Fractal dimension of tree crowns explains species functional-trait responses to urban environments at different scales

Georgios Arseniou 🔳 and David W. MacFarlane[1]

Department of Forestry, Michigan State University, East Lansing, Michigan 48824 USA

Abstract. The evolution of form and function of trees of diverse species has taken place over hundreds of millions of years, while urban environments are relatively new on an evolutionary time scale, representing a novel set of environmental constraints for trees to respond to. It is important to understand how trees of different species, planted in these anthropogenically-structured urban ecosystems, are responding to them. Many theories have been advanced to understand tree form and function, including several that suggest the fractal-like geometry of trees is a direct reflection of inherent and plastic morphological and physiological traits that govern tree growth and survival. In this research, we analyzed the "fractal dimension" of thousands of tree crowns of many different tree species, growing in different urban environments across the United States, to learn more about the nature of trees and their responses to urban environments at different scales. Our results provide new insights regarding how tree crown fractal dimension relates to balances between hydraulic- and light-capture-related functions (e.g., drought and shade tolerance). Our findings indicate that trees exhibit reduced crown fractal dimension primarily to reduce water loss in hotter cities. More specifically, the intrinsic drought tolerance of the studied species arises from lower surface to volume ratios at both whole-crown and leaf scales, preadapting them to drought stress in urban ecosystems. Needle-leaved species showed a clear trade-off between optimizing the fractal dimension of their crowns for drought vs. shade tolerance. Broad-leaved species showed a fractal crown architecture that responded principally to inherent drought tolerance. Adjusting for the temperature of cities and intrinsic species effects, the fractal dimension of tree crowns was lower in more heavily urbanized areas (with greater paved area or buildings) and due to crowns conflicting with utility wires. With expectations for more urbanization and generally hotter future climates, worldwide, our results add new insights into the physiological ecology of trees in urban environments, which may help humans to provide more hospitable habitats for trees in urbanized areas and to make better decisions about tree selection in urban forest management.

Key words: fractal dimension; functional traits; tree physiology; urban ecology.

Introduction

Tree species have inherent traits that constrain their form and function, but these traits are also plastic to some degree (Weiner 2004), to allow them to survive and reproduce in different types of environments. On an evolutionary timescale, urban environments are new and represent a novel set of environmental constraints for trees to respond to. While features like tall buildings or pavement may have natural analogs, like canyons or natural rock concretions, urban trees often experience very different life histories than their rural counterparts. Urban trees are often planted, rather than naturally germinated, and usually have fewer tree neighbors, unlike trees growing in natural forests, and the number of

neighbors of a tree has been shown to affect light availability and wind resistance (MacFarlane and Kane 2017). In urban areas, there are many factors that negatively affect tree growth: e.g., pollutants, compacted soil, barriers to roots due to paving and asphalt, and intensive pruning (Moran 1984, McHale et al. 2009, Troxel et al. 2013, Ferrini et al. 2014). On the other hand, urban areas may supply larger availability of nutrients, warmer temperatures and increased carbon dioxide emissions, factors that usually enhance tree growth, and the net effect of all these factors combined is not well known (Gregg et al. 2003). Such differences between urban and natural environments make urban environments novel places to study the plasticity of tree species traits.

Many "fractal"-based theories have been advanced to understand tree form and function (e.g., pipe-model theory [Valentine 1985, Mäkelä and Valentine 2006], metabolic scaling theory [West et al. 1997]). These theories suggest that the fractal-like geometry of trees is a direct

reflection of both inherent and plastic morphological and physiological traits that govern tree growth and survival. Indeed, there has been a rapid increase in the use of fractal methodologies to study organismal, population and even landscape-level ecological phenomena (Halley et al. 2004). In the case of trees, fractal geometry (Mandelbrot 1983) provides a unique way to explore the structural complexity of tree crowns (Seidel 2018).

Crowns may be the ideal unit to study, for understanding tree species functional-trait responses to environments. Crowns contain the leaves and branches, thus connecting key theories that unify our understanding of commonalties and differences in tree function. Among major theories, the "worldwide leaf economics spectrum" (Wright et al. 2004) suggests that tree species leaf traits are part of a continuum from fast to slow responses to investments of energy and nutrients in leaves, and the WBE theory (West et al. 1997) theorizes that plant vascular networks are "space-filling" fractal networks of branches.

In theory, tree branches are fractal-like or self-similar across different scales (Noordwijk and Mulia 2002). Self-similarity in branching implies that any branching point looks the same whether we observe the first or the last tree branching point. However, self-similarity of branches does not hold true across all levels of a tree branching hierarchy (Malhi et al. 2018) and the departure of real tree branches from perfect symmetry has significant implications for tree hydraulic properties, mechanical stability, photosynthesis, and metabolic scaling (Smith et al. 2014). Therefore, it is important to understand what ecological factors influence the "realized" fractal dimension of trees.

Modern, urban environments can affect the expression of a tree's fractal dimension. In particular, the lower number, or complete lack, of tree neighbors in urban environments, typically gives them an open growth form, which might better allow them to express their inherent fractal branching architecture, which should be otherwise expected to be disrupted when shaded or crowded by other trees (Mäkelä and Sievänen 1992, MacFarlane et al. 2014). In this sense, studying the fractal dimension of tree crowns in urban ecosystems might reveal a purer signal of species functional-trait responses to environmental stimuli, than might be detected in the presence of tree-to-tree competition. On the other hand, anthropogenic stressors (e.g., pruning) and structures (e.g., buildings) may have major impacts on tree growth and metabolism, which manifest in a different fractal architecture for the tree.

Our study provides an understanding of how the regional- and local-scale growing environments of urban trees affect their fractal architecture, which has important management implications. We expect that the growing environment of an urban tree affects its socioecological benefits (e.g., shading) by affecting its crown architecture and, by studying this, we can inform arborists about how to better manage urban forests for optimizing their benefits.

We analyzed the fractal dimension of tree crowns of many different tree species, growing in different urban environments, across the United States, to learn more about their responses to urban environments at different scales. Our major questions were the following: (1) How does the fractal dimension of urban tree crowns reflect their life-form and life-history traits, as members of different species? (2) How do crown fractional-dimensional traits, expressed at the tree level, relate to functional traits at the leaf level? (3) How does the fractal dimension of the crowns of communities of urban trees of many species vary between cities in different climatic regions? (4) What is the effect of the local growing environment within cities (e.g., urban land use) on the fractal dimension of tree crowns?

We hypothesized that the life-history functional traits (i.e., drought and shade tolerance), of different tree species with different leaf types (i.e., needle-leaved and broad-leaved), relate to the fractal dimension of their crowns. Species with higher drought tolerance should have lower fractal dimension in order to minimize heat gain and water loss through transpiration. A positive relationship is expected between the fractal dimension of tree crowns and their shade tolerance (Zeide and Pfeifer 1991). Furthermore, we expected that drought-tolerant species with higher leaf mass per unit area to have lower crown fractal dimension, in order to prevent excessive water loss through transpiration.

The fractal dimension of the crowns of trees in urban forest communities should be affected by the climatic conditions of the cities in different regions, such as atmospheric drought responses, but should also be affected by the local growing environment within cities. Urban land use must be an important factor, and more specifically, we expected that less developed areas (e.g., parks, vacant lots) would have a positive effect on the fractal dimensionality of urban trees. We expected that tree crowns close to buildings should have lower fractal dimension, because buildings restrict tree crown expansion. Finally, we expected a negative effect of urban infrastructure (utility wires, in particular) on the fractal dimension of urban tree crowns, due to the pruning treatments enacted to reduce tree conflicts with urban structures.

MATERIALS AND METHODS

Urban tree data

The main source of data for this study was an extensive, publicly-available, urban tree data set, published by McPherson et al. (2016). To produce this data set, the United States was divided into 16 climatic zones and a reference city was selected within each zone. About 20 of the most abundant species were selected within each reference city. Trees were chosen based on a stratified random sampling design; approximately 5–10 trees of each species were randomly sampled within nine classes of

stem diameter at breast height (DBH) (McPherson et al. 2016). Typical tree measurements were taken (e.g., DBH, total tree height, crown width), along with many other variables that helped describe each tree's growing environment within cities (e.g., distance from a building, land-use). However, the key aspect of the data that allowed for this study was that the data had independent measurements of leaf area and crown volume, which allowed for estimation of the fractal dimension of the crown of every tree (explained below). Leaf area was estimated for every tree using a novel photographic method developed by Peper and McPherson (2003), and crown volume was estimated from individual measurements of crown dimensions and a geometric shape (e.g., cone, parabola) being assigned to each crown (McPherson et al. 2016). In total, we used data from 11,038 trees, of 80 species (66 broad-leaved species and 14 needle-leaved species), in 15 climatic regions, available for analysis from this database (see Appendices S1 and S2).

We obtained regional scale climatic data (e.g., mean annual temperature) for different cities from U.S. Climate Data to characterize the climatic region that the trees were growing in, in terms of mean annual precipitation (MAP) and mean annual temperature (MAT; data *available online*).[2] We used cooling degree days (CDD), which is the number of degrees that a day's average temperature is above 18.5°C, summed over 1 yr, as a third measure of the city's climate, following McPherson et al. (2016), who considered CCD because it is used to quantify the demand for energy needed to cool buildings and relevant to the role of urban trees in cooling the environment of cities.

From the McPherson et al. (2016) data, we selected three variables to account for the effect of local urban growing environments, within cities, which we hypothesized would affect tree crowns. The first was the distance of a tree from the nearest heated or air-conditioned building, a factor that had four levels: 1, 0–8 m; 2, 8.1–12 m; 3, 12.1–18 m, 4, ≥18.1 m. The second was crown conflicts with utility wires, where 0 indicates no wires are present in or around the crown and 1 indicates that wires are present (this variable was rescaled to have only two levels based on the original factor levels from McPherson et al. 2016). The third factor was urban land use, which had four levels: 1, single and multi-family residential; 2, industrial, institutional, and large or small commercial areas; 3, park, vacant, and other areas, e.g., agricultural; 4, transportation corridor (this variable was rescaled to have these four levels based on the original factor levels from McPherson et al. 2016).

Measuring the fractal dimension of tree crowns

There is some ambiguity in quantifying the fractal dimension of trees. Halley et al. (2004) noted that applying fractal values to natural objects is, in general,

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[2] https://www.usclimatedata.com/climate/united-states/us

dependent on the method used. Even Mandelbrot (1983), who is credited with articulating fractal geometry, warned against the underlying ambiguity of a precise mathematical interpretation of fractal dimension (Halley et al. 2004). Due to this ambiguity, one can use different methods for quantifying fractal dimension. For example, the 'path-fraction' metric quantifies to what extent a branch network differs from an ideally self-similar branch network and it ranges between 0 and 1 (Smith et al. 2014). The 'box-dimension' metric quantifies the structural complexity of trees based on fractal analysis derived from laser scanning of the three-dimensional structure of the tree; it takes values between 1 and 3 (Seidel 2018).

In this study, the fractal dimension of the urban trees was estimated using a variant of the 'two-surface' method (Zeide and Gresham 1991, Zeide and Pfeifer 1991, Zeide 1998). The two-surface-method assumes that the fractal dimension of a tree's crown can be derived from the relationship between the total leaf area of a tree and the surface area of the convex hull that covers the crown, but also has a variant that uses crown volume instead of crown area (Zeide and Pfeifer 1991). The fractal dimension of a tree crown based on the latter method refers to the distribution of leaf surface area within a crown volume occupied by the leaves and branches.

Due to the irregular distribution of "holes" in a tree's crown volume (empty spaces within the crown volume), a crown cannot be simply treated as a two-dimensional surface or a three-dimensional solid (Zeide 1998). Instead, it has a fractal dimension (unlike a Euclidean dimension) that exceeds its corresponding topological dimension (Zeide and Gresham 1991). This measure of fractal dimension takes values between 2 and 3. Fractal dimension equal to 2 means that the foliage is distributed on the crown's periphery and the crown surface is a classic, flat Euclidean surface. As the fractal dimension increases (i.e., fractal dimension >2), the crown surface becomes more fractal until the fractal dimension is equal to 3, when the foliar surface is evenly distributed within a given crown volume (Zeide and Gresham 1991, Zeide and Pfeifer 1991).

The model (from Zeide and Pfeifer 1991) to estimate the fractal dimension of urban tree crowns is a power function

$$\mathrm{LA} = a * Cvol^{\frac{D}{3}} + \varepsilon, \qquad (1)$$

where LA and Cvol are the leaf area and the crown volume of the trees, D is the fractal dimension of tree crowns, and ϵ is the error term of the model. The normalization constant a corresponds to the overall leaf density, i.e., leaf area per unit crown volume (Zeide 1998), with D describing how leaf-area–crown-volume relationships change with increasing crown volume.

To help visualize the meaning of D in this context, Fig. 1 shows a regression line relating LA to Cvol on a log-log scale, fitted to all 11,038 trees, along with other,

hypothetical lines representing two theoretical values of D at the same a value. On a log-log scale, the slope of the line (D) shows the level of exponential increase in leaf area of a crown of a given volume. We can see (in Fig. 1) a high degree of variation from tree to tree in terms of LA at a given Cvol, with the underlying trend of $D = 2.27$ indicating a trend of leaf surface area more likely to be concentrated toward the periphery of the crown.

An important assumption of the method is that the relationship between LA and Cvol is linear on the logarithmic scale, with no significant inflection points (Zeide and Pfeifer 1991). A second-order polynomial regression that predicted leaf area from crown volume on the logarithmic scale was fitted to the data and it was found that the second-order term was not statistically significant ($P = 0.1049$; $\alpha = 0.05$). Only the coefficient of the crown volume to the first power was statistically significant (shown in Fig. 1), which enabled us to validate the assumption and use the method for our study population.

Species functional trait data

We expected tree-to-tree variation in D to indicate physiological performance at the whole-tree level, in terms of light energy capture and water-use efficiency, so we determined a shade- and drought-tolerance value for each tree, based on the work of Niinemets and
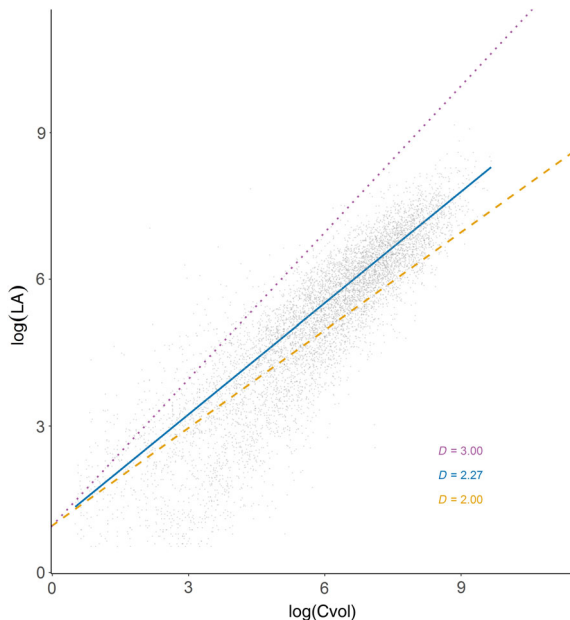

FIG. 1. The linear relationship between log(LA) and log(Cvol) for all trees in this study (blue solid line), based on log-linear regression of Eq. 1 and two theoretical lines for $D = 2$ (orange, dashed line) and $D = 3$ (purple, dotted line), respectively, holding coefficient a (in Eq. 1) at the same value estimated from the regression. LA and Cvol are the leaf area (m^2) and the crown volume (m^3) of the trees; D is the fractal dimension of tree crowns.

Valladares (2006), who produced numerical tolerance indices, ranging from 1 to 5, for 806 woody species in the temperate Northern Hemisphere (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant). We also determined the leaf mass per unit area (LMA) for the study trees, which has been linked to physiological performance of plants at the leaf level, in terms of photosynthetic and water-use efficiency (Roderick et al. 2000). LMA values were assigned to species based on publicly available data produced from the work of Wright et al. (2004, the GLOPNET data set) for as many study tree species that data were available (see Appendix S1).

Statistical analyses

All statistical analyses for this study were done with custom coding and available packages written in the R software language (R Core Team 2015).

We used a hierarchical, mixed-effects, modeling approach, where fixed-effects coefficients were estimated using Eq. 1, and all categorical variables related to the effects of species, climatic region, and local urban growing environment on the fractal dimension were treated as random (grouping) effects; these random effects were included to help explain variation in the overall trend (Fig. 1). We looked at each of the major factors, species, climatic region, and local environment, individually, and then at various combinations of models, all of which predicted leaf area as a power function of crown volume (Eq. 1). Thus, the mixed-effects version of Eq. 1 is written as

$$LA = a \times Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon, \qquad (2)$$

where S, R, and L are random effects that modify the coefficient D estimated for all urban trees, depending on their species, region, and local urban environment, respectively. The coefficient a (the intercept) varies in all models, but it is not modified by any random effect. The random effect of species (S) has 80 levels (i.e., 80 different species), given in Appendix S1. The random effect of climatic region (R) has 15 levels, given in Appendix S2. It is important to note that the experimental design (of McPherson et al. 2016) selected only one city to represent each climatic region, so the effects of different climatic regions are confounded with the effects of the reference city itself. Within-city local environmental effects (L) were described under *Urban tree data,* above.

When fitting models, assumptions of variance homoscedasticity and error normality were checked by plotting the model residuals against the fitted values, and the Q-Q plots and the histograms of the model residuals. Eqs. 1 and 2 assumed a multiplicative error structure, which is additive on a log-log scale. The best model was selected considering both the coefficient of determination (adjusted R^2) and the Akaike Information Criterion (AIC). All relationships were quantified with

the Pearson correlation coefficient and the significant relationships were evaluated at α = 5% level of significance.

After the best-fit model (Eq. 2) was developed, the fractal dimension (*D*) of urban tree crowns was determined for trees (based on their species, region, and local environment) and related to drought and shade tolerance and LMA. The Standardized Major Axis Tests and the Routines R package (Warton et al. 2012) was used to conduct hypothesis tests regarding the slopes of the subpopulation (*S*, *R*, or *L*) regression lines. Since crown and leaf traits are typically different between needle-leaved and broad-leaved tree species, we also refit some of the models to only trees of these "leaf types" (Appendix S1), in addition to fitting the models to all trees.

Quantile regressions were also used in order to examine relationships at different quantiles of crown fractal dimension. The quantile regression is based on the minimization of the sum of the absolute values of the model residuals and it is very robust against outliers (Niinemets and Valladares 2006, Pretzsch et al. 2015).

RESULTS

Influence of species, regional and local environments on variation in fractal dimension

The coefficients of the fixed and random effects of all models fitted to the data (listed in Table 1) can be found in Appendix S3. Species exhibited an important influence on the fractal dimension (*D*) of urban trees and the model with species effects was superior to the corresponding fixed-effects-only model (Table 1). The climatic region of the cities the trees were growing in was also an important variable influencing the *D* of trees and explained a slightly larger proportion of the variation than species. Together, species and region explained slightly more variation than either by themselves (Table 1). Local effects of the urban environment further helped explain an individual tree's fractal dimension. The model with all three local effects included

(Dist.build/Wire.Conf/Land.Use, in addition to Species and Region, Table 1) explained the most variation in *D* and had the lowest AIC. This latter model predicts an individual *D* for each tree depending on its species, region, and the three local environments within the city it's growing in.

Species and leaf type effects on D: drought and shade tolerance and LMA

Across all trees, the mean *D* was estimated to be 2.277 (see Table 2 and Fig. 1), with needle-leaved species (2.147) having a lower average *D* than broad-leaved species (2.290). There was also a greater variability in the estimated *D* for needle-leaved species, though there were many more broad-leaved species in the sample population. Each of the three models (all trees, broad-leaved only, and needle-leaved only) also had a different estimated minimum and maximum *D* for the species included in the model (Table 2), which represents the smallest and largest estimated divergence of a species in that group from the mean trend.

We hypothesized that the species with higher drought tolerance would have lower fractal dimensionality. When we examined this, the average D for trees of a species was found to be significantly negatively correlated with the drought tolerance of the species ($r = -0.46$, $P = 0.00$, Fig. 2), across all cities and locations within cities. The negative relationship between *D* and drought tolerance was stronger for needle-leaved species ($r = -0.74$, $P = 0.0027$), than for broad-leaved species ($r = -0.47$, $P = 0.0000$), such that needle-leaved species had a much lower *D* at higher drought tolerance levels (Fig. 2).

The quantile regression for *D* predicted from drought tolerance indicated that species with lower drought tolerance are more elastic in their fractal dimension, meaning a wider range of *D* values at the same drought tolerance level, whereas species with higher drought tolerance had a smaller range of *D* values (Fig. 3). For all quantiles of *D*, the relationship between *D* and drought tolerance

TABLE 1. Candidate models for Eq. 2 including species (*S*), regional (*R*), or local (*L*) random effects influencing the fractal dimension (*D*), with the fixed-effects model, including none of these variables.

Model	Model form	Adjusted R^2	AIC values
Fixed-effects only (Eq. 1)	$LA = a \times Cvol^{(D/3)} + \epsilon$	0.678	113,847
Species (Eq. 2 with *S* only)	$LA = a \times Cvol^{(D + S/3)} + \epsilon$	0.734	112,592
Region (Eq. 2 with *R* only)	$LA = a \times Cvol^{(D + R/3)} + \epsilon$	0.752	111,853
Species/region (Eq. 2 with *S* and *R*)	$LA = a \times Cvol^{(D + S + R/3)} + \epsilon$	0.796	110,864
Species/Region/Land Use (Eq. 2 with *S*, *R*, and *L*)	$LA = a \times Cvol^{(D + S + R + L/3)} + \epsilon$	0.807	99,406
Species/Region/Dist. Build. (Eq. 2 with *S*, *R*, and *L*)	$LA = a \times Cvol^{(D + S + R + L/3)} + \epsilon$	0.820	97,873
Species/Region/Wire Conf. (Eq. 2 with *S*, *R*, and *L*)	$LA = a \times Cvol^{(D + S + R + L/3)} + \epsilon$	0.808	93,805
Species/Region/Dist. Build./Wire Conf./Land Use (Eq. 2 with *S*, *R*, and *L*)	$LA = a \times Cvol^{(D + S + R + L/3)} + \epsilon$	**0.841**	**71,963**

Notes: Nested models are characterized by a "/", e.g., Species/Region/Land Use, meaning a tree was of a specific species, growing in a certain region in a certain land use within that city; distance from buildings (Dist. Build.), conflicts with wires (Wire Conf.), and land-use (Land Use). Models are sorted by AIC. Statistics for the best model are shown in boldface type.

TABLE 2. Estimated fractal dimension of tree crowns (coefficient D) from Eq. 2, with species-random effects, fitted for all trees and for broad- and needle-leaved trees, separately.

Tree type	No. species	D.mean	D.mean SE	D.min	D.max
All trees	80	2.277	0.021	2.092	2.719
Broad-Leaved	66	2.290	0.022	2.124	2.487
Needle-Leaved	14	2.147	0.088	1.843	2.588

Notes: The minimum and maximum D value, respectively, come from adding the largest and smallest (most negative) species-random effect to D.mean.
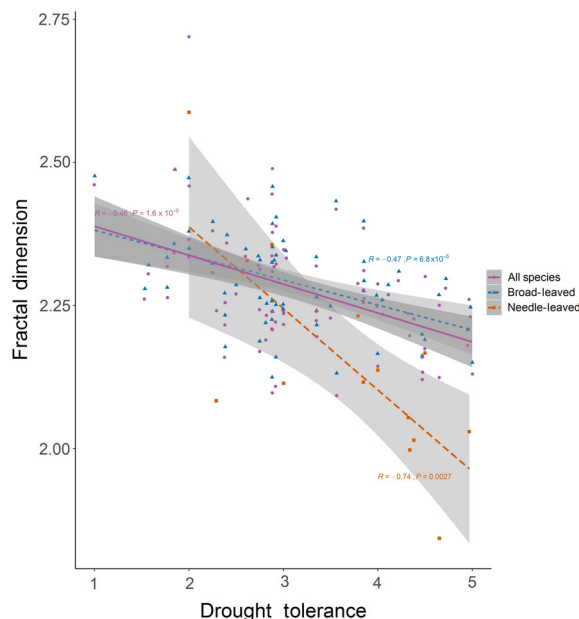

FIG. 2. Mean fractal dimension of tree crowns for species as a function of species-specific drought tolerance (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant). Data was fitted to Eq. 2 with S only as a random effect (see Table 1).

was negative and the strongest relationship was observed for the species at the highest quantile of D.

A positive relationship was also found between D and the shade tolerance of urban trees ($r = 0.22$, $P = 0.05$, Fig. 4), though the relationship was much weaker than that found for drought tolerance. When separating out needle- vs. broad-leaved species, a strong positive relationship was found between D and shade tolerance of urban needle-leaved trees ($r = 0.84$, $P = 0.00$, Fig. 4). However, no significant relationship was found between D and shade tolerance of urban broadleaved trees ($r = 0.1$, $P = 0.41$, Fig. 4). Quantile regressions showed no clear pattern of elasticity in D relative to shade tolerance.

A negative relationship was found between D and the LMA of the urban trees ($r = -0.5$, $P = 0.0008$, Fig. 5). Needle-leaved trees showed a stronger relationship
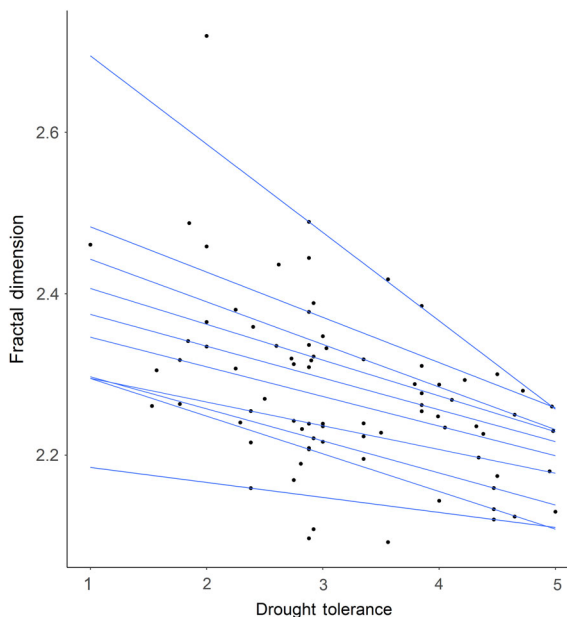

FIG. 3. Quantile regressions for fractal dimension vs. drought tolerance (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant) at species level for 10 quantiles of D (i.e., from bottom to top 5%, 15%, 25%, 35%, 45%, 55%, 65%, 75%, 85%, 95%). The line of the 5% quantile is a nonsignificant regression. Fractal dimension was estimated from Eq. 2 with S only as a random effect (see Table 1).

($r = -0.82$, $P = 0.046$, Fig. 5) than the corresponding relationship for broadleaved trees ($r = -0.41$, $P = 0.012$, Fig. 5). Quantile regressions showed no discernable difference in the elasticity of D at low vs. high LMA.

Regional climatic effects on fractal dimension

To examine the effects of climatic region on D, we computed the mean D for all trees of all species in each city-region and then regressed those values against key climatic variables describing each region (Appendix S2). We found D to be strongly related to the mean annual temperature (MAT) of the climatic regions ($r = -0.58$, $P = 0.024$, Fig. 6). The relationship was negative, indicating that trees of a wide variety of species exhibited lower fractal dimensions, when growing in a city with a hotter climate. There was a similar negative relationship between the average D of trees and the cooling degree days (CDD) of each climatic region ($r = -0.51$, $P = 0.05$). MAP was not significantly correlated with tree average D.

Influence of local urban environments on fractal dimension

The local urban environmental effects (L in Eq. 2) on the fractal dimension of tree crowns were interpreted by looking at the sign of the coefficients influencing D (see Appendix S3 for full details). Trees that were in the first
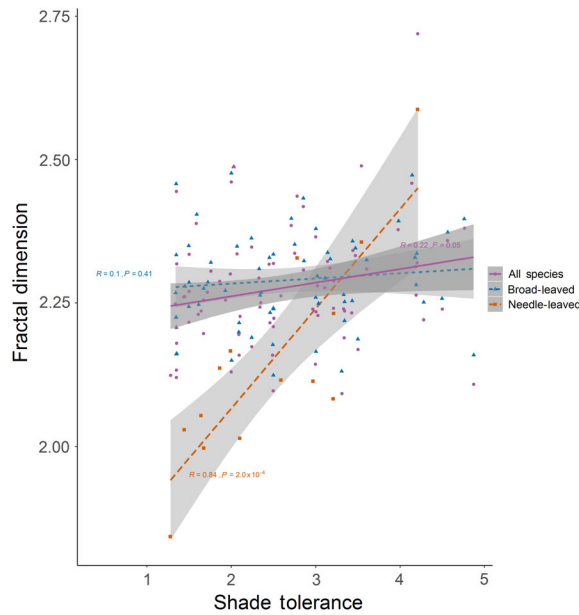
FIG. 4. Mean fractal dimension of tree crowns for species as a function of species-specific shade tolerance (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant). Data was fitted to Eq. 2 with S only as a random effect (see Table 1).
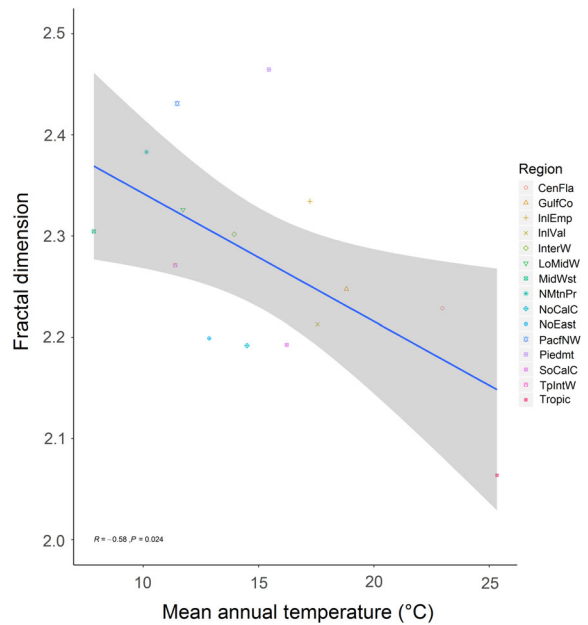

FIG. 6. Mean fractal dimension of tree crowns in a region plotted against the mean annual temperature (MAT) for that region (the abbreviated names of the regions are explained in Appendix S2). Data were fitted to Eq. 2 with R only as a random effect (see Table 1).
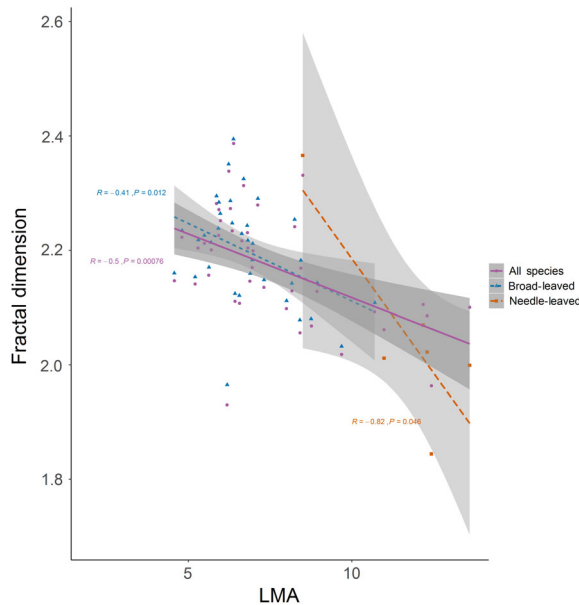

FIG. 5. Mean fractal dimension of tree crowns for species as a function of species-specific leaf mass per unit area (LMA). Data was fitted to Eq. 2 with S only as a random effect (see Table 1).

level of the Dist. Build. factor (0–8 m distance from a building) exhibited a lower D (L has a negative effect on D), controlling for species and region. The effect was positive in the other three classes (>8 m away), which indicates that being relatively close to a building generally lowers a tree's fractal dimension. Trees that had conflicts with utility wires had lower-than-average D values, and higher-than-average values when no wires were present. Land use within a city showed positive effects on D when trees were growing in single and multi-family residential land uses, or in parks, vacant lots, and other areas. The other two land-use categories (industrial, institutional, and large or small commercial areas and transportation corridors) exhibited a negative effect on D.

DISCUSSION

Drought and shade tolerance in crown and leaf fractal dimensions of different species

A major finding of this study is that both the drought and shade tolerance of different species relates to the fractal dimension of their crowns. This indicates that species-specific crown architecture is part of an evolutionary strategy associated with tolerance of key environmental stressors, namely too much energy in the form of heat (causing water losses), or not enough energy due to shade. Niinemets and Valladares (2006) noted that trees may not have the morphological and physiological characteristics that allow simultaneous tolerance to several environmental stresses and found negative correlations between the drought and shade tolerance values for different species.

There appeared to be a clear trade-off for the needle-leaved species we examined, with higher D for shade-tolerant species and lower D for drought-tolerant trees, while the D of broad-leaved species appeared only to be influenced by species-specific drought tolerance. This suggests that urban trees, across the diverse city-regions we examined in the United States, are adapting the dimensionality of their crowns to minimize heat gain or water loss, but inherent shade tolerance is having a smaller influence. This result makes sense, given that lower tree densities in urban areas make trees less likely to be shaded by other trees (McHale et al. 2009, MacFarlane and Kane 2017), but more likely to experience drought (Close et al. 1996), than their (rural) forest-growing counterparts.

Our results provide new insights regarding how the fractal architecture of trees relates to balances between hydraulics and light capture (also noted by Smith et al. 2014). Mäkelä and Valentine (2006) suggested that deviations from the WBE fractal-scaling model for trees, arise from the senescence of twigs inside the crown, as foliage expands toward the surface, where light can be more readily captured, leading to empty space in the interior of crown volume. This suggests that shade from neighboring trees and shade from one's own leaves (self-shading) should influence D, such that shade tolerance should be an important species characteristic determining D. A study by Zeide and Pfeifer (1991) also suggested a positive relationship between D and shade tolerance for coniferous species, which we also found here, but their study was before the advent of the numerical shade-tolerance scale we employed here and a directly comparable numerical scale of drought tolerance (compliments of Niinemets and Valladares 2006).

Our results suggest that, for trees growing in urban environments, with fewer tree neighbors to cast shade, differences in D might be better explained by hydraulic limitations, because both broad- and needle-leaved trees showed a negative response in D to drought tolerance. It is possible that these results could also apply to open-grown trees in general, where only tolerance to self-shading would be an issue, unlike in a natural forest, where shelf-shading is confounded with shading from other trees.

Zeide and Gresham's (1991) method of estimating D should produce values bounded between 2 and 3 (see Fig. 1), so it was notable that our model predicted a value <2 for one species, *Juniperus virginiana* ($D = 1.843$, Table 2), a species with very high drought tolerance (4.65 out of a maximum of 5). This "out-of-bounds" value likely reflects statistical uncertainty in this method of estimating D (Zeide 1998), which reflects uncertainty from both the method used to estimate tree leaf area and the method used to estimate crown volume, as well as model error. Seidel (2018) recently proposed a direct method to estimate D for trees, using terrestrial laser-scanning technology, but this method shows values consistently lower than $D = 2$. However, Seidel's method (applied to forest-grown trees) also includes the tree's trunk below the crown, and it has been noted that trunk length does not scale with crown fractal dimensions (Mäkelä and Valentine 2006). Nonetheless, Zeide and Gresham's (1991) method of estimated D proved a highly useful index of comparison in this study. It allowed us to quantify functional relationships between crown architecture and stress tolerance for a variety of tree species.

One of the most interesting features of fractals is that the patterns reproduce themselves at different scales (Mandelbrot 1983). While we understand that trees are not truly fractals, it was interesting that our results showed a similar, negative relationship between D and LMA, to that observed between D and drought resistance. We know that LMA is proportional to the inverse of leaf surface to volume ratio (Roderick et al. 2000), so a lower D at the crown level could be a direct consequence of a higher LMA at the leaf level. Further analysis revealed a positive relationship between the drought tolerance of tree species and LMA ($r = 0.67$, $P < 0.0001$), which were estimated independently from each other (Niinemets and Valladares 2006, Wright et al. 2004, respectively) in this study. Lower LMA implies thinner and larger leaves, which transpire more easily than smaller or thicker leaves as their local temperature increases, increasing water loss (Pallardy 2008). Conversely, higher LMA is associated with thicker leaf blades and smaller cells with thicker walls, which allow leaves to continue functioning in arid and semiarid regions (Wright et al. 2004).

Our analysis also revealed a negative relationship between shade tolerance of all tree species and LMA ($r = -0.43$, $P = 0.0045$), which may explain the positive relationship that was found between D and species shade tolerance ($r = 0.22$, $P = 0.05$). According to Lusk and Warton (2007) and Lusk et al. (2010), a positive relationship is expected between species shade tolerance and LMA. However, Lusk and Warton (2007) concluded that this relationship can change depending on the tree ontogeny and the light environment; they found a negative relationship between shade tolerance and LMA of deciduous saplings. Overall, our results also support the premise that development of a fractal-like crown architecture in urban tree crowns is heavily influenced by water transportation as a limiting factor for photosynthesis (Smith et al. 2014).

We expected greater drought resistance for needle-leaved trees compared to broadleaved trees, given their higher LMA (Wright et al. 2004), as well as a wood anatomy that should increase resistance to drought cavitation (Markesteijn et al. 2011), e.g., thicker walled and shorter water-conducting tracheid elements for needle-leaved species (Sperry et al. 2006, Pallardy 2008). Both a different branching architecture and different branch anatomy may help explain why needle-leaved species showed a strong differentiation in crown D over the range of drought tolerance examined (note the steep

slope in Fig. 2). This idea is supported by a study by Pittermann et al. (2012) who showed that the evolution of drought tolerance within the Cupressaceae family of gymnosperms occurred in response to Cenozoic climate change that favored the evolution of lower xylem-specific conductivity and imbricate needles over a higher xylem-specific conductivity and bilaterally flattened needles; the former conferring greater drought resistance in hotter, arid environments at the expense of growth rate. Our estimates of D at the crown level appeared to capture this divergence; the highest value of D predicted by our three species-group models (Table 2) was $D = 2.719$ for *Sequoia sempervirens*, a species with bilaterally flattened needles that evolved in once humid, warm climates, abundant during the Cretaceous and Paleocene. Whereas the lowest D estimated was for *Juniperus virginiana* (see Table 2). Pittermann et al. (2012) showed that slower-growing, imbricate-leaved *Juniperus spp.* evolved more recently, in response to the advent of cooler, drier woodland/grassland environments of the Eocene.

The strong, opposite trend between D and shade tolerance that we observed for needle-leaved species supports the idea that drought-tolerant, needle-leaved species likely lose significant capacity to tolerate shade, as a result of adopting a crown architecture with a lower D. Niinemets and Valladares (2006) noted that shade-tolerant, drought-intolerant conifers (e.g., trees in the genera *Abies*, *Picea*, or *Tsuga*) are generally species of cool, temperate forests, where growing-season length is similar for deciduous and evergreen species. In natural environments, these needle-leaved species may need a higher D, at the crown level, to capture the necessary light in competition with broad-leaved species, and in accordance with shorter growing seasons at higher latitudes. In the context of our results, this suggests that shade-tolerant, needle-leaved species, may have the highest *intrinsic* vulnerability to relatively droughty urban environments, where urban "heat island" effects and harsh rooting environments are likely influential, and shading from neighboring trees is of much lower importance.

In the sections that follow, we discuss the environmental (extrinsic) effects on D, to contrast with, and further explain the intrinsic effects on D associated with species life history traits, discussed here.

Climatic region influences on crown architecture and management implications

The negative relationship between the average D of all trees within each reference city and the mean annual temperature (MAT) of the reference city reinforces the notion that atmospheric drought responses are driving urban forest crown architecture. Trees of the same species and across all species had a lower D when growing in a hotter city/region. This was also seen in the relationship with CDD. According to McPherson et al. (2016), CCD is used to quantify the demand for energy needed

to cool buildings. So, based on the negative relationship between CDD and D, trees are showing a reduced D in cities where air conditioners are running more.

Climatic regions with higher MAT are typically arid, with a larger vapor pressure deficit that drives water vapor movement from leaf stomata to the atmosphere. Trees growing in hotter regions should reduce their fractal dimension, where possible, in order to minimize transpiration costs; this could be adaptive or simply a consequence of leaf and shoot die back due to stress. In urban areas, when trees are growing with reduced competition from other trees, they may have more flexibility to modify their crown shape to reduce D. We did not find the expected, opposite relationship with MAP (more rain increases D), but it is possible that precipitation is a more variable measure of the drought experienced by trees than MAT, rather than indicating that rainfall levels are not important to tree crown architecture. Nonetheless, the fact that MAP and MAT for the cities (Appendix S2) were essentially uncorrelated ($R^2 = 0.0049$) indicates that the trees we studied were responding to a full range of climatic conditions from cool and dry to warm and wet, but responding mainly to temperature in terms of their D.

Another consideration is that urban forest communities do not undergo natural assembly processes, but rather are the result of anthropogenic structuring (sense Sattler et al. 2010). The above-mentioned negative relationship could be attributed to the tendency of arborists to plant drought-tolerant species in warmer regions. Indeed, the mean drought tolerance of all study trees within each climatic region, was significantly higher in cities with a higher MAT ($r = 0.54$, $P = 0.04$). Further analysis showed that both MAT and mean drought tolerance of trees in a region together explained more variation in mean D than either of them separately (VIF = 1.00 for both variables), indicating that both the nature of trees planted and the climate of the cities influenced D. Taken with the lower elasticity of D relative to drought resistance (Fig. 3), this suggests that there is a limit to how far a tree of a given species can modify its crown architecture to adapt to the conditions of a hotter city, and that arborists are similarly limited in what species they can plant as urban conditions become hotter. This result has important implications for adapting urban forests to global warming.

It is no coincidence that there were many more broad-leaved, deciduous species than needle-leaved, evergreen species in the extensive data base of U.S. city trees that we examined. One of the much-cited benefits of urban trees are the cooling effects of shade provided by broad-leaved trees, who can also provide heat-energy benefits, because they lose their leaves during the cooler, darker winters in the northern hemisphere, letting sunlight through the crown (McPherson et al. 2018). However, the negative relationship that we observed between the fractal dimension of urban trees and the cooling degree days (CDD) suggests that the amount of shade a tree

can cast should be lower in hotter cities (lower D). It appears difficult to build a canopy architecture that can cast a deep shade while also trying to reduce D to reduce water loss. The latter notion could provide insight into the choices of species to be planted for adapting urban ecosystems to climate change. As examples, in regions with arid and warm climates, arborists could select drought-tolerant species with lower D or they could water trees more often in order to maintain their hydraulic balance and develop crowns that can cast deeper shade. The latter implies higher water maintenance costs for managing a higher D for urban tree cover in hotter, drier regions.

Local growing environments influence crown architecture

Environments within cities are heterogeneous and may present more or less challenging growing conditions than natural forest settings. Urban trees are both nurtured by people and harmed by various edifices and anthropogenic processes that define urban ecosystems (Vogt et al. 2015). In our study, the less-developed areas within cities (single or multi-family residential areas, parks, and vacant areas), had a positive effect on D, whereas the more developed ones had negative effects on D (these were industrial, institutional, and commercial areas and transportation corridors). Since it has been suggested that fractal dimension relates to tree growth rate (Seidel 2018), and we know that crown dieback relates to tree stress, we interpret such negative effects on D to represent reduced vigor for urban trees in more developed urban areas, after accounting for differences due to species and region.

Other studies also indicate that family-residential areas or parks offer more favorable tree habitats than commercial-industrial areas and transportation corridors. According to Lu et al. (2010), trees planted in single- and two-family residential areas had the lowest mortality rates, whereas street trees planted in industrial areas had the highest rates of mortality. It is possible that trees may receive more care, such as watering, in areas with family-residential land uses, so there may be a social-ecological component associated with tree survival and growth, depending on the socio-demographic characteristics of local neighborhoods (Vogt et al. 2015). Studies by Iakovoglou et al. (2001, 2002) showed that streets and commercial settings with high soil pH and high concentration of deicing salts negatively affect tree growth compared to urban parks and residential areas. Other characteristics of industrial areas that relate to reduced tree growth are restricted growing space, limited soil moisture, lack of nutrient balance, and high evaporative levels (Iakovoglou et al. 2001). In general, paved surfaces in cities are associated with reduced tree growth because of soil compaction and reduced soil aeration, water deficit or excessiveness, increased local soil temperature, and excess of Na and Cl ions (Krizek and Dubik 1987, Grabosky and Gilman 2004). A greater extent and spatial distribution of paved surfaces determines the corresponding level of negative impact on trees (Kostić et al. 2019). This can help explain why traffic volume has a negative effect on tree survival (Lu et al. 2010). These findings support the idea that more-developed urban areas are likely causing greater stress to trees, that is reflected in a lower value for D.

Our analyses also showed that the D of urban tree crowns is typically lower whenever a tree is close to a building. Buildings may be regarded as anthropogenic barriers to tree crown expansion, which might explain the observed reduction in D. Trees growing close to buildings may experience enhanced wind loads that can disrupt the architecture of the crown (Telewski et al. 1997). On the other hand, Bang et al. (2010) found that trees surrounded by buildings can be sheltered from wind and this can increase productivity. Ultimately, the relative wind load a tree receives is a complex function of building heights and street geometry (e.g., urban street canyons) and any adjacent trees, thus difficult to translate into a direct effect on D. However, new approaches are being developed to simulate wind flows in urban areas, inside and above street canyons and over the roofs of buildings (Mohamed and Wood 2015, Salim et al. 2015).

Another consideration for buildings is to what extent they affect the temperatures experienced by trees. While we have already seen that trees in hotter cities have a generally lower D, the local growing environment within a city may be relatively hotter or cooler. We could expect the local temperature close to buildings to be relatively higher, due to cooling and heating systems, and the fact that ground surfaces around buildings are typically paved. However, buildings also provide shade, which might cool trees off and benefit shade tolerant species, presumably those with intrinsically higher D.

Kostić et al. (2019) argued in their study that street canyons were associated with the most stressful conditions for trees. Kjelgren and Clark (1992) found that direct solar radiation in a canyon was limited to 4 h in the middle of summer, while the direct solar radiation in plaza sites was not inhibited and therefore the afternoon air temperature and vapor pressure deficits were greater in plaza sites. Bourbia and Boucheriba (2010) found that urban "canyons" can be 3–6°C warmer than surrounding rural environments, which could negatively affect D. So, we expect that the distance of trees from buildings should affect the mechanisms of crown development, since buildings alter both the wind and sunlight environments. Collectively, these studies suggest that the heat and drought effects of being close to buildings might be much more important than any shading effect.

Another important factor influencing the D of urban trees was the negative effect when they were growing in conflict with wires. We assume this negative effect is mainly an effect of pruning treatments to reduce these conflicts, such as raising, reduction, and thinning (Pavlis et al. 2008). Trees naturally self-prune as they grow,

shedding unhealthy and non-productive branches and rearranging foliage to minimize self-shading of foliage (Pugnaire and Valladares 2007), which alters the fractal dimension of the trees vascular system (under Pipe Model theory; Mäkelä and Valentine 2006). Natural (self-) pruning likely restores a healthy balance of leaf area relative to water-conducting systems, but it is less clear how anthropogenic pruning may affect the long-term structure and physiology of urban trees (Fini et al. 2015). Vogt et al. (2015) noted that pruning branches can remove photosynthetic (leaf) area and reduce growth rates, but correctly performed, can enhance tree growth and vigor. We expect that the negative effect on *D* observed in our study reflects a reduction in vigor, likely due to a prioritization of reducing wire conflicts over enhancing crown architecture for the tree's benefit. "Topping," where pruning cuts are made in the middle of internodes to chop a tree back from wires, appears to have a particularly damaging effect; these cuts increase crown dieback, but also reduce the LMA of regenerating leaves (Fini et al. 2015); this likely leads to a lower drought resistance, based on our results. So, pruning, which is a regular part of urban forest management, might have positive or negative effects on *D*, but our results indicate that pruning to protect wires is having a net negative effect, on balance.

Conclusions

The evolution of the form and function of trees of diverse species has taken place over hundreds of millions of years, but trees have only had to adapt to structures like buildings, roads, and sidewalks for millennia. Many studies of human–tree interactions emphasize the many "ecosystem services" provided by trees to humans; urban forests provide, e.g., temperature regulation, carbon dioxide sequestration, noise reduction, filtering of air pollutants, biodiversity, pollination, human health, recreation, water management, energy saving for buildings, and aesthetics (Heisler 1986, McPherson et al. 1994, McPherson 1998, Nowak and Crane 2002, MacFarlane 2007, Casalegno et al. 2017, Tigges and Lakes 2017). However, it is equally important to study the reciprocal effects that our built environment has on the trees that we depend on. We conclude by summarizing our key findings in this regard.

Species can differ in their functional traits (e.g., leaf traits) independently from the ecosystem or the biome where they grow (Reich et al. 1997), so that when we put a tree into a novel environment, it may or may not thrive. Our main results show that drought-stress tolerant trees seem to be inherently better adapted to urban environments, which are likely hotter and with more restrictions in the rooting zone, than rural and wild places, in the same climatic region. Tree drought tolerance relates to the fractal dimension of both leaves and the whole crown, as expressed by LMA and *D*, respectively, in this study. Our results also suggest that shade

tolerance, which is very important for succeeding in competition with other trees (e.g., the positive relationship between *D* and shade tolerance for coniferous species found by Zeide and Pfeifer 1991), is of much less importance in urban ecosystems, likely due to the much lower presence of tree neighbors. Trees appear to have some plasticity in shaping the architecture of their crowns, to adapt to stresses in the urban environment, by lowering the fractal dimension of their crowns to reduce drought stress. However, we also revealed that trees have an underlying inherent constraint in both their leaf type and their crown architecture, due to genetics, which limits their adaptability to urban ecosystems.

With expectations for more urbanization and a generally hotter climate in a period of history that has been dubbed the "Anthropocene," our results add some new insights into the physiological ecology of trees in urban environments, which may help humans to provide more hospitable habitats for trees in urbanized areas and make better decisions about tree selection and climate change adaptation in urban forest management.

Literature Cited

Bang, C., J. L. Sabo, and H. F. Stanley. 2010. Reduced wind speed improves plant growth in a desert city. PLoS ONE 5:1–8.

Bourbia, F., and F. Boucheriba. 2010. Impact of street design on urban microclimate for semi arid climate (Constantine). Renewable Energy 35:343–347.

Casalegno, S., K. Anderson, S. Hancock, and K. J. Gaston. 2017. Improving models of urban green space: from vegetation surface cover to volumetric survey, using waveform laser scanning. Methods in Ecology and Evolution 8:1443–1452.

Close, R. E., J. J. Kielbaso, P. V. Nguyen, and R. E. Schutzki. 1996. Urban vs. natural sugar maple growth: II. Water relations. Journal of Arboriculture 22:187–192.

Ferrini, F., F. Bussotti, M. Tattini, and A. Fini. 2014. Trees in the urban environment: response mechanisms and benefits for the ecosystem should guide plant selection for future plantings. Agrochimica 58:234–246.

Fini, A., P. Frangi, M. Faoro, R. Piatti, G. Amoroso, and F. Ferrini. 2015. Effects of different pruning methods on an urban tree species: a four-year-experiment scaling down from the whole tree to the chloroplasts. Urban Forestry & Urban Greening 14:664–674.

Grabosky, J., and E. Gilman. 2004. Measurement and prediction of tree growth reduction from tree planting space design

in established parking lots. Journal of Arboriculture 30:154–164.

Gregg, J. W., C. G. Jones, and T. E. Dawson. 2003. Urbanization effects on tree growth in the vicinity of New York City. Nature 424:183–186.

Halley, J. M., S. Hartley, A. S. Kallimanis, W. E. Kunin, J. J. Lennon, and S. P. Sgardelis. 2004. Uses and abuses of fractal methodology in ecology. Ecology Letters 7:254–271.

Heisler, G. M. 1986. Energy savings with trees. Journal of Arboriculture 12:113–125.

Iakovoglou, V., L. Burras, and R. Kipper. 2001. Factors related to tree growth across urban-rural gradients in the Midwest, USA. Urban Ecosystems 5:71–85.

Iakovoglou, V., J. R. Thompson, and L. Burras. 2002. Characteristics of trees according to community population level and by land use in the U.S. Midwest. Journal of Arboriculture 28:59–69.

Kjelgren, R. K., and J. R. Clark. 1992. Microclimates and tree growth in three urban spaces. Journal of Environmental Horticulture 10:139–145.

Kostić, S., J. Čukanović, S. Orlović, M. Ljubojević, and E. Mladenović. 2019. Allometric relations of sycamore maple (*Acer pseudoplatanus*) and its red leaf cultivar (*A. pseudoplatanus* "Atropurpureum") in street and park habitats of Novi Sad (Serbia, Europe). Journal of Forestry 117:114–127.

Krizek, D. T., and S. P. Dubik. 1987. Influence of water stress and restricted root volume on growth and development of urban trees. Journal of Arboriculture 13:47–55.

Lu, J. W. T., E. S. Svendsen, L. K. Campbell, J. Greenfeld, J. Braden, K. L. King, and N. Falxa-Raymond. 2010. Biological, social, and urban design factors affecting young street tree mortality in New York City. Cities and the Environment. 3:15, article 5.

Lusk, C. H., Y. Onoda, R. Kooyman, and A. Gutiérrez-Girón. 2010. Reconciling species-level vs plastic responses of evergreen leaf structure to light gradients: shade leaves punch above their weight. New Phytologist 186:429–438.

Lusk, C. H., and D. I. Warton. 2007. Global meta-analysis shows that relationships of leaf mass per area with species shade tolerance depend on leaf habit and ontogeny. New Phytologist 176:764–774.

MacFarlane, D. W. 2007. Quantifying urban saw timber abundance and quality in southeastern lower Michigan, U.S. Arboriculture & Urban. Forestry 33:253–263.

MacFarlane, D. W., and B. Kane. 2017. Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistanc. Functional Ecology 31:1624–1636.

MacFarlane, D. W., S. Kuyah, R. Mulia, J. Dietz, C. Muthuri, and M. V. Noordwijk. 2014. Evaluating a non-destructive method for calibrating tree biomass equations derived from tree branching architecture. Trees 28:807–817.

Mäkelä, A., and R. Sievänen. 1992. Height growth strategies in open-grown trees. Journal of Theoretical Biology 159:443–467.

Mäkelä, A., and H. T. Valentine. 2006. Crown ratio influences allometric scaling in trees. Ecology 87:2967–2972.

Malhi, Y., T. Jackson, L. Patrick Bentley, A. Lau, A. Shenkin, M. Herold, K. Calders, H. Bartholomeus, and M. I. Disney. 2018. New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. Interface Focus 8:20170052.

Mandelbrot, B. B. 1983. The fractal geometry of nature. W. H. Freeman, New York, New York, USA.

Markesteijn, L., L. Poorter, F. Bongers, H. Paz, and L. Sack. 2011. Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. New Phytologist 191:480–495.

McHale, M. R., I. C. Burke, M. A. Lefsky, P. J. Peper, and E. G. McPherson. 2009. Urban forest biomass estimates: is it important to use allometric relationships developed specifically for urban trees? Urban Ecosystems 12:95–113.

McPherson, E. G. 1998. Atmospheric carbon dioxide reduction by Sacramento's urban forest. Journal of Arboriculture 24:215–223.

McPherson, E. G., J. D. Nowak, and A. R. Rowan, editors. 1994. Chicago's urban forest ecosystem: results of the Chicago Urban Forest Climate Project. General Technical Report NE-186. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA.

McPherson, E. G., N. S. Van Doorn, and P. J. Peper. 2016. Urban tree database. Forest Service Research Data Archive, Fort Collins, Colorado, USA.

McPherson, E. G., Q. Xiao, N. S. Van Doorn, N. Johnson, S. Albers, and P. J. Peper. 2018. Shade factors for 149 taxa of in-leaf urban trees in the USA. Urban Forestry & Urban Greening 31:204–211.

Mohamed, M. A., and D. H. Wood. 2015. Computational study of the effect of trees on wind flow over a building. Wind, Water, and Solar 2:2.

Moran, M. A. 1984. Influence of adjacent land use on understory vegetation of New York forests. Urban Ecology 8:329–340.

Niinemets, Ü., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76:521–547.

Nowak, D. J., and D. E. Crane. 2002. Carbon storage and sequestration by urban trees in the USA. Environmental Pollution 116:381–389.

Pallardy, S. G. 2008. Physiology of woody plants. Third Edition. Academic Press, Cambridge, Massachusetts, USA.

Pavlis, M., B. Kane, J. R. Harris, and J. R. Seiler. 2008. The effects of pruning on drag and bending moment of shade trees. Arboriculture & Urban Forestry 34:207–215.

Peper, P. J., and E. G. McPherson. 2003. Evaluation of four methods for estimating leaf area of isolated trees. Urban Forestry & Urban Greening 2:019–029.

Pittermann, J., S. A. Stuart, T. E. Dawson, and A. Moreau. 2012. Cenozoic climate change shaped the evolutionary ecophysiology of the Cupressaceae conifers. Proceedings of the National Academy of Sciences USA 109:9647–9652.

Pretzsch, H., et al. 2015. Crown size and growing space requirement of common tree species in urban centers, parks, and forests. Urban Forestry & Urban Greening 14:466–479.

Pugnaire, F. I., and F. Valladares, editors. 2007. Functional plant ecology. Taylor and Francis, New York, New York, USA.

R Core Team 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences USA 94:13730–13734.

Roderick, M. L., S. L. Berry, and I. R. Noble. 2000. A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. Functional Ecology 14:423–437.

Salim, M. H., K. H. Schlünzen, and D. Grawe. 2015. Including trees in the numerical simulations of the wind flow in urban areas: Should we care? Journal of Wind Engineering and Industrial Aerodynamics 144:84–95.

Sattler, T., D. Borcard, R. Arlettaz, F. Bontadina, P. Legendre, M. K. Obrist, and M. Moretti. 2010. Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology 91:3343–3353.

Seidel, D. 2018. A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution 8:128–134.

Smith, D. D., J. S. Sperry, B. J. Enquist, V. M. Savage, K. A. McCulloh, and L. Patrick Bentley. 2014. Deviation from symmetrically self-similar branching in trees predicts altered hydraulics, mechanics, light interception and metabolic scaling. New Phytologist 201:217–229.

Sperry, J. S., U. G. Hacke, and J. Pittermann. 2006. Size and function in conifer tracheids and angiosperm vessels. American Journal of Botany 93:1490–1500.

Telewski, F. W., B. A. Gardiner, G. White, and A. Plovanich-Jones. 1997. Wind flow around multi-storey buildings and its influence on tree growth. G. Jeronimidis and J.F.V. Vincent, Pages 179–183 in Conference Proceedings I of Plant Biomechanics, The University of Reading: Centre for Biomimetics.

Telewski, F. W., B. A. Gardiner, G. White, and A. Plovanich-Jones. 1997. Wind flow around multi-storey buildings and its influence on tree growth. Pages 179–183. Plant Biomechanics. Centre for Biomimetics, Univ of Reading, Reading, UK.

Tigges, J., and T. Tobia Lakes. 2017. High resolution remote sensing for reducing uncertainties in urban forest carbon offset life cycle assessments. Carbon Balance and Management 12:17.

Troxel, B., M. Piana, M. S. Ashton, and C. M. Dunning. 2013. Relationships between bole and crown size for young urban trees in the northeastern USA. Urban Forestry & Urban Greening 12:144–153.

Valentine, T. H. 1985. Tree-growth models: derivations employing the pipe-model theory. Journal of Theoretical Biology 117:579–585.

Van Noordwijk, M., and R. Mulia. 2002. Functional branch analysis as tool for fractal scaling above and belowground trees for their additive and non-additive properties. Ecological Modeling 149:41–51.

Vogt, J. M., S. L. Watkins, S. K. Mincey, M. S. Patterson, and B. C. Fischer. 2015. Explaining planted-tree survival and growth in urban neighborhoods: A social–ecological approach to studying recently-planted trees in Indianapolis. Landscape and Urban Planning 136:130–143.

Warton, D. I., R. A. Duursma, D. S. Falster, and S. Taskinen. 2012. SMATR 3—an R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3:257–259.

Weiner, J. 2004. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology Evolution and Systematics 6:207–215.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Zeide, B. 1998. Fractal analysis of foliage distribution in loblolly pine crowns. Canadian Journal of Forest Research 28:106–114.

Zeide, B., and C. A. Gresham. 1991. Fractal dimensions of tree crowns in three loblolly pine plantations of coastal South Carolina. Canadian Journal of Forest Research 21:1208–1212.

Zeide, B., and P. Pfeifer. 1991. A Method for estimation of fractal dimension of tree crowns. Forest Science 37: 1253–1265.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2297/full

Data Availability

The main source of data for this study was an extensive, publicly available, urban tree data set, published by McPherson et al. (2016). LMA values were assigned to species based on publicly available data produced from the work of Wright et al. (2004), the GLOPNET supplementary data set file, for as many study tree species that data were available. Shade and drought tolerance values were assigned to each tree based on publicly available data produced from the work of Niinemets and Valladares (2006). Regional scale climatic data for different cities was obtained from U.S. Climate Data, as outlined in *Materials and Methods: Urban tree data.*