Plant sizes and shapes above and belowground and their interactions with climate

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Summary

- Although the above and belowground sizes and shapes of plants strongly influence plant competition, community structure, and plant–environment interactions, plant sizes and shapes remain poorly characterized across climate regimes. We investigated relationships among shoot and root system size and climate.
- We assembled and analyzed, to our knowledge, the largest global database describing the maximum rooting depth, lateral spread, and shoot size of terrestrial plants – more than doubling the Root Systems of Individual Plants database to 5647 observations.
- Water availability and growth form greatly influence shoot size, and rooting depth is primarily influenced by temperature seasonality. Shoot size is the strongest predictor of lateral spread, with root system diameter being two times wider than shoot width on average for woody plants.
- Shoot size covaries strongly with rooting system size; however, the geometries of plants differ considerably across climates, with woody plants in more arid climates having shorter shoots, but deeper, narrower root systems. Additionally, estimates of the depth and lateral spread of plant root systems are likely underestimated at the global scale.

Introduction

The vertical and horizontal extents of plants partly define plant architecture above and belowground (Lynch, 1995; Schenk & Jackson, 2002a; Hunt, 2016; Pawlik & Kasprzak, 2017). Plant architecture, the three-dimensional organization of the plant body (Reinhardt & Kuhlemeier, 2002), is plastic; plants compensate for resource limitations by altering allocation among above and belowground organs to optimize growth, survival, and reproduction (Poorter et al., 2012; Díaz et al., 2016). To understand plant responses to changes in resource availability and climate (Dybinski et al., 2011; Farrior et al., 2015), several global studies have examined plant biomass partitioning across climates (Cheng & Niklas, 2006; Mokany et al., 2006; Reich et al., 2014). However, the vertical and horizontal extents of plants have traditionally been ignored, despite the fact that plants with similar biomass allometries may have different dimensions. In this study we seek to understand how the maxima of plant extents respond to climate through changes among shoot height and width and rooting depth and spread.

Understanding the relationships between the size of plants above and belowground will improve our knowledge of plant form and function. For example, the global spectrum of plant form and function (plant economic spectrum; PES), proposed by Diaz et al. (2016), posits that the size of plants and their organs represents the first major dimension of the PES. Consequently, most PES studies have focused on leaf, seed, and stem traits; however, these studies have typically used only shoot height to represent overall plant size (Verbeek et al., 2019). Additionally, root traits, such as maximum depth and spread, considered to be an important missing link, have mostly been excluded from such analyses due to a scarcity of data (Joswig et al., 2022). When root traits have been included in studies of the global spectrum of plant form and function, the focus has usually been on fine root traits, not root system size traits, such as maximum depth and spread (Carmona et al., 2021).

Variation in belowground plant traits remains poorly quantified compared with shoot traits (Jackson et al., 1996; Vogt et al., 1996; Norby & Jackson, 2000; Reich, 2014; Iversen & McCormack, 2021). The size and shape of root systems rely, first, on resource demand of the plant (for water and nutrients), depending on overall plant size and growth strategy (Jackson et al., 2000; Enquist & Niklas, 2002; Niklas & Enquist, 2002; Poorter et al., 2012); second, on resource availability belowground (Poorter & Nagel, 2000; Schenk, 2008a); third, on soil constraints, such as horizons, bedrock, hardpans, and groundwater

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To rectify the scarcity of root-system size data, we assembled, to our knowledge, the largest global database describing the maximum rooting depth, lateral spread, and shoot size of terrestrial plants. The Root Systems of Individual Plants (RSIP) database was developed in 2002 to quantify the maximum depth $D_R$ and lateral spread $L_R$ of plant root systems (Schenk & Jackson, 2002a; Fig. 1; Supporting Information Fig. S1a). Here, we more than doubled the database to 5647 total observations across a broad range of terrestrial climates and geographies (Figs 2, S1c).

We use the expanded RSIP database to examine large-scale patterns related to plant size and shape both above and belowground. Specifically, we seek to (1) characterize the root and shoot sizes of different plant functional types (PFTs), (2) understand how plant size, climate, and environment influence the vertical and horizontal extents of plants globally, (3) evaluate how plant dimensions shift above and belowground along climatic gradients, and (4) compare individual-plant-scale rooting depths to ecosystem-scale rooting depths across biomes and climates.

**Materials and Methods**

**Dataset**

The RSIP dataset integrates observations of the vertical and horizontal extents of individual plants with data for other plant traits. The RSIP data come from published observations of maximum plant root system dimensions, 361 publications (Appendix A1), covering 2989 species from 263 plant families (Fig. 3). The first
version of the RSIP (Fig. S1a; Schenk & Jackson, 2002a) included 1305 observations for water-limited ecosystems, and second version (Fig. S1b; Schenk & Jackson, 2005) included 2449 observations across a broader range of climates. Our expanded RSIP, with 5647 total observations (Fig. S1c), includes a range of root and shoot sizes spanning more than four orders of magnitude (Fig. 4) across most of the Earth’s climates and environments (Fig. 2).

The RSIP entries are classified by physiology and functional traits (see Tables S1, S2 for a full list of RSIP variables), including six growth forms: forbs (30% of observations), grasses (18%), semi-shrubs (shrub species and suffrutescent forbs that rarely reach 1 m in height; 10%), shrubs (12%), stem succulents (2%), and trees (28%). We also record coarse-scale information on the plant’s environment and location, such as biome, elevation, and spatial coordinates (see Tables S1, S2). However, fine-scale environmental parameters, such as soil traits, cannot be accurately estimated based on the spatial coordinates for the RSIP entries.

The spatial coordinates allowed us to estimate related climate information, such as mean annual precipitation (MAP), when it was unavailable in the source literature. The estimated climate parameters came from WorldClim2, specifically 1 km spatial resolution climate surfaces for global land areas, providing historical (1970–2000) monthly and annual estimates of temperature and precipitation (Fick & Hijmans, 2017). Estimates for mean annual potential evapotranspiration (MAE) came from the Global Aridity Index and Potential Evapotranspiration Climate Database v.2 (Trabucco & Zomer, 2019). Nineteen additional bioclimatic variables were calculated following Fick & Hijmans (2017), providing long-term metrics for precipitation and temperature seasonality (Table S1, BIO1-19).

Bioclimatic variables allowed us to test how seasonality and climate affect the size of plants. Additionally, we calculated the seasonality of precipitation metric $S_w = \min[P_{sur}, P_{def}]$ described in Schenk & Jackson (2005). To calculate $S_w$, we used long-term monthly average precipitation (Fick & Hijmans, 2017) and potential evapotranspiration (Trabucco & Zomer, 2019) to calculate the sum of the seasonal surplus $P_{sur}$ or deficit $P_{def}$ of water. See Table S1 for the equations and definitions for $S_w$, $P_{def}$, and $P_{sur}$, along with a description of each of the climate metrics, growth extents, plant traits, and environmental metrics.

**Describing plant size**

The RSIP contains measurements describing the maximum above and belowground dimensions of individual plants at the time of measurement. Maximum rooting depth $D_R (n = 5633)$ is defined as the deepest soil depth reached by the roots of an individual plant (Fig. 1; Table 1). Two additional belowground dimensions in the database include lateral spread $L_R (n = 2874)$, the maximum one-sided horizontal distance from the stem of an individual plant reached by its roots (i.e. the radius), and root system width $W_R (n = 1756)$, the maximum root system diameter, which is not always the same as $2 \times L_R$ because most root systems are asymmetrical (Fig. 1). The main aboveground dimensions in the database are shoot height $H_S (n = 2373)$ and shoot width $W_S (n = 2074)$; Fig. 1), the maximum shoot diameter. Shoot volume $V_S$ was estimated using an ellipsoid shape ($V_S (m^3) = \pi \times H_S \times W_S^2 / 6$). We excluded from the analyses
of shoot width $W_z$ and lateral spread $L_R$ those observations from species known to have clonal, rhizomatous, or stoloniferous growth habits ($n=101$), such as Populus tremuloides and Poa pratensis, so as not to give a misleading view of their functional morphology by only measuring the widths of individual ramets. The maximum dimensions of an individual plant at the time of excavation had to be directly measured to be included in the RSIP; observations were excluded from the RSIP if the sampling depth was less than the perceived max rooting depth, if allometric equations or other formulas were used to predict plant dimensions, or if the measurements were an aggregate of multiple observations and were not the dimensions of an individual plant.

**Phylogenetic analysis**

To understand the importance of phylogeny on the main variables ($D_R$, $L_R$, $H_S$, and $W_z$), we calculated the phylogenetic signal using Pagel’s lambda (Pagel, 1997, 1999) and performed phylogenetically independent contrasts (PICs) between above and belowground plant extents and across the main climate metrics (MAE, MAP, aridity index $A_i$, and $S_j$). The phylogeny of RSIP observations was constructed using the v.phylomaker R package (Jin & Qian, 2019) with the GBOTB.extented mega-tree (Zanne et al., 2014; Smith & Brown, 2018). The plant names were standardized using the The Plant List (2013; v.1.1; www.theplantlist.org/) to...
of the phylogeny (Freckleton et al., 2002). A lambda value of zero indicates no phylogenetic influence on plant traits, whereas a lambda value of one represents high phylogenetic signal. To calculate Pagel’s lambda and the log likelihood statistic we used the PHYLTOOLS::phylosig R function (Revell, 2012) to run 100 simulations for each of the resolved phylogenies using the ape and stats R packages (Paradis & Schliep, 2019; R Core Team, 2020). Phylogenetic relatedness was calculated and used as a predictor variable in the random forest analysis (see next section) via an analysis of the phylogenetic pairwise distance between species using the ape package (Paradis & Schliep, 2019), as suggested in Bergmann et al. (2017).

Evaluating variable importance for shoot and root extents
To determine factors influencing maximum root ($D_R$ and $L_R$) and shoot extents ($H_S$ and $W_S$), we estimated the importance of covariates using a random forest approach (Breiman, 2001). The list of covariates included aboveground plant traits and climate metrics (see Table S1 for a full list of RSIP parameters). The random forest models for belowground extents were run with (Fig. 6c,d see later) and without (Fig. 6a,b see later) aboveground metrics ($H_S$, $W_S$, and $V_S$) as predictors; however, belowground extents ($D_R$ and $L_R$) were not used as predictors for $H_S$ and $W_S$.

For the random forest approach, we utilized the RANGER package (Wright & Ziegler, 2017), which is an implementation of the original random forest (Breiman, 2001) suited for high-dimensional data (Boehmke & Greenwell, 2020). We split the RSIP dataset using stratified sampling into a model training

**Table 1** A list of commonly used abbreviations (see Supporting Information Table S1 for a list of all RSIP parameters).

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant size</td>
<td></td>
</tr>
<tr>
<td>$D_R$</td>
<td>Maximum rooting depth of plant (m)</td>
</tr>
<tr>
<td>$L_R$</td>
<td>Maximum lateral root spread, one-sided (radius) linear distance from stem reached by roots (m)</td>
</tr>
<tr>
<td>$W_R$</td>
<td>Rooting spread or diameter (m)</td>
</tr>
<tr>
<td>$H_S$</td>
<td>Height of plant shoot (m)</td>
</tr>
<tr>
<td>$W_S$</td>
<td>Width of plant shoot (m)</td>
</tr>
<tr>
<td>$V_S$</td>
<td>Canopy volume, calculated using an ellipsoidal shape: $V_S (m^3) = \pi \times H_S \times W_S^2/6$</td>
</tr>
<tr>
<td>DBH</td>
<td>Stem diameter (diameter at breast height) of trees (cm)</td>
</tr>
<tr>
<td>Plant shape</td>
<td></td>
</tr>
<tr>
<td>$Y : X_{root}$</td>
<td>Aboveground dimensional aspect ratio</td>
</tr>
<tr>
<td>$Y : X_{noot}$</td>
<td>Belowground dimensional aspect ratio</td>
</tr>
<tr>
<td>$S : R_y$</td>
<td>Vertical shoot : root ratio ($S : R_y = H_S/D_R$)</td>
</tr>
<tr>
<td>$S : R_s$</td>
<td>Horizontal shoot : root ratio ($S : R_s = W_S/W_R$)</td>
</tr>
<tr>
<td>Climate</td>
<td></td>
</tr>
<tr>
<td>MAP</td>
<td>Mean annual precipitation (m)</td>
</tr>
<tr>
<td>MAE</td>
<td>Mean annual potential evapotranspiration (m)</td>
</tr>
<tr>
<td>$A_i$</td>
<td>Aridity index ($A_i = MAP/MAE$)</td>
</tr>
<tr>
<td>$S_a$</td>
<td>Seasonality index or annual water storage index: $S_a = \min(P_{sum}, P_{def})$</td>
</tr>
<tr>
<td>Datasets</td>
<td></td>
</tr>
<tr>
<td>RSIP</td>
<td>Root Systems of Individual Plants</td>
</tr>
<tr>
<td>RPGE</td>
<td>Root Profiles for Global Ecosystems (Schenk &amp; Jackson, 2003)</td>
</tr>
</tbody>
</table>
subset containing 70% of the entries and a model testing subset using the RSAMPLE package (Silge et al., 2021). Because random forests cannot handle missing values, we used the MISSRANGER package (Mayer, 2019) to impute missing values through a non-parametric approach for mixed-type data using chains of random forests (Stekhoven & Bühlmann, 2012). The training data were used to adjust the random forest model using a hyperparameter grid to search for the optimal parameter values, resulting in the greatest reduction in root-mean-square error (Probst et al., 2019). The hyperparameter tuning resulted in an average 4% improvement compared with the baseline model. The random forest model was then rerun using the selected hyperparameters to calculate the permutation-based variable importance for each predictor. We chose the permutation-based method because it is not biased towards variables with high cardinality (Strobl et al., 2008), such as for many climate variables. Although the permutation-based approach is more computationally intensive (because of the constant shuffling of features across the decision trees), it is generally a more accurate method than the standard mean-decrease-in-impurity importance (Strobl et al., 2007).

Additionally, we sought to determine how plant size differed across categorical variables such as plant characteristics and growth form (Table 2). Significant differences between the plant extents of categorical parameters were tested using ANOVA and post hoc Tukey honest significant difference tests (de Mendiburu, 2021).

### Shifts in plant shape across climate

Whereas our initial analysis focused on factors influencing single measures of plant vertical or horizontal size, we further sought to understand how the shapes or dimensions of plants shift along climatic/resource gradients. To do this, we calculated four new plant shape ratios: two that we call ‘dimensional aspect’ ratios ($Y : X_{shoot}$ and $Y : X_{root}$) and two ‘shoot : root’ ratios ($S : R_y$ and $S : R_x$). We plotted the four indicator ratios (Eqns 1–4) against a

<table>
<thead>
<tr>
<th>Table 2</th>
<th>Mean belowground (rooting depth ($D_R$), lateral spread ($L_R$), shoot height ($H_S$) and shoot width ($W_S$)) extents across plant traits.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Belowground extents (m)</td>
</tr>
<tr>
<td>Growth form</td>
<td>$D_R$</td>
</tr>
<tr>
<td>Forb</td>
<td>1.02</td>
</tr>
<tr>
<td>Grass</td>
<td>1.14</td>
</tr>
<tr>
<td>Semi-shrub</td>
<td>1.42</td>
</tr>
<tr>
<td>Shrub</td>
<td>2.36</td>
</tr>
<tr>
<td>Succulent</td>
<td>0.56</td>
</tr>
<tr>
<td>Tree</td>
<td>3.64</td>
</tr>
<tr>
<td>Lifespan</td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>0.76</td>
</tr>
<tr>
<td>Perennial</td>
<td>2.12</td>
</tr>
<tr>
<td>Tissue</td>
<td></td>
</tr>
<tr>
<td>Herbaceous</td>
<td>1.06</td>
</tr>
<tr>
<td>Woody</td>
<td>2.88</td>
</tr>
<tr>
<td>Seed category</td>
<td></td>
</tr>
<tr>
<td>Dicot</td>
<td>2.24</td>
</tr>
<tr>
<td>Gymnosperm</td>
<td>1.92</td>
</tr>
<tr>
<td>Monocot</td>
<td>1.08</td>
</tr>
<tr>
<td>Leaf longevity</td>
<td></td>
</tr>
<tr>
<td>Deciduous</td>
<td>2.96</td>
</tr>
<tr>
<td>Evergreen</td>
<td>3.1</td>
</tr>
<tr>
<td>Leaf form</td>
<td></td>
</tr>
<tr>
<td>Broadleaf</td>
<td>3.59</td>
</tr>
<tr>
<td>Needle-leaf</td>
<td>1.87</td>
</tr>
<tr>
<td>Photosynthetic pathway</td>
<td></td>
</tr>
<tr>
<td>C3</td>
<td>2.04</td>
</tr>
<tr>
<td>C3–C4</td>
<td>1.13</td>
</tr>
<tr>
<td>CAM</td>
<td>1.75</td>
</tr>
<tr>
<td>CAM</td>
<td>0.61</td>
</tr>
</tbody>
</table>

CAM, Crassulacean acid metabolism.

*These are the only two categories where rooting extents relative to aboveground volume showed significant differences between groups, where both annual and herbaceous plants had $D_R/V_T$ values greater than perennial and woody plants, therefore differing from the pattern shown by $D_R$, $D_R$ and $L_R$ relative to shoot volume ($V_S$) did not differ across all other classifications. The lowercase letters represent significant differences between groups via Tukey’s honest significance difference tests.
global climate gradient of aridity (Fig. 7, see later). Nonlinear regressions were fit to the mean ratio values for each aridity class.

The two-dimensional aspect ratios ($Y : X_{\text{shoot}}$ and $Y : X_{\text{root}}$) depict a plant’s dimensions shifting towards either lengthening or widening their maximum extents (Eqns 1, 2). A high $Y : X$ ratio represents a relative narrowing of plant morphology, whereas a low ratio represents a widening. As water availability increases, we expect to see relatively shallow plant growth belowground and a narrowing aboveground because plants may not need to root deeply in search of water and shoot heights are less limited by plant water potential. We calculated the dimensional aspect ratios as follows:

$$Y : X_{\text{shoot}} = \frac{H_S}{W_S} \quad \text{Eqn 1}$$

$$Y : X_{\text{root}} = \frac{D_R}{W_R} \quad \text{Eqn 2}$$

($H_S$, height of the plant; $W_S$, aboveground width of the plant (shoot diameter); $D_R$, maximum rooting depth; $W_R$, maximum width of the root system). When $W_R$ was not reported but $L_R$ was, we used $2 \times L_R$ in Eqn 2.

The second pair of growth indicator ratios, the shoot : root size ratios ($S : R_y$ and $S : R_x$), depict a plant’s vertical and horizontal allometry (Eqns 3, 4). These metrics are similar to traditional shoot-to-root biomass ratios, but with biomass replaced by vertical length ($S : R_y$) and horizontal width ($S : R_x$). A high $S : R$ ratio represents relatively greater aboveground investment, whereas a lower ratio represents relative belowground investment. We calculated the shoot : root size ratios as follows:

$$S : R_y = \frac{H_S}{D_R} \quad \text{Eqn 3}$$

$$S : R_x = \frac{W_S}{W_R} \quad \text{Eqn 4}$$

Comparing individual plant rooting depth observations with ecosystem and plant-functional-type estimates

Because many terrestrial biosphere models rely on ecosystem-level estimates of maximum rooting depth (Warren et al., 2015; McCormack et al., 2017; Drewniak, 2019), we compared how our rooting depth estimates for individual plants differ from ecosystem-level estimates across biomes and climates. For ecosystem-level data, we used the Root Profiles for Global Ecosystems (RPGE) dataset (Schenk & Jackson, 2002b) available online through the Oak Ridge National Laboratory Distributed Active Archive Center (Schenk & Jackson, 2003). We compared average individual plant rooting depth estimates by biome from the RSIP with (1) the ecosystem rooting depths ($D_{50}$ and $D_{95}$) by biome from the RPGE, and (2) the PFT rooting depth estimates used by the Energy Exascale Earth System Land Model (ELM; Fig. S2; Drewniak, 2019). ELM uses RPGE data to inform PFT rooting depth estimates (Drewniak, 2019).

To analyze the effect that climate parameters have on individual-plant ($D_0$) and ecosystem-level rooting depths ($D_{50}$ and $D_{95}$), we used linear mixed effect regression models (LMERs) with biome as a random effect, the climate metrics as fixed effects, and rooting depth ($D_{50}$, $D_{95}$, and $D_0$) as the dependent variable. The LMERs were performed using the lme4 package (Bates et al., 2015). We evaluated the LMERs using likelihood ratio tests, which compare the ANOVA of the full LMER with the fixed effects with the ANOVA of a null LMER with only random effects. Through the likelihood ratio test we computed the corrected Akaike information criterion AICc and $P$-values to analyze only significant predictors (Winter, 2013; Hajduk & Bailey, 2017; Mazerolle, 2020). Using the model results for $D_{50}$ and $D_{95}$, we compared the standardized coefficients with that of individual plant maximum rooting depth $D_R$ (Fig. S3).

Results

Rooting extents covary with shoot size

The two main plant rooting extents we examined, $D_R$ and $L_R$, differed substantially across growth forms, with woody plants, especially trees (mean $D_R$ of 3.64 m), rooting the deepest and the widest (Fig. 4; Table 2). Semi-shrubs, succulents, forbs, and grasses all had shallower, significantly indistinguishable rooting depths, with $D_R$ being only c. 30% as deep as trees on average (Fig. 4a; Table 2; $P < 0.001$). Trees and shrubs had the widest lateral spreads (average $L_R$ of 7.04 m and 3.35 m, respectively), whereas the average $L_R$ for succulents was 2.22 m, 4.5 times wider than $L_R$ for herbs (forbs and grasses; Fig. 4b; Table 2; $P < 0.001$). Relative to aboveground volume, $L_R$ ($L_R/V_S$; Kruskal–Wallis $P = 0.173$) and $D_R$ ($D_R/V_S$; Kruskal–Wallis $P = 0.053$) ratios did not significantly differ across growth forms.

Both rooting depth and spread scaled linearly with shoot size – specifically shoot height and width – across all growth forms (Fig. 5; Table 3). Whereas stem diameter (DBH) had a strong positive linear relationship with both maximum rooting depth and spread for trees (Table 3; $P < 0.0001$), $W_S$ and $H_S$ had stronger positive linear relationships with the rooting extents for both woody and herbaceous plants (Table 3).

High phyllogenetic signals for woody plant root system lateral spreads ($L_R$) and aboveground size ($H_S$, $W_S$, $V_S$, and DBH)

Pagel’s lambda values for woody plants showed high phylogenetic signals for aboveground size traits ($H_S \lambda = 0.934$; $W_S \lambda = 0.750$; $V_S \lambda = 1.0$; DBH $\lambda = 0.922$) and for root lateral spread ($L_R \lambda = 0.865$; Table S3). Lambda values for herbaceous plants were much lower than those of woody plants, suggesting a lower phylogenetic signal, except for maximum rooting depth, where the phylogeny of herbs accounted for more of the variation in $D_R$ values (herb $D_0 \lambda = 0.644$ and woody $D_0 \lambda = 0.271$; Table S3). For herbaceous $L_R$, $W_S$, and $V_S$ the phylogeny accounted for little to no variation in trait values across species ($\lambda < 0.2$), whereas phylogeny had a moderate effect on shoot height ($H_S \lambda = 0.558$).
There remained a positive relationship between shoot size and root system size (Table 3), even when using phylogenetically independent contrasts for woody and herbaceous plants, except for the relationship between $H_S$ and belowground extents ($D_R$ and $L_R$) when combining woody and herbaceous plants (Figs S4a, S5a). The negative PIC slopes ($\beta_1$) for $D_R$ ($\beta_1 = -0.19, P < 0.0001$) and $L_R$ ($\beta_1 = -0.05, P = 0.18$) when regressed against $H_S$ were due to the strong phylogenetic signal for $H_S$ ($\lambda = 0.985$), and the large differences between the shoot heights of woody and herbaceous plants (Table 3; Figs S4a, S5a). Overall, the PIC regressions and correlations of above to belowground plant size (Figs S4, S5) tended to be consistent with the linear relationships between plant extents (Fig. 5; Table 3).
Plant size extents differed significantly across the leaf and morphological traits we collected (i.e. lifespan, tissue, seed category, leaf longevity, leaf form, and photosynthetic pathway; Table 2). The average absolute extents ($D_R$ and $L_R$) of perennials were more than six times greater than for annuals, but their extents relative to shoot volume were four times greater (Table 2). The $D_R$ and $L_R$ of woody plants were, respectively, six times and 10 times greater than for herbs, but the $D_R/V_S$ of herbs was 2.3 times greater than for woody plants.

Among woody plants (trees and shrubs), deciduous plants had lateral spreads that were an average of 5.67 m (twice the width of evergreens), and broadleaf plants had an average $D_R$ of 3.59 m (two times deeper than needle-leaf plants) (Table 2). Moreover, we found similar trends, with perennial and woody plants having greater shoot heights $H_S$ and widths $W_S$ (Table 2) than annual and herbaceous plants did. Deciduous trees had average shoot widths of 2.6 m, which is twice that of evergreen trees. The $H_S$ values of needle-leaf plants were 7.74 m, also two times the $H_S$ of broadleaf plants, whereas $D_R$ was two times deeper for broadleaf plants than for needle-leaf plants.

Deeper roots in drier and more seasonal climates

We found significant linear relationships between the rooting extents and the primary climate metrics (MAE, MAP, $A_i$, and $S_i$; see Table 1 for abbreviation definitions) we analyzed (Fig. S6; Table S4). Rooting depth $D_R$ correlated positively with MAE and negatively with $A_i$ and MAP ($P < 0.0001$). Lateral spread $L_R$ was positively related to MAP and $A_i$ for all plants. $L_R$ was negatively related to MAE for herbs, and with $S_i$ for woody plants ($P < 0.0001$; Fig. S6; Table S4).

Though the PIC results tended to agree with the trends shown with the linear regressions (Table S4; Figs S6–S8) there were a few instances where the trends of the PIC results differed from the log-linear regressions. For example, there was a positive linear relationship between $L_R$ and MAP for woody plants ($\beta_1 = 0.21 \pm 0.04; P < 0.0001$; Table S4), whereas the PIC regression showed a negative relationship ($\beta_1 = -0.45; P < 0.0001$; Table S4).

Differences in predictor importance for shoot and root extents

Our random forest approach highlighted the important predictors for each of the plant size extents, with climate and temperature seasonality being important for $D_R$ and shoot size and plant characteristics being the most important for $L_R$ (Fig. 6a–d). Climate descriptors such as MAE, mean annual temperature, temperature seasonality, and maximum temperature were the most important predictors of $D_R$ (Fig. 6a,c), with $D_R$ increasing with warmer and more seasonal climates. $L_R$ was mostly affected by shoot size ($H_S$ and $W_S$, Fig. 6d) and plant descriptors (i.e. growth form and family; Fig. 6b,d). Partial dependencies showed that $L_R$ was greatest in woody plants, and in less seasonal climates (i.e. climates where temperature seasonality $< 500$, annual temperature range $< 25^\circ$C, and isothermality $> 50$). When shoot size ($W_S$, $H_S$, and $V_S$) was omitted from the random forest analyses (Fig. 6a,b) it had little effect on the variable importance ranking for $D_R$, but it led to growth form, family, phylogeny, and isothermality becoming the most important variables for predicting $L_R$.

Aboveground, the growth form and family were among the most important predictors of $H_S$ and $W_S$, followed by various climate metrics (Fig. 6c,d). The partial dependencies showed that trees, and plant families primarily made up of trees, represented the greatest $H_S$ and $W_S$ values. Additionally, $H_S$ and $W_S$ were greatest in less arid climates ($A_i > 1$). $H_S$ was greatest in climates with high precipitation and high seasonal water surplus ($P_{out} > 0.3$). $W_S$ was greatest in climates with low seasonal water deficits ($P_{def} < 0.2$) and colder climates (mean annual temperature $< 10^\circ$C).

Divergence in woody plant dimensions across aridity

The dimensions of woody plants shifted towards deeper and narrower root systems in more arid climates and towards taller and narrower shoots in relatively humid climates (Fig. 7a). Significant shifts in $Y$: $X$ and $S$: $R$ values with climate were seen only for woody plants (Fig. 7; Table S5). The aspect ratios of shoots and roots ($Y_i$: $X_{shoot}$ and $Y_i$: $X_{root}$) for woody plants in arid climates ($A_i < 0.2$) did not differ significantly ($P = 0.308$) (Fig. 7a). The average $Y_i$: $X_{shoot}$ and $Y_i$: $X_{root}$ values of woody plants in climates where $A_i < 0.5$ were 1.8 and 1.3, respectively. As $A_i$ increased, the aspect ratio curves diverged, crossing at an $A_i$ of 0.43, near the arid–humid threshold ($A_i = 0.5$; Fig. 7a). The $Y_i$: $X_{shoot}$ curve saturated in humid climates ($A_i > 0.5$). $Y_i$: $X_{root}$ decreases as climates become more humid, with root systems being wider relative to their depth ($Y_i$: $X_{root} < 1$) at an $A_i$ of 0.73. The average $Y_i$: $X_{shoot}$ and $Y_i$: $X_{root}$ values of woody plants in humid climates were 1.6 and 0.7, respectively.

Woody plants, on average, had shoots taller relative to rooting depth in humid climates ($S_i$: $R_S > 1$ when $A_i > 0.34$), but in arid climates the rooting depth is generally greater than shoot height (Fig. 7b). In arid climates, woody plants tended to be both wider and deeper belowground than aboveground, with $S_i$: $R$ values $< 1$ (Fig. 7b, purple). Horizontal allometry does not shift much across $A_i$ and the mean $S_i$: $R_S$ is 0.44, indicating that woody plants are, on average, more than two times wider belowground than aboveground. Herb $S_i$: $R$ and $Y_i$: $X$ values do not shift substantially across $A_i$ (Fig. 7c,d), with mean $S_i$: $R$ values $< 1$ ($S_i$: $R_S = 0.654$; $S_i$: $R_S = 0.452$), indicating that herbs generally take up more vertical and horizontal space belowground relative to aboveground dimensions.

Comparing RSIP individual plant data to broader scale estimates of maximum rooting depth

We compared the average RSIP maximum rooting depths ($D_R$) across growth forms and biomes with the biome-based estimates from the RPGE ($D_{RS}$; Fig. 8). For all biomes with trees, the average tree $D_R$ was significantly deeper than $D_{RS}$ (ecosystem-scale
maximum rooting depth; Table 1), sometimes by several meters, except for boreal forests, where $D_{95}$ was deeper. Tropical and seasonally dry climates had the largest disagreement between the RPGE and RSIP values, with $D_R$ values for multiple growth forms being significantly deeper than $D_{95}$ (Fig. 8). The ELM PFT parameters closely resembled RPGE $D_{95}$ estimates, except that ELM assigns tropical forest trees a maximum rooting depth of 3 m (Drewniak, 2019).

The ecosystem-scale $D_{50}$ (50th percentile rooting depth) was more sensitive to climate than the individual-plant ($D_R$) and ecosystem-scale ($D_{95}$) rooting depths were. The $D_{50}$ climate coefficients are greater than the $D_R$ coefficients, showing that $D_{50}$ is more heavily skewed by climate variables than $D_R$ is (Fig. S3). This is exemplified by the slope of the linear regression across the coefficients, where a unit slope is a one-to-one relationship between $D_R$ and $D_{95}$ coefficients; however, the slope was 0.52 with an $R^2 = 0.81$ ($y = 0.52x - 0.016$; Fig. S3). The opposite was true for $D_{95}$ vs $D_R$, where the slope of the regression across the climate coefficients was 2.62 ($y = 2.62x - 0.04$, $R^2 = 0.71$; Fig. S3), indicating that individual plant rooting depth $D_R$ is

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**Fig. 6** Random forest variable importance for (a) maximum rooting depth $D_R$, (b) maximum lateral spread $L_R$, (c) $D_R$ with shoot size included as predictors, (d) $L_R$ with shoot size as predictors, (e) shoot height $H_S$, and (f) shoot width $W_S$. The predictors are colored by predictor type, according to the figure key. The $y$-axis is the 15 most important predictors in descending order, and the $x$-axis is a scaled variable importance. Scaled variable importance $= \frac{\text{variable importance}}{\max(\text{variable importance})}$. The predictors used for the random forest analysis can be found in the fourth column of Supporting Information Table S1. Measures of aboveground size were not included as predictors in (a) and (b), whereas shoot height, shoot width, and shoot volume $V_S$ were included as predictors in (c, d). Belowground extents ($D_R$ and $L_R$) were not included as predictors for $H_S$ and $W_S$. 
more variable across climates than ecosystem-level rooting depth. At both the individual plant and ecosystem scales, roots were deeper in climates with higher mean and maximum temperatures and in climates with greater seasonal deficits of precipitation (Fig. S3). Shallower roots were found in humid climates and in climates with greater surpluses of precipitation (Fig. S3).

Discussion

Using our expanded RSIP database, we found the following patterns in plant size and shape globally: shoot size and root system size strongly covary; water availability and plant characteristics greatly influence shoot size, whereas rooting depth is primarily

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**Fig. 7** Woody plant shapes diverge across aridity classes. Point range represents the mean and confidence intervals grouped by aridity index categories for the four shape ratios with fitted nonlinear regressions. (a) Dimensional aspect ratios for woody plants, (b) shoot : root ratios for woody plants, (c) dimensional aspect ratios for herbaceous plants, and (d) shoot : root ratios for herbaceous plants. Either log-normal \( y = a \exp\left(-0.5 \log_b(x/x_0)/b^2\right) \) or nonlinear saturation curves \( y = ax/(b+x) \) were fitted to the means of each shape ratio across aridity classes, and the \( R^2 \) values are stated (see Supporting Information Table S5 for full equations). The aridity index categories, delimited by light gray dashed lines, are arid (0–0.2), semi-arid (0.2–0.5), subhumid (0.5–0.75), humid (0.75–1.0), per-humid (1.0–1.5), and hyper-humid (1.5–2.0). The dashed black line represents ratio values equal to one. (e) The color-coded schematics represent the relative dimensions for each ratio value. MAP, mean annual precipitation; MAE mean annual potential evapotranspiration; \( D_{R95} \), max rooting depth; \( W_R \), root system width, \( H_S \), shoot height; \( W_S \), shoot width.
influenced by temperature seasonality and lateral spread by shoot size; woody plants have deeper, narrower root systems in more arid climates and taller shoots in humid climates; and estimates of the depth and lateral spread of plant root systems are likely underestimated at the global scale.

Shoot size covaries strongly with root system size across plant functional groups

Both rooting depth \( D_R \) and lateral spread \( L_R \) scale linearly with aboveground size extents (\( H_S, W_S, V_S \), and DBH; Table 3), as expected with allometric scaling (Niklas & Enquist, 2001; Enquist & Niklas, 2002). Furthermore, multiple tropical forest studies have highlighted the link between shoot size and root system size (Ivanov et al., 2012; Brum et al., 2019; Smith et al., 2019). Of all the aboveground variables, shoot width \( W_S \) had the strongest positive relationship to rooting depth and spread across all plants (Table 2). Traditionally, stem diameter DBH is the most common metric used for allometric scaling in forestry and plant physiology (Cermák et al., 1998; Ledo et al., 2017), including long-standing allometric relationships between DBH and crown radius (Dawkins, 1963; O’Brien et al., 1995). DBH has also been used to estimate coarse root biomass (Tobin et al., 2007; Gou et al., 2017) and effective rooting depth (Brum et al., 2019). However, though DBH strongly correlated with shoot height and width, DBH did not correlate with rooting depth in our analysis (Fig. S9). We suggest that shoot width may be better used to estimate the size of root systems, as it correlates positively with both rooting depth and spread (Table 3; Fig. S9).

As expected, woody plants, especially trees, had the largest rooting (\( D_R \) and \( L_R \)) and shoot extents (\( W_S \) and \( H_S \)) and herbs had the smallest extents. Succulents have unique root system shapes, having the shallowest root systems yet wider lateral extents than herbs do (Fig. 4). One explanation for the shape of succulent root systems may be that succulents are found in regions with extremely dry soils, where shallow and elongated root systems are adapted to acquiring intermittent rainfall and fog (Jordan & Nobel, 1984; February et al., 2013). Additionally, there can be a large degree of rooting depth plasticity within the same species and environment. For example, a study on the rooting depth of Panicum maximum, a tropical perennial bunchgrass, in the state of São Paulo, Brazil, found rooting depths for mature grasses ranging from 0.85 to 4.85 ms across > 50 observations (Villares et al., 1953).

We found that the rooting depths of annuals and herbs relative to shoot volume (\( D_R/V_S \)) were much greater than that of perennials and woody plants, demonstrating an investment in belowground organs by shorter-lived plants. John Ernest Weaver (1958) observed the rooting patterns of forbs and found that some forbs can root deeply below the root zone of neighboring plants to avoid competition, quickly occupying depths of greater than 1.2 m in their first growing season and up to 4.6 m at maturity. The deepest-rooted forb in the RSIP, Alhagi maurorum – commonly known as camelthorn – reached rooting depths of 20 m but rarely exceeded 1.2 m in height (Nechaeva, 1985). The need of some plants to root deeply could also be due to competition in the form of root territoriality or resource depletion (Schenk, 2006, 2008a). The ability of plants such as herbs (which we often think of as being ‘small’ aboveground) to root at times several meters in depth is surprising.

Maximum lateral root spreads were strongly influenced by shoot size, even more than maximum rooting depth (Figs 5, S9; Table 3), further evidenced by the high variable importance of shoot height, width, and volume in the lateral extent random forest model (Fig. 6d). Modeling studies have demonstrated that lateral roots are more efficient at anchoring larger aboveground
plants than deep roots are (Ennos, 1993), and a strong linear relationship has been found between lateral spread and stem diameter (Schwarz et al., 2010). The relationship between lateral extent and shoot size highlights the potential importance of lateral root reinforcement for shoot anchorage.

Not surprisingly, there were strong phylogenetic signals for several size and shape traits, especially for aboveground traits, but also for the lateral spread of root systems. Plant species within a genus tend to be similar in growth form, and many plant families consist predominantly of woody plants, herbs, or succulents; and some woody families include mostly trees, whereas others include mostly shrubs and smaller trees. Different environments that favor trees, smaller woody plants, or herbs will therefore cause ecological and evolutionary sorting of genera and families, and historical effects will contribute to this sorting as well (Herrera, 1992), leaving what appears to be a strong phylogenetic signal in plants sizes and shapes (see Table S3).

The effect of temperature and precipitation seasonality on rooting depth

Relationships among above and belowground plant traits that we found are not static across the climate space. Our results agree with Schenk & Jackson (2002a), who found that plants root deeper relative to shoot size in arid climates. A global meta-analysis of forest biomass allocation found contrasting results, where root biomass decreased with temperature – analogous with MAE – but found no relation with aridity (Reich et al., 2014), potentially highlighting the difference between the space occupied by roots and overall biomass. A decrease in root system size relative to shoot size as climates become less arid would be expected under a plant resource economics framework, where increased water availability would allow plants to invest in aboveground growth when there are no longer limited by water availability belowground (Shipley & Meziane, 2002; Farrior et al., 2015; Anderegg et al., 2016; O’Brien et al., 2017).

Metrics of climate seasonality, specifically temperature seasonality and proxies for water availability, are important for understanding global rooting patterns. The relationship between precipitation seasonality and deep rooting has been well documented in seasonally dry ecosystems (Nepstad et al., 1994; Oliveira et al., 2005; Singh et al., 2020), although predicting deep rooting using global climate metrics is difficult given the complexities of plant–soil–water interactions. However, we provide ample evidence that deeper roots are more likely to occur in arid climates with hotter temperatures and seasonal precipitation (Figs 6a, S3, S6).

The exact relationships between rooting extents and seasonality are still unclear because we need root data at finer scales coupled with measures of seasonality that serve as better proxies for plant-available water, such as plant-accessible water storage capacity, dry-season water drawdown, and climatic water deficit (Fellows & Goulden, 2017; Ledo et al., 2017; Klos et al., 2018). Additionally, as climates change, metrics of interannual seasonality may provide insight on the climates that a plant is adapted to and its rooting response (Fischer et al., 2013; Pratt & Mooney, 2013; Stocker et al., 2013; Knapp et al., 2015). For instance, a study in an arid grassland found that increased interannual variability in precipitation causes a shift in community composition towards deeply rooted shrubs (Weltzin & McPherson, 2000; Gherardi & Sala, 2015). One promising method to understand spatial patterns in maximum rooting depth is to consider the climatology of the cumulative water deficit to estimate the rooting zone water storage capacity to which plants are adapted (Gao et al., 2014; Stocker et al., 2021).

Above and belowground woody plant geometries diverge across climates

Woody plants shift their shapes across climates more than other plant types do (i.e. herbs), with woody root systems being relatively narrower in arid climates and relatively wider in humid climates (Fig. 7a, red). In arid climates, woody plants are short and wide aboveground ($Y$: $X_{\text{root}} < 1$); an important transition occurs at the semi-arid to subhumid boundary, where plants become taller in relation to their width (Fig. 7a). Shoot height increases as plants compete for light, especially when plants are no longer limited by other resources (Falster & Westoby, 2003; Craine & Dybzinski, 2013). In humid climates, the aspect ratio of shoots (Fig. 7a, blue) does not change much, potentially because of the biological limits to the possible shoot size that plants can support and plants could be limited by other resources (Reich et al., 2003; Koch et al., 2004; Westoby & Wright, 2006; Niklas, 2007; Moles et al., 2009; Krishnamurthy, 2015). Overall, the shapes of woody plants above and belowground diverge across the climate space, where, as aridity decreases, root systems widen and shoots narrow (Fig. 7a). The aspect ratio of root systems decreases with increasing humidity, representing a relative widening of root systems. This could demonstrate a shift in resource priority, where, as plants become less limited by water availability, root systems may prioritize lateral growth to increase nutrient foraging (Lynch, 2005) and to anchor larger aboveground plants (Gilman, 1990; Dupuy et al., 2007).

Woody and herbaceous plants’ root systems exhibit widths that are more than twice their shoot widths on average ($S: R_x$ values of 0.44 and 0.45, respectively). Our results are consistent with the literature review by Schwarz et al. (2010), who found that the lateral radius of tree roots is typically one to three times the shoot radius. The greater widths reached by plants belowground contradicts the common misconception that the width of root systems mirrors the width of shoots (Day et al., 2010; Sinclair et al., 2017). For example, a whole-tree harvest study found that, unlike the tightly packed crowns of forest trees, roots overlap greatly with their neighbors, resulting in root system radii being twice that of crown radii (Sinacore et al., 2017). We postulate that $S: R_x$ may display plasticity across other resource and competition gradients, such as nutrients belowground (Lynch, 2005), light aboveground (Takenaka, 1994; Cermák et al., 1998; Viellefont et al., 2010), or increased competition with neighboring plants (Schenk et al., 1999; Schenk, 2006; Cahill et al., 2010; Lepik et al., 2021).
Whereas woody plants growing in more arid climates had deeper, narrower root systems than woody plants in humid climates did, herbs—wher forbs and grasses—did not show the same trend. Herb root systems may rely on other trait-based strategies to cope with resource stress (Roumet et al., 2016; Freschet et al., 2018; Wang et al., 2020), such as going dormant or shedding fine roots during the dry season (Eissenstat & Yanai, 1997), increasing root density to avoid dehydration (Norton et al., 2016; Singh et al., 2020), and optimizing for fast resource uptake by having a high specific root length (Roumet et al., 2006). However, we did find that herbs occupy much more space belowground compared with aboveground (Fig. 7), which could be part of a stress or disturbance-copying strategy (Singh et al., 2020).

Are we underestimating plant rooting depth?

The RPGE dataset has been a primary source of rooting depth data used by many Earth system models, usually incorporated to parameterize biome-level or PFT rooting depth distributions (Schenk & Jackson, 2002b, 2005; Warren et al., 2015). For example, the US Department of Energy’s ELM uses the RPGE to inform its PFT maximum rooting depth, a static parameter, with the exception that tropical tree PFT maximum rooting depths were set to 3 m based on expert opinion (Fig. S2; Drewniak, 2019), considerably deeper than the RPGE estimates. Across several biomes, our analysis found that RSIP rooting depths averaged by growth form were much deeper than the RPGE biome-level estimates (Fig. 8). This is especially true for biomes with high seasonality and deeply rooted woody plants, such as tropical, Mediterranean, xeric, and forested biomes (Fig. 8).

Comparing RSIP Dr values with the RPGE, we found that D50 was very sensitive to changes in temperature, whereas individual plant maximum rooting depth Dr was slightly more sensitive to climate parameters than D50 was (Fig. S3). The correlations between climate and estimates of rooting depths are important because the estimates are generally used to characterize entire biomes or PFTs without considering environmental changes within biomes. Furthermore, studies have shown that terrestrial-biosphere models are sensitive to changes in plant rooting depth, leading to significant global variations in gross primary productivity, evapotranspiration, nitrogen uptake, and more—suggesting a more accurate and dynamic approach to modeling the size of plant root systems is needed (Kleidon & Heimann, 1998; Warren et al., 2015; McCormack et al., 2017; Drewniak, 2019). Based on our findings, we suggest the following: rooting depth distribution should be modelled dynamically, by accounting for resource availability and plant optimality, as suggested in previous studies (Schenk, 2008b; Drewniak, 2019), and that the RSIP Dr data could be used to parameterize maximum rooting depth across PFTs, whereas the RPGE D50 could inform the relative distribution of roots within the vertical soil column.

Significance and pitfalls

Our study provides a global synthesis of maximum plant extents and dimensions and shows that the lateral spread of root systems covaries strongly with aboveground plant size, whereas rooting depth is much more influenced by temperature and climate seasonality. As suggested by Tumber-Dávila & Malhotra (2020), in addition to climate variables, future studies should also focus on root system characteristics across resource gradients. Future studies could also characterize plant volumes above and belowground more explicitly. There are additional environmental constraints on root systems that should be investigated, such as the temporal or vertical availability of plant-accessible water and plant–soil interactions that we were unable to accurately test at the global scale, leaving a need for additional studies at the ecosystem or individual plant scales (Brantley et al., 2017; Erkten et al., 2018).

We present novel findings on relationships of plant size and shape above and belowground, and across the climate spectrum. Given that aboveground plant size is a major axis of variation in the global spectrum of plant form and function (Díaz et al., 2016; Joswig et al., 2022) and that our results characterized strong links between above-and belowground plant size, our analysis and the RSIP can contribute to an improved understanding of plant size trade-offs above and belowground. Better predicting these trade-offs would have far-reaching consequences for understanding nutrient, water, and carbon cycling of ecosystems.

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Author contributions

SJT-D wrote the manuscript with critical input and revisions from RBJ, HJS and ED. All authors contributed significantly to the design of the study and the analyses. HJS and RBJ created the original RSIP database that the study builds upon.

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Data availability

The RSIP can be found as Dataset S1. The RPGE data (Schenk & Jackson, 2003) are openly available in the ORNL DAAC at https://doi.org/10.3334/ORNLDAAC/660.

References


### Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Dataset S1** Root systems of individual plants database.

**Fig. S1** Map of Root Systems of Individual Plants Database (RSIP) observations by versions.

**Fig. S2** Comparison of Root Profiles for Global Ecosystems (RPGE) rooting depth estimates to the plant functional type (PFT) estimates.

**Fig. S3** The effect that climate variables have on individual plant rooting depth vs ecosystem-scale rooting depth.

**Fig. S4** PIC of maximum rooting depth ($D_R$) to aboveground plant size ($H_S$, $W_S$, $V_S$, and DBH).

**Fig. S5** PIC of maximum lateral spread ($L_R$) to aboveground plant size ($H_S$, $W_S$, $V_S$, and DBH).

**Fig. S6** The influence of climate metrics on max rooting depth ($D_R$) and maximum lateral spread ($L_R$).

**Fig. S7** PIC of maximum rooting depth ($D_R$) to climate metrics (MAE, MAP, $A_i$ and $S_i$).

**Fig. S8** PIC of maximum lateral spread ($L_R$) to climate metrics (MAE, MAP, $A_i$ and $S_i$).

**Fig. S9** Correlation matrix for the above and belowground plant size metrics.

**Table S1** Description of RSIP parameters ($n$ is the total number of observations).

**Table S2** RSIP categorical groups. The number of total observations $n$, and unique species, geographic locations, and studies for each class are shown.

**Table S3** Pagel’s lambda values for the above and belowground plant measurements.

**Table S4** Comparison of absolute extents ($D_R$ and $L_R$) with climate metrics.

**Table S5** Nonlinear regression curves for the shape ratios plotted in Fig. 7.

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### Appendix A1

#### Citations used in the database


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