared these values with the record tree heights and dbh values listed in the 2021 National Register of Champion Trees, a list maintained by the nonprofit American Forests (americanforests.org). It is quite possible

that FIA crews have inadvertently identified champion trees; thus, if the maximum H or D for the tree in the FIA database was greater than 1.5 times the H or D for that same species in the National Register of Champions Trees, the largest tree that was ≤1.5 times the record tree for that species was used to record maximum sizes for our analysis.

To examine the central tendency and shape of the distribution for the allometric slopes for the three relationships (H vs. D, H vs. M and D vs. M), we generated histograms for each collection of slopes and measured the skew of the distribution following the standard formula. We also counted the number of species slope values that fell between the elastic similarity and flow similarity model predictions.

To test the curvature in each allometric relationship, we fit a second-order polynomial function to each bivariate relationship (log–log axes) and then recorded the sign of the second derivative of that polynomial which indicates if the curve is concave (sign is negative) or convex (sign is positive).

To examine the covariation in allometric slopes, we plotted empirical slope values for each relationship (H vs. D, H vs. M, D vs. M) against one another, and overlayed the covariation functions predicted in Price et al. (2022; Table 2).

To examine how the maximum recorded size (H, D or M) for each species influences species level allometric slopes, we fit a locally weighted regression slope (lowess or loess regression; Cleveland, 1979) across the range of recorded sizes within a sliding window that has a span corresponding to 20% of the data. Given that the tallest tree species in the North American flora are gymnosperms, we also plotted angiosperms and gymnosperm species separately to visually inspect whether there are differences between these clades in allometric covariation or in allometric trends with size.

RESULTS

Following filtering for sample size, we retained 8,794,737 individual records representing 285 species for an average of ~30,799 samples per regression. The distribution of number of individuals measured per species are strongly biased, however, with a handful of species that are represented by very large sample sizes substantially increasing the mean. The median number of individuals per species was 4313 and the mode 60 (recall sample size cutoff of 20). Among the maximum recorded sizes per species, the tallest individual was 99 m (325 feet) tall (*Sequoia sempervirens*) and the shortest 5.79 m (19 feet) (*Thrinax morrisii*). The tallest individual with a dbh (D) of 12.7 cm (5 inches) was 10.97 m (36 feet) (*Carya carolinae-septentrionalis*) and the shortest 0.60 m (2 feet) (*Juniperus occidentalis*). The mean height of the tallest recorded individual for each species for angiosperms was 34.35 m (112.7 feet) (206 species) and for gymnosperms was 47.06 m (154.4 feet) (79 species).

Two hundred thirteen individual trees had height measures that were larger than that recorded in the National Register of Champion Trees (https://datadryad.org/stash/share/ah18bY3oc9EYgtle8pLLVW5EckRAFvoXBkRw5UDF6yY [FIA_BigTree_Comparison.xlsx]). Of those, 81 had recorded heights that were >1.5 times the Champion tree height. Twenty-nine individuals had dbh values larger than what was found for that species in the Champion tree register. Of those, eight had dbh values >1.5 times the Champion tree value.

The distributions of scaling slopes (Figure 2) are right-skewed for H vs. D (Figure 2A, skewness = 3.74) and H vs. M (Figure 2C, skewness = 0.786) relationships, and left-skewed for the D vs. M (Figure 2E, skewness = −1.67) relationship, with the skew in the direction of the flow similarity model in all three cases. As indicated in each panel, the mean slope (black star), and a majority of the species' empirical slope values fell between elastic (green star) and flow similarity (red star) model predictions. Notably, 65.61% of the H vs. D slopes, 96.14% of the H vs. M slopes, and 51.58% of the D vs. M slopes fell between the two models' predictions. Across all three relationships, 71.1% of empirical slopes fell between the two model predictions. The mean H vs. D slope was 0.713 with a mean R^2 of 0.715, the mean H vs. M slope was 0.329 with a mean R^2 of 0.631, and the mean D vs. M slope was 0.371 with a mean R^2 of 0.897. The range of the observed slopes was 1.65 (H vs. D), 0.395 (H vs. M), and 0.397 (D vs. M). Regression slope estimates, intercepts, R^2 values, maximum sizes, sample sizes and the results from each test for concavity/convexity are available from Dryad (https://doi.org/10.5061/dryad.p2ngf1vwk).

Also seen in Figure 2, the curvatures of the fitted polynomial relationships were consistent with predictions (Table 1) in a majority of cases (88.1% across relationships). Notably, 82.5% of the polynomial fits to the H vs. D relationships were concave (Figure 2B), 86.3% of the polynomial fits to the H vs. M relationships were concave (Figure 2D), and 95.4% of the polynomial fits to the D vs. M relationships were convex (Figure 2F).

While substantial variability exists in the relationships analyzed, the overall directional trends in exponent covariation were well captured by the theoretical covariation model (Figure 3, Table 2). The predicted covariation function in Figure 3A is linear (black line), and while the data appear somewhat flat, a standardized major axis (SMA) regression model fit to the data (red line) reveals that the slope is negative as is the predicted function.

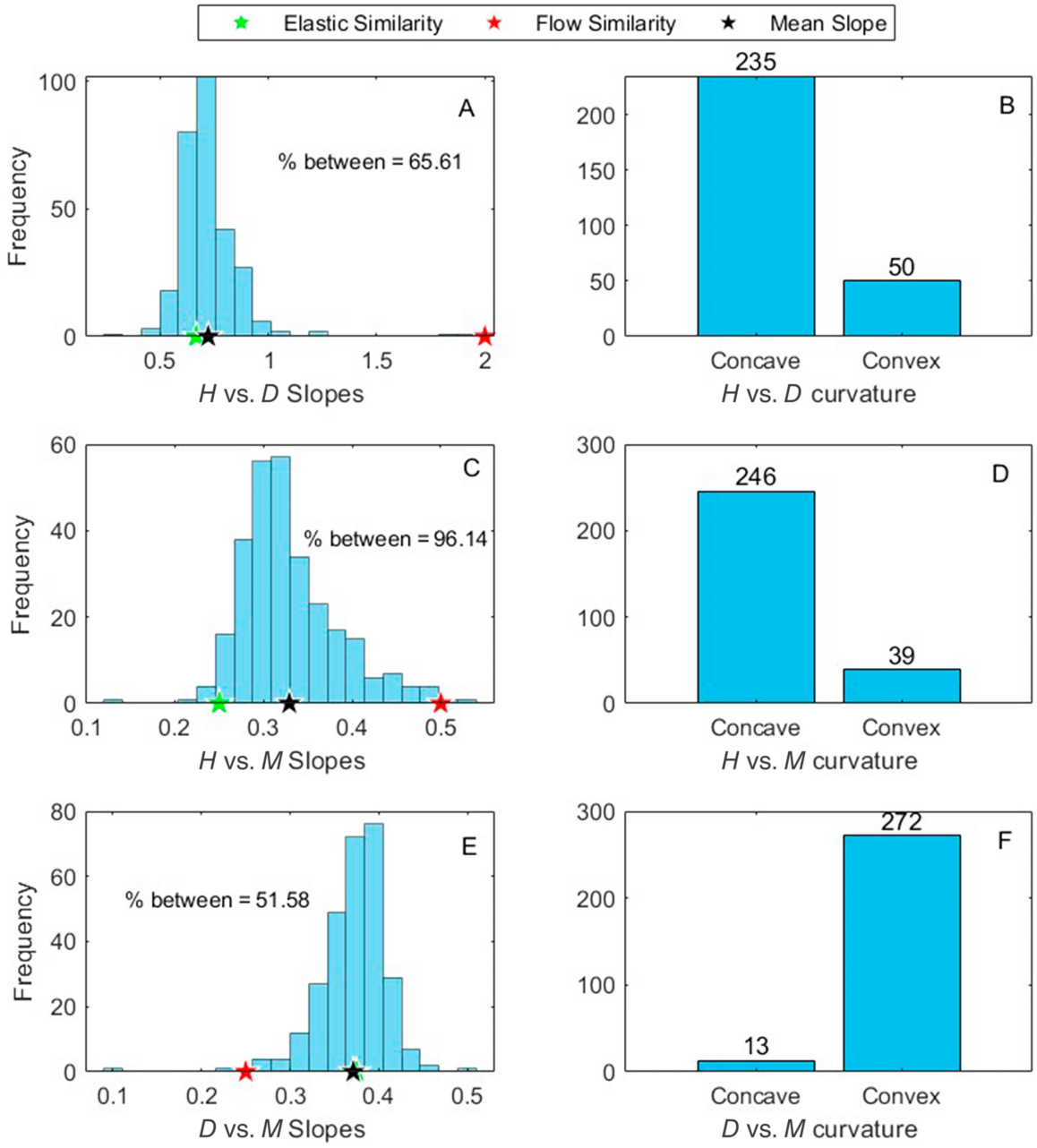

FIGURE 2 Slope distributions and curvature tests. Histograms of the frequencies of allometric slopes for relationships among the three variables height (*H*), diameter (*D*), and mass (*M*); *H* vs. *D* (A), *H* vs. *M* (C), and *D* vs. *M* (E). Note the right skew in (A) and (C) and left skew in (E). Observed means (black stars) are in between the predicted values from the elastic similarity (green stars) and flow similarity models (red stars). As indicated in each panel, the majority of the slope values in each case fall between the two model predictions. A majority of the curvature tests were consistent with model predictions in all three cases. 82.5% of *H* vs. *D* curves were concave (B), 86.3% of *H* vs. *M* curves were concave (D), and 95.4% of *D* vs. *M* curves were convex (F). Across all three relationships 88.1% of the tests were consistent with model expectations.

Our results show a strong size dependence of the fitted allometric slopes, with high variability at small sizes and convergence to values closer to the predictions of the elastic similarity model at large sizes (Figure 4), in both angiosperms and gymnosperms. Lowess regressions capture the shift in mean slopes at smaller sizes toward values closer to those predicted by the flow similarity (Figure 4).

DISCUSSION

Terrestrial plants exhibit considerable variability in their architectural form, some of which can be explained by systematic changes due to increases in mature size. In particular, the degree of apical dominance tends to correlate with maximum tree height. The tallest tree species

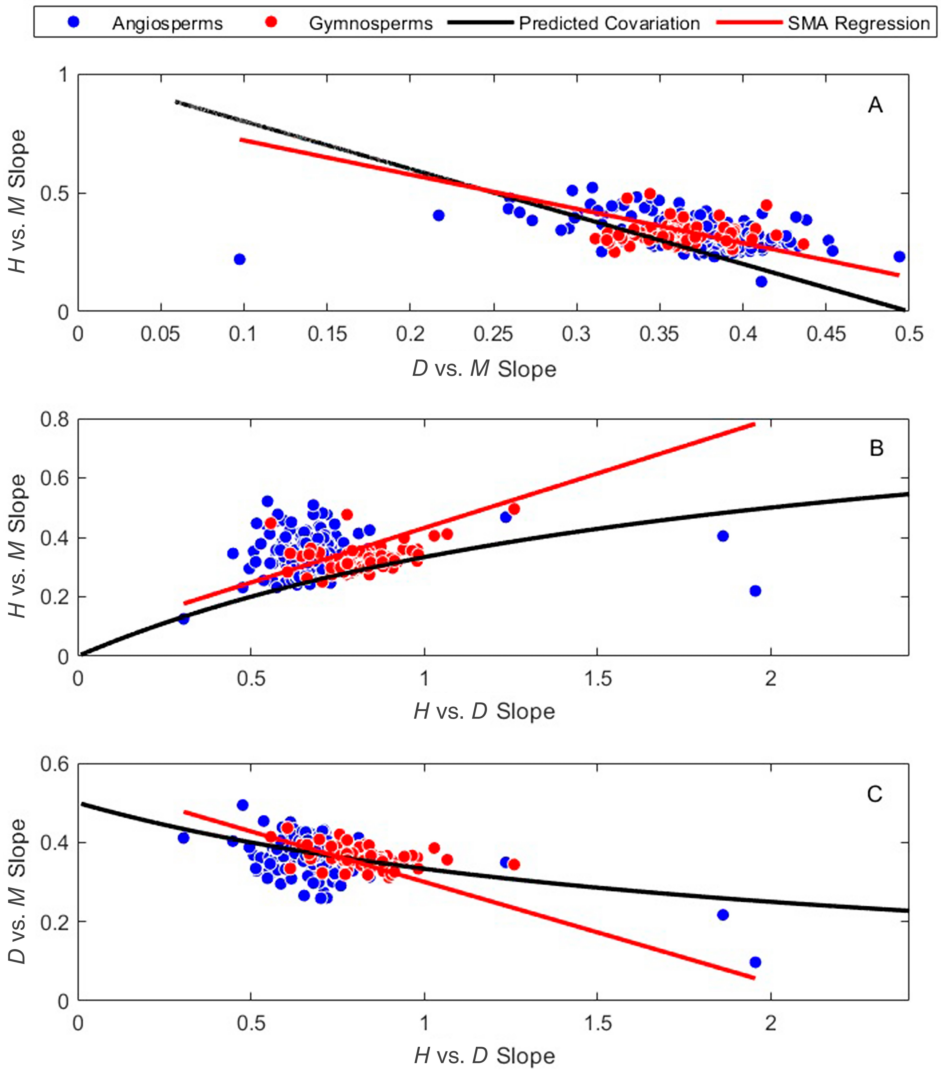

FIGURE 3 Interspecific allometric covariation. Trends in the covariation between pairwise allometric exponents for the three variables height (*H*), diameter (*D*), and mass (*M*) are fairly consistent with model predictions in all three cases. Note in (A), the data *appear* fairly flat, yet an standard major axis (SMA) regression line fit (red line) to the data reveals a negative trend consistent with model predictions. The general trends in panels (B) and (C) are also consistent with model predictions.

on Earth and in our US woody plant data are gymnosperms and are exclusively those which exhibit strong apical dominance and have large, fairly cylindrical, tapering boles supporting smaller lateral branches and thus most closely resemble the idealized columnar form of the elastic similarity model (Greenhill, 1881; Niklas, 1994). In contrast, smaller species exhibit much more variability in architecture including succulents, prostrate species, minimally branched species, highly branched species with weak apical dominance, and all manner of intermediate variant forms (Hallé et al., 1978). These trends are captured in Figure 4 where there is much more allometric variability at small sizes and much less at large sizes, with slopes converging near the expectations of elastic similarity at large sizes and mean values approaching flow similarity at small sizes, albeit with increasing variation.

Our results suggest that elastic buckling due to self-loading and/or external loading may be more of a constraint as tree species become large (Holbrook & Putz, 1989). The mean slope in all three relationships is near to the expectation for elastic similarity (Figure 2A,C,E), and slopes converge on values closer to the elastic similarity expectation as maximum size increases (Figure 4). While mechanical damage due to self-loading or external stress events can certainly occur in smaller species, it is easy to conceive that the greater threat to function in many species and habitats is hydraulic stress or failure (cavitation, embolism), particularly when one considers the strong relationship between plant size and aridity (Hulshof et al., 2015; Maherali et al., 2004; Meinzer et al., 2009). Along gradients in aridity, we also see systematic changes in canopy structure, with intense

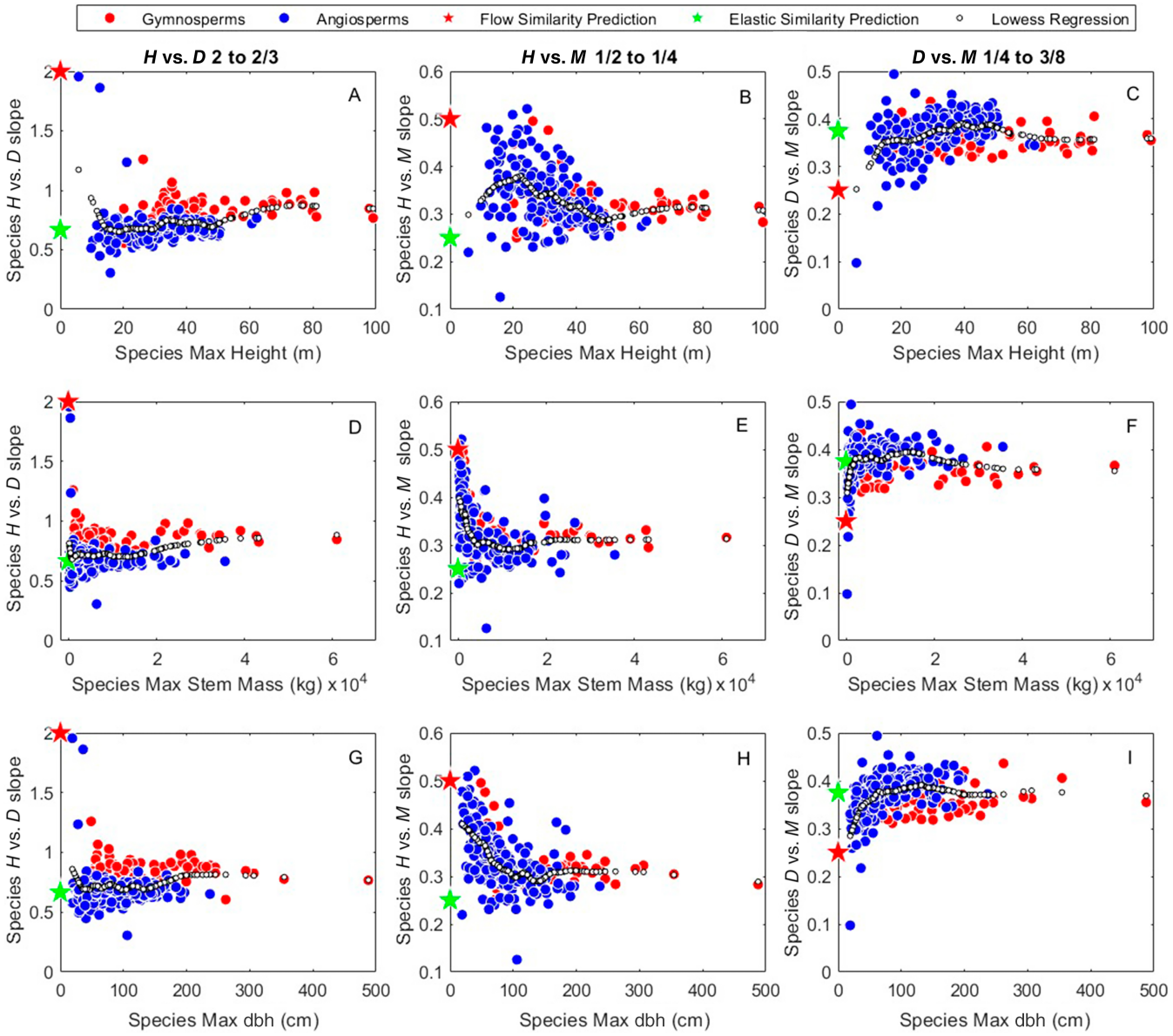

FIGURE 4 Size dependence of allometric slopes. Both the variance and locally weighted mean value of the fitted regression slopes for the pairwise allometric exponents for the three variables height (*H*), diameter (*D*), and mass (*M*) show strong size dependent trends for the *H* vs. *D* relationships (A, D, G), *H* vs. *M* relationships (B, E, H), and *D* vs. *M* relationships (C, F, I) when plotted against maximum size data for each species (height, mass, and dbh). In all cases, the lowess regression fits demonstrate that the data trends closer elastic similarity predictions at large sizes with reduced variance, and in most cases toward flow similarity at small sizes albeit with increasing variance.

light competition in closed canopy forests in hydric systems, and little to no light competition in arid systems. One can find taller species in arid systems along riparian corridors where water availability supports vertical growth and competition for light, but such habitats comprise a small proportion of the area of arid land systems.

Height to diameter allometries have been linked to trade-offs in growth rate versus survival and tree species that grow rapidly in height in order to reach the forest canopy may sacrifice mechanical stability through having narrower trunks at a given height (King et al., 2006; Niklas, 1994). The allometry of tree height to diameter across climatic gradients has been examined by several groups. A full exploration of this literature is beyond the scope of our efforts here, but a brief survey indicates that this relationship has been shown to be related to temperature (Lines et al., 2012; Wang et al., 2006), competition, aridity (Lines et al., 2012), precipitation seasonality, stem density, solar radiation, and wood density (Banin et al., 2012). Within the FIA data, Hulshof et al. (2015) examined height-diameter variability at the landscape scale and found it correlated with coarse

phylogenetic affiliation (Angiosperms and Gymnosperms) and the degree of shade tolerance. Clearly, the extent to which trees grow vertically or horizontally is a plastic trait. We hope to have added to this conversation by showing how this parameter space is bounded and linked to maximum plant size (Figures 2–4).

The flow similarity model predicts the form and allometry of the branches of woody plants as a function of branch network topology. The model predicts that the dimensions of subtrees within trees will most closely align with scaling predictions due to the conservation of mass in stochastically branching networks. For example, predicted length within the model is the total path length of branches distal to any branching point. Thus, the data presented here do not constitute the strongest test of the model: plant height is quantitatively and qualitatively different than branch path length. Nevertheless, the four predictions we evaluated here appear to have empirical support (Figures 2–4).

We evaluated the predicted curvature for each of the three relationships by fitting second-order polynomials to bivariate relationships. Polynomial fits to clouds of data are sensitive to outliers and non-homogeneity, and allometric data in the FIA database may contain noise due to the large number of individuals collecting data, and the large environmental gradients over which some species in the data set are growing, and due to the fact that mass estimates are nondestructively generated and thus contain error. These caveats are counterbalanced by the sheer number of observations that the FIA dataset contains. Height and dbh are collected using standard protocols, and the nondestructive mass estimates within FIA are among the most researched and vetted in the field (Burrill et al., 2021; Jenkins et al., 2003), underpinning numerous efforts to estimate timber volumes, carbon stocks, and forest health for land managers across the country (see review in Tinkham et al., 2018).

The predicted covariation functions capture the trends in data (Figure 3) with unexplained variability around each relationship. This is not surprising as the model predicts the dimensions of the branching architecture irrespective of how that form is embedded in 3D space. While relatively easy to measure, the relationship between plant height and dbh is a coarse representation of plant form. Understandably this relationship is widely used due to the ease and speed with which these parameters can be estimated, allowing measurements of millions of trees. However, this approach fails to capture differences in size and form due to architecture, such as differences in apical dominance, branch size, and frequency, or the degree of side branching, which likely accounts for much of the unexplained variation we see here (Hallé et al., 1978; Kohyama, 1987). Moreover, allometric relationships are inherently somewhat noisy, sensitive to outliers, and confounded here by plants growing across a wide range of habitats and environmental conditions which may influence allometric relationships (Archibald & Bond, 2003; Banin et al., 2012; Hulshof et al., 2015; Lines et al., 2012; Wang et al., 2006). Moreover, despite standardized collection protocols and robust quality assurance procedures, measuring (and remeasuring) H and dbh can be challenging, especially in rugged terrain and dense stand conditions; thus, there will inevitably be uncertainty introduced when conducting large scale forest inventories.

The predicted allometric covariation functions for the three relationships examined here (Figure 3) are identical in form to those predicted by Price et al. (2007) (other functions differ however; see Price et al., 2022). Price et al. (2007) utilized a two-parameter model derived from the underlying framework of the West, Brown, and Enquist hierarchical fractal model (West et al., 1999) to predict allometric covariation. The flow similarity model also follows a hierarchical branching framework (as any model for tree branching might) but differs in the physical constraints it invokes and relies on a single parameter for the covariation predictions (Table 1). Comparing identical functions that differ in the number of parameters using a metric such as Akaike information criteria, would trivially favor the flow similarity model; thus, we have not performed such an analysis here.

Among the most interesting of our findings is the strong size dependence of observed allometric slopes (Figure 4). The interspecific data for all three allometric slope estimates trend from high variability at small sizes to narrowing variability as size increases, whether size is indexed by plant height, dbh or estimated mass, in both angiosperms and gymnosperms. Moreover, lowess regression fits show convergence toward elastic similarity predictions at large sizes and movement toward flow similarity predictions at small sizes, consistent with model predictions (Price et al., 2022). FIA does not measure trees below 5 inches dbh in their subplots, and whether or not these trends would continue at even smaller sizes remains an open question.

As species become smaller, the central tendency in allometric exponents with size approaches the flow similarity expectation in Figure 4 in most, but not all cases (i.e., Panel I vs. Panel B). One interpretation of these trends is that, on average, small tree species have scaling properties that are more similar to those found in the terminal branches of large trees. However, we recognize that because allometric exponents are bounded by zero (typically), any increase in variability may tend to increase the mean observed exponent and that the agreement we see here is simply a statistical artifact. Subsequent examinations exploring the physiology,

dimensions, and topology of small trees versus the terminal portions of large trees may shed light on this issue.

We recognize that it may seem inconsistent to suggest that allometric relationships are non-linear, then evaluate their variability using linear fits to log-transformed data. This is done for several reasons. First, while polynomial fits to allometric data will reveal curvature, the overwhelming majority of the relationships are still well described by a linear model with relatively high correlation coefficients (see *Results*). Thus, a linear model fit is a good approximation to the data. Additionally, linear model fits allow for more straightforward comparisons with other regressions slopes and model predictions. We note that the correlation coefficients observed here are likely lower than those derived from studies examining allometric relationships in a single species within a constrained geographic area, which tend to be higher. Examining species across a broad array of habitats and management units surely increases the variability of recorded plant sizes and dimensions.

As suggested by Chamberlin (1897) over a century ago and reiterated by Platt (1964), science progresses more rapidly when one compares the predictions of multiple models and allows the data to indicate which is favored. In that spirit we have compared the predictions of two models here, elastic similarity and flow similarity. The data we have presented demonstrate that allometric exponents vary greatly across species, and thus, any model that predicts a single exponent for each scaling relationship, such as elastic similarity, will fail to capture this variability. We have also shown that the majority of slope estimates fall within the predicted bounds, exhibit the predicted curvature, and covary with other slopes and with plant size in a manner that is consistent with broad scale expectations described by the flow similarity model (Price et al., 2022). While our analysis is admittedly coarse scale, it does provide support for approaches that allow for variability in allometric exponents, both within and across tree species. Subsequent tests that explore how measures of plant branching topology, conduit anatomy, and physiology all vary with plant size will help us to understand the extent to which the flow similarity model is a useful abstraction of the dimensions of growing plants.

AUTHOR CONTRIBUTIONS

Charles A. Price conceived the analyses. Charles A. Price and Todd A. Schroeder performed the analyses and wrote the paper.

ACKNOWLEDGMENTS

We would like to thank the hard-working individuals of the USFS Forest Inventory and Analysis group, without whom the data would not be available.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Price, 2024) are available from Dryad: https://doi.org/10.5061/dryad.p2ngf1vwk. FIA data are available from the USFS FIA Datamart: https://apps.fs.usda.gov/fia/datamart/datamart.html. Details are available in *Materials and methods*.

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REFERENCES

Archibald, S., and W. J. Bond. 2003. "Growing Tall vs Growing Wide: Tree Architecture and Allometry of *Acacia karroo* in Forest, Savanna, and Arid Environments." *Oikos* 102: 3–14.

Banin, L., T. R. Feldpausch, O. L. Phillips, T. R. Baker, J. Lloyd, K. Affum-Baffoe, E. J. M. M. Arets, et al. 2012. "What Controls Tropical Forest Architecture? Testing Environmental, Structural and Floristic Drivers." *Global Ecology and Biogeography* 21: 1179–90.

Brown, J. H., and G. B. West, eds. 2000. *Scaling in Biology*. Oxford: Oxford University Press.

Burrill, E. A., A. M. DiTommaso, J. A. Turner, S. A. Pugh, J. Menlove, G. Christiansen, C. J. Perry, and B. L. Conkling. 2021. *The Forest Inventory and Analysis Database: Database Description and User Guide Version 9.0.1 for Phase 2*. Asheville, NC: U.S. Department of Agriculture, Forest Service. 1026 pp.

Calder, W. A. 1984. *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.

Chamberlin, T. C. 1897. "The Method of Multiple Working Hypotheses." *Journal of Geology* 5: 837–848.

Charnov, E. L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. "Towards a Worldwide Wood Economics Spectrum." *Ecology Letters* 12: 351–366.

Cleveland, W. S. 1979. "Robust Locally Weighted Regression and Smoothing Scatterplots." *Journal of the American Statistical Association* 74: 829–836.

Greenhill, A. G. 1881. "Determination of the Greatest Height Consistent with Stability That a Vertical Pole or Mast Can Be Made, and of the Greatest Height to Which a Tree of Given Proportions Can Grow." *Proceedings of the Cambridge Philosophical Society* 9: 65–73.

Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical Trees and Forests: An Architectural Analysis*. New York: Springer-Verlag.

Heath, L., M. Hansen, J. Smith, W. Smith, and P. Miles. 2009. "Investigation into Calculating Tree Biomass and Carbon in the FIADB Using a Biomass Expansion Factor Approach." In *Forest Inventory and Analysis (FIA) Symposium 2008*, ed. W. McWilliams, G. Moisen, R. Czaplewski, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Holbrook, N. M., and F. E. Putz. 1989. "Influence of Neighbors on Tree Form: Effects of Lateral Shade and Prevention of Sway on the Allometry of *Liquidambar styraciflua* (Sweet Gum)." *American Journal of Botany* 76: 1740–49.

Hulshof, C. M., N. G. Swenson, and M. D. Weiser. 2015. "Tree Height–Diameter Allometry across the United States." *Ecology and Evolution* 5: 1193–1204.

Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. Birdsey. 2003. "National Scale Biomass Estimators for United States Tree Species." *Forest Science* 49: 12–35.

King, D., S. Davies, and N. S. Muhammad Noor. 2006. "Growth and Mortality Are Related to Adult Tree Size in a Malaysian Mixed Dipterocarp Forest." *Forest Ecology and Management* 223: 152–58.

Koch, G. W., S. C. Sillett, G. M. Jennings, and S. D. Davis. 2004. "The Limits to Tree Height." *Nature* 428: 851–54.

Kohyama, T. 1987. "Significance of Architecture and Allometry in Saplings." *Functional Ecology* 1: 399–404.

Lewis, A. M., and E. R. Boose. 1995. "Estimating Volume Flow-Rates through Xylem Conduits." *American Journal of Botany* 82: 1112–16.

Lines, E., M. Zavala, D. Purves, and D. Coomes. 2012. "Predictable Changes in Aboveground Allometry of Trees along Gradients of Temperature, Aridity and Competition." *Global Ecology and Biogeography* 21: 1017–28.

Maherali, H., W. Pockman, and R. Jackson. 2004. "Adaptive Variation in the Vulnerability of Woody Plants to Xylem Cavitation." *Ecology* 85: 2184–99.

McMahon, T. A., and R. E. Kronauer. 1976. "Tree Structures: Deducing the Principle of Mechanical Design." *Journal of Theoretical Biology* 59: 443–466.

Meinzer, F. C., D. M. Johnson, B. Lachenbruch, K. A. McCulloh, and D. R. Woodruff. 2009. "Xylem Hydraulic Safety Margins in Woody Plants: Coordination of Stomatal Control of Xylem Tension with Hydraulic Capacitance." *Functional Ecology* 23: 922–930.

Niklas, K. J. 1994. *Plant Allometry: The Scaling of Form and Process*. Chicago, IL: University of Chicago Press.

Niklas, K. J., and H.-C. Spatz. 2004. "Growth and Hydraulic (Not Mechanical) Constraints Govern the Scaling of Tree Height and Mass." *Proceedings of the National Academy of Sciences of the United States of America* 101: 15661–63.

Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Platt, J. R. 1964. "Strong Inference." *Science* 146: 347–353.

Price, C. A. 2023. "Flow Similarity Model Predicts the Allometry and Allometric Covariation of Petiole Dimensions." *Plant Direct* 7: e510.

Price, C. A. 2024. "Allometric Regression Statistics for 285 North American Tree Species." Dryad. Dataset. https://doi.org/10.5061/dryad.p2ngf1vwk.

Price, C. A., P. Drake, E. J. Veneklaas, and M. Renton. 2022. "Flow Similarity, Stochastic Branching, and Quarter-Power Scaling in Plants." *Plant Physiology* 190: 1854–65.

Price, C. A., B. J. Enquist, and V. M. Savage. 2007. "A General Model for Allometric Covariation in Botanical Form and Function." *Proceedings of the National Academy of Sciences of the United States of America* 104: 13204–9.

Price, C. A., J. S. Weitz, V. M. Savage, J. C. Stegen, A. Clarke, D. A. Coomes, P. S. Dodds, et al. 2012. "Testing the Metabolic Theory of Ecology." *Ecology Letters* 15: 1465–74.

Raile, G. K. 1982. *Estimating Stump Volume*. St. Paul, MN: Forest Service, U.S. Department of Agriculture, North Central Forest Experiment Station.

Ryan, M. G., and B. J. Yoder. 1997. "Hydraulic Limits to Tree Height and Tree Growth: What Keeps Trees from Growing beyond a Certain Height?" *Bioscience* 47: 235–242.

Savage, V. M., E. J. Deeds, and W. Fontana. 2008. "Sizing up Allometric Scaling Theory." *PLoS Computational Biology* 4: 17.

Schmidt-Nielsen, K. 1984. *Scaling: Why Is Animal Size So Important?* Cambridge: Cambridge University Press.

Shinozaki, K., K. Yoda, K. Hozumi, and T. Kira. 1964. "A Quantitative Analysis of Plant Form—The Pipe Model Theory. I. Basic Analysis." *Japanese Journal of Ecology* 14: 97–105.

Shipley, B., and D. Meziane. 2002. "The Balanced-Growth Hypothesis and the Allometry of Leaf and Root Biomass Allocation." *Functional Ecology* 16: 326–331.

Sibly, R. M., J. H. Brown, and A. Kodric-Brown. 2012. *Metabolic Ecology: A Scaling Approach*. Oxford: Wiley-Blackwell.

Tinkham, W., P. Mahoney, A. T. Hudak, G. Domke, M. Falkowski, C. Woodall, and A. Smith. 2018. "Applications of the United States Forest Service Forest Inventory and Analysis Dataset: A Review and Future Directions." *Canadian Journal of Forest Research* 48: 1251–68.

Venturas, M. D., J. S. Sperry, and U. G. Hacke. 2017. "Plant Xylem Hydraulics: What We Understand, Current Research, and Future Challenges." *Journal of Integrative Plant Biology* 59: 356–389.

Wang, X., J. Fang, Z. Tang, and B. Zhu. 2006. "Climatic Control of Primary Forest Structure and DBH-Height Allometry in Northeast China." *Forest Ecology and Management* 234: 264–274.

Warton, D. I., I. J. Wright, D. S. Falster, and M. Westoby. 2006. "Bivariate Line-Fitting Methods for Allometry." *Biological Reviews* 81: 259–291.

West, G. B., J. H. Brown, and B. J. Enquist. 1999. "A General Model for the Structure and Allometry of Plant Vascular Systems." *Nature* 400: 664–67.

West, G. B., J. H. Brown, and B. J. Enquist. 2001. "A General Model for Ontogenetic Growth." *Nature* 413: 628–631.

How to cite this article: Price, Charles A., and Todd A. Schroeder. 2024. "Flow Similarity Model Predicts Allometric Size Dependence, Curvature, and Covariation of 285 North American Tree Species." *Ecosphere* 15(4): e4835. https://doi.org/10.1002/ecs2.4835