NEW APPROACHES FOR STUDYING THE ARCHITECTURE OF URBAN TREES

By

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ABSTRACT

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The study of the architecture of urban trees is important for the management of urban forests to optimize their ecological and socioeconomic services. Trees have a fractal-like architecture which is disrupted by competition for light. Therefore, studying the architecture of open-grown urban trees should provide a better understanding of the inherent fractal-like character of trees. Terrestrial Laser Scanning (TLS) technology provides detailed data of tree architecture. The main scope of this dissertation was to model the fractal-structural complexity of urban trees based on different fractal analysis methods in relation to their physiological and functional traits.

In the second chapter of the dissertation, a variant of the "two-surface" method was used to estimate the fractal dimension of thousands of urban tree crowns from a publicly-available dataset across the USA. It was found that urban trees reduced their crown fractal dimension to reduce water loss through transpiration in hotter cities depending on the level of urbanization at smaller spatial scales. The functional group and the life-history traits of the studied urban trees significantly affected their crown fractal dimension in response to their growing environment.

In the third chapter, forty-five trees of different deciduous species (*Gleditsia triacanthos* L., *Quercus macrocarpa* Michx., *Metasequoia glyptostroboides* Hu & W.C. Cheng) were laser scanned in leaf-on and -off conditions on the Michigan State University campus to study the role of leaves in the fractal-structural complexity of urban trees using the "box-dimension" (D_b) metric. It was found that the presence of leaves significantly increased the D_b metric of all study

trees, and the contribution of leaves decreased as branch network complexity increased. The leafon laser point clouds of the study trees were also virtually defoliated with a leaf-removal algorithm. It was found that the algorithmic leaf-removal caused biased estimates of the D_b of the *G. triacanthos* and *M. glyptostroboides* trees.

In the fourth chapter, the leaf-off laser point clouds of fifty-six urban trees of the aforementioned species were used to generate quantitative structural models (QSMs) to quantify their woody surface area (WSA) allometry. It was found that the variation in the above-ground WSA of the study trees related to their fractal dimension quantified with the D_b metric and the distribution of "path" lengths from the tree base to every branch tip. It was also found that the urban trees allocated the largest portion of their WSA to their branches, which varied with branch order, branch-base diameter, and branch-base height. This study also showed a positive relationship between the WSA and the crown surface area of the urban trees.

The fifth chapter included laser point clouds of thirty-one trees of deciduous and evergreen species that were sampled on the Michigan State University campus and the Harvard Forest in Petersham, MA, USA to model their above-ground woody biomass. QSMs were generated to estimate the total tree volume and component volumes of the study trees. Biomass estimates were produced by multiplying the TLS-based volumes with measurements of tree basic density from sample disks from stems and branches obtained after destructively sampling the trees, and also with published basic density values at species level. The leaves of the trees that were scanned in leaf-on condition were artificially removed before QSM generation. It was found that TLS technology can be used to produce reliable total and component biomass estimates of trees. The biomass estimates quality can be affected by the growing environment, the leaf condition of the laser-scanned trees and the basic density values that are used. This dissertation is dedicated to my beloved parents, Anastasia and Stefanos.

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KEY TO ABBREVIATIONS

| %RE | Percent Relative Error |
|-----------------------|---|
| AGB | Above-Ground Biomass of a Tree |
| AGB _{Ref} | Reference Above-Ground Biomass of a Tree |
| AGB _{TLS} | TLS-Based Above-Ground Biomass of a Tree |
| AIC | Akaike Information Criterion |
| ANOVA | Analysis of Variance Test |
| BD | Broad-Leaf Deciduous |
| BD _{disk} | Basic Density of a Disk (of a branch or main stem) |
| BMS | Branch to the Main Stem Woody Surface Area Ratio |
| BWSA | Branch Woody Surface Area |
| CCC | Concordance Correlation Coefficient |
| CDD | Cooling Degree Days |
| CI | Competition Index |
| CSA | Crown Surface Area |
| CV | Coefficient of Variation |
| Cvol | Crown Volume |
| D | Crown Fractal Dimension Based on the "Two-Surface" Method |
| D _b | Box-Dimension |
| DBH | Diameter at Breast Height |
| DW _{disk} | Dry Weight of a Disk (of a branch or main stem) |
| DW _{section} | Dry Weight of a Section (of a branch or main stem) |
| GLTR | Gleditsia triacanthos |
| | |

| GV _{disk} | Green Volume of a Disk (of a branch or main stem) |
|------------------------------|---|
| GW _{section} | Green Weight of a Section (of a branch or main stem) |
| LA | Leaf Area |
| LCC | Leaf Complexity Contribution Index |
| LMA | Leaf Mass Per Unit Area |
| MAP | Mean Annual Precipitation |
| MAT | Mean Annual Temperature |
| Max | Maximum |
| MC _{disk} | Moisture Content of a Disk (of a branch or main stem) |
| MEGL | Metasequoia glyptostroboides |
| Min | Minimum |
| MRE% | Mean Relative Error |
| NE | Needle-Leaf Evergreen |
| QSM | Quantitative Structure Model |
| QUMA | Quercus macrocarpa |
| RE | Relative Error |
| RF | Rural Forest |
| RMSE | Root Mean Square Error |
| SD | Standard Deviation |
| SPP | Species |
| TLS | Terrestrial Laser Scanning |
| UF | Urban Forest |
| WSA | Woody Surface Area |

CHAPTER 1

INTRODUCTION

1.1. Dissertation Scope and Objectives

The main scope of this dissertation was to quantify the fractal- architectural complexity of urban trees based on different methods and metrics of fractal analysis and to better understand how their architectural complexity relates to their physiological and functional traits adapting them to the urban growing conditions. In order to achieve this goal, two main methods were employed: the "two-surface" method (Zeide and Pfeifer 1991) which requires data for the leaf area and the crown dimensions of trees, and the "box-counting" method (Da Silva et al. 2006) which requires laser point clouds of trees (see section 1.5). This dissertation also aimed to explore the accuracy of the Terrestrial Laser Scanning (TLS) technology to model urban tree architecture and allometry, specifically, the total above-ground woody surface area and woody biomass of urban trees which have important physiological and management implications (e.g., carbon balance and carbon stocks of trees; Kinerson 1975, Kim et al. 2007, MacFarlane 2015).

The four objectives of this dissertation were the following:

- Understand how the fractal dimension of the crowns of communities of urban trees of many species varies at different spatial scales (local growing environment within cities, and between cities in different climatic regions); and explore how fractal dimension reflects the life-form and life-history traits of different tree species adapting them to the urban environment.
- Disentangle the two main components of the fractal-like character of trees i.e., the photosynthetic and non-photosynthetic parts; and quantify the role of foliage in the fractal dimension of urban trees in terms of structural complexity using TLS data.
- 3. Quantify the total above-ground allometry of the woody surface area of urban trees and understand how it relates to their fractal-structural complexity using TLS data.

 Evaluate the accuracy of TLS-based estimates of the above-ground biomass of urban trees compared to the accuracy of TLS-based estimates of the above-ground biomass of rural forest trees in different leaf conditions.

1.2. Dissertation Outline

Chapter 1 is the introductory chapter and it outlines the main scope and the objectives of the dissertation research. Furthermore, it provides the overall theoretical background and the motivation for the dissertation research. The fundamental theories of tree architecture are described, the ecological services of urban trees are also described, and their architectural characteristics are explored in comparison to the architecture of rural forest trees. Finally, the technology of TLS, to study tree structure and important considerations for laser scanning trees, is described.

Chapter 2 focuses on the first dissertation objective. More specifically, the fractal dimension of thousands of tree crowns of many different tree species, growing in different urban environments across the USA was estimated based on the "two-surface" method (Zeide and Pfeifer 1991). The tree data for this study was a publicly-available, urban tree dataset, published by McPherson et al. (2016). The analysis allowed for the study of the fractal dimension and the physiological responses of the trees to urban environments at different scales. The results provided a better understanding on how tree crown fractal dimension relates to balances between hydraulic- and light capture-related functions (e.g., drought and shade tolerance). It was shown that trees reduced their fractal dimension at both whole-crown and leaf scales in order to reduce water loss in hotter cities and depending on the level of urbanization at smaller spatial scales.

environment were observed, which were dependent on their functional group and life-history traits, i.e., needle-leaved versus broad-leaved species, and drought versus shade tolerance.

Chapter 3 focuses on the second objective of the dissertation. Terrestrial laser scanning data was used to study the role of foliage in the structural complexity of urban trees. More specifically, forty-five trees of three deciduous species (Gleditsia triacanthos L., Quercus macrocarpa Michx., Metasequoia glyptostroboides Hu & W.C. Cheng) were sampled on the Michigan State University campus and were laser-scanned in both leaf-on and leaf-off conditions. The box-dimension (D_b) metric, which is computed based on the "box-counting" method (Da Silva et al. 2006), was used to quantify the fractal dimension in terms of structural complexity of the leaf-on and leaf-off point clouds of the study trees. The leaf-on point clouds were also algorithmically defoliated to assess the effect of artificial leaf-removal on the estimated structural complexity. The study results showed that the presence of leaves significantly increased the D_b metric of all study trees and the contribution of leaves decreased as branch network complexity increased. The leaf-removal algorithm caused biased estimates of the D_b of the G. triacanthos and M. glyptostroboides trees, indicating that the shape and the type of leaves affects the performance of the algorithm, while the maximum branch order of the G. *triacanthos* trees was significantly related to the underestimation of their D_b.

Chapter 4 focuses on the third objective of the dissertation. Fifty-six trees of three species (*Gleditsia triacanthos* L., *Quercus macrocarpa* Michx., *Metasequoia glyptostroboides* Hu & W.C. Cheng) were sampled and laser-scanned on the Michigan State University campus in leaf-off condition. The TLS point clouds were used to generate quantitative structural models of the study trees to quantify their woody surface area allometry, considering the anatomy and the physiology of urban trees. The study results showed that the variation in the woody surface area

of the main stem and branches of the trees related to the fractal dimension of tree architecture quantified with the D_b metric and the distribution of "path" lengths from the tree base to every branch tip. It was also found that the urban trees allocated the largest portion of their total woody surface area to their branches and this varied with branch order, branch-base diameter, and branch-base height. Finally, this study showed a positive relationship between the woody surface area and the crown surface area of the urban trees, which has important implications for their carbon balance.

Chapter 5 focuses on the fourth objective of the dissertation. In this study, thirty-one trees of deciduous and evergreen species were sampled and laser-scanned in urban and rural forest conditions. The TLS point clouds were used to generate quantitative structural models to estimate the total tree woody volume and component volumes (main stem and branches) of the study trees. The woody volume estimates were converted to biomass estimates by multiplying with estimates of tree basic density from sample disks from stems and branches obtained after scanning and felling the trees, and also by multiplying with published basic density values at the species level. Furthermore, the leaves of the trees of evergreen species and some deciduous species, scanned in leaf-on condition, were algorithmically removed before generating quantitative structural models; the effect of the leaf-removal algorithm on the biomass estimates was assessed. Total woody above-ground biomass, main stem and branch biomass were also computed from destructive sampling data, as reference values to compare to TLS-based values. The study results showed that TLS technology can be used to produce reliable total and component woody biomass estimates of trees and the quality of the estimates can depend on the growing environment (urban versus rural forest conditions), the leaf condition of the laserscanned trees and the basic density values that are used.

Chapter 6 provides a synthesis of all previous chapters of the dissertation. The analysis methods are evaluated to identify challenges and remaining knowledge gaps about the fractallike architecture of urban trees and the use of TLS data to study tree structural complexity and architecture. Prospects of future research investigations are also discussed.

1.3. Tree Architecture: The Allometry of Trees Considering the Crowding Conditions

Size-dependent variation of tree architecture is explained by allometric scaling laws of power form (West et al. 1999, Sileshi 2014). Trees allocate available resources to their different organs in a way that increases the uptake of the most limiting resource for their growth, implying that allocation is a partitioning process of trees. Allometry is the quantitative relationship between allocation and tree growth (Weiner 2004). According to MacFarlane (2015) the main theories that describe the architecture of trees as a result of their allometric growth are the following: the metabolic scaling theory (branches have a fractal-like architecture described by a general allometric scaling based on quarter-power allometric models; West et al. 1997, West et al. 1999), the pipe model theory (the cross-sectional area of stems is preserved when they bifurcate into branches and the vascular system of trees consists from active and inactive pipes whose surface area scales with their volume; Shinozaki et al. 1964, Chiba 1998), various allometric models that assume that tree form is significantly affected by the wind loads (McMahon 1973, Niklas 1995, Eloy 2011, Telewski 2012), and different models that account for hydraulic limitations which are an important force affecting the size and the hydraulic architecture of tall trees (Ryan and Yoder 1997, Niklas and Spatz 2004, Ryan et al. 2006).

Both the metabolic scaling theory and the pipe model theory assume that trees have an inherent fractal-like branching architecture (Noordwijk and Mulia 2002, Mäkelä and Valentine 2006) based on fractal geometry principles (Mandelbrot 1983). However, tree branching networks are not perfect fractals because they lack self-similarity across all scales of branching hierarchy (Halley et al. 2004, Mäkelä and Valentine 2006, Malhi et al. 2018). According to MacFarlane et al. (2014) competition for light from neighboring trees significantly disrupts the inherent fractal character of trees growing in closed forest canopies.

Trees adapt their allometric patterns to the various growing conditions, which makes them plastic. Plasticity is the ability of trees to change their inherent allometric trajectories due to environmental factors (e.g. competition for light), which implies that plasticity is the flexibility of a tree's genotype to support different phenotypes depending on biotic and abiotic factors (Weiner 2004). Trees can develop various degrees of plasticity depending on the crowding conditions they face from tree neighbors. According to Coomes and Grubb (1998) competition for light is asymmetric and light-demanding, fast-growing species tend to be less "branchy" in their juvenile growth stage, which affects their fractal-like architecture. It has been found that trees growing in open areas (e.g., open-grown urban trees) have larger crowns, and sharper trunk taper when compared to rural forest trees, that grow in closed canopies, indicating that open grown trees allocate more mass to their branches (Zhou et al. 2015). Lines et al. (2012) found that trees grow taller and have narrower crowns when they grow in closed canopies, compared to trees that grow in the open. Similarly, MacFarlane and Kane (2017) found that branch traits change under different crowding conditions and they suggest that urban open-grown trees tend to have a squat growth form and allocate the largest portion of their aboveground biomass to their branches, in order to resist the strong wind loads in urban settings.

Open-grown and forest-grown trees can also have different wood properties. More specifically, Zhou et al. (2011) observed that within the same geographic region the stem specific gravity of open grown trees was greater than the stem specific gravity of forest grown trees, while they did not observe a significant difference in branch specific gravity. However, MacFarlane (2020) found that trees of different species facing reduced competition from their neighbors had greater branch wood density compared to their main stem wood density. Considering all the above studies, it becomes apparent that urban open-grown and forest-grown trees can have fundamentally different allometric and architectural patterns which reflect different conditions of competition for light, mechanical loads (e.g., wind), and local growing environment in cities (e.g., paved-impermeable surfaces, buildings).

1.4. Studying the Architecture of Urban Trees to Understand Their Ecological Services

Urban forests sequester large amounts of atmospheric carbon dioxide and they provide several other important ecological services e.g., shade, temperature regulation, noise reduction, air pollutants uptake, biodiversity, pollination, water purification, energy savings for buildings etc. (Heisler 1986, McPherson et al. 1994, McPherson 1998, Nowak and Crane 2002, Casalegno et al. 2017). However, our understanding of these ecological services and particularly the carbon offset of urban forests on global scale remains limited (Tigges and Lakes 2017). There are several reasons for this knowledge gap: a lack of accurate and detailed data about the architecture of urban trees at large spatial and temporal scales, a shortage of robust models describing urban tree architecture, limited information about the effects of natural and human-

induced disturbances on urban forest dynamics, and scarce information about the carbon that is stored in urban trees (Tigges and Lakes 2017).

The architecture of urban trees can be studied based on the principles of fractal analysis. Urban trees should have more evident fractal-like architecture compared to rural forest trees due to the typically lower number, or complete absence of neighboring trees and competition for light (MacFarlane et al 2014). However, the growing conditions in cities can be significantly heterogeneous (Moran 1984, Kjelgren and Clark 1992, Iakovoglou et al. 2002, Lu et al. 2010, Jensen et al. 2012, Ferrini et al. 2014, Kostić et al. 2019), which affects the fractal dimension of urban trees (Arseniou and MacFarlane 2021). More specifically tree architecture in cities is affected by systematic tree pruning (Pavlis et al. 2008, Vogt et al. 2015), increased atmospheric temperatures and reduced water infiltration (Kjelgren and Clark 1992, Bourbia and Boucheriba 2010, Nowak and Greenfield 2020), anthropogenic barriers to root and crown expansion (Krizek and Dubik 1987, Rhoades and Stipes 1999, Vogt et al. 2015), and heterogeneous soil properties (Iakovoglou et al. 2001, McHale et al. 2009). On the other hand, in urban areas there is a large availability of nutrients, and there are increased carbon dioxide emissions that usually enhance tree growth; the net effect of all these environmental factors combined is not well known yet (Gregg et al. 2003). It is expected that the fractal-like character of open-grown urban trees should be stronger compared to trees growing in closed-canopy forest conditions based on the hypotheses for the effect of competition for light on tree architecture (MacFarlane et al 2014, Arseniou et al. 2021).

1.5. Use of Laser Scanning Technology in Forest Measurements

1.5.1. Laser Scanning Systems

Remote sensing provides important technological tools that can be used to study the architecture of urban trees across several spatial and temporal scales, including laser scanning(Tigges and Lakes 2017). Laser scanners are instruments that emit laser pulses and capture "point clouds" consisting of millions of three-dimensional points of the surrounding environment i.e., Light Detection and Ranging (LiDAR) data (Liang et al. 2016). Range measurements and precise angular measurements through the optical beam deflection mechanism of the laser instrument are needed to capture three-dimensional point coordinates (Liang et al. 2016). There are different types of laser scanning systems depending on the platform that lasers are mounted e.g., spaceborne, airborne, Unmanned Aerial Vehicle (UAV), mobile, terrestrial (Calders et al. 2020). Terrestrial Laser Scanners (TLS) are mounted on a tripod and they create point clouds of trees by analyzing the returned energy of the emitted laser pulses as a function of either time (time-of-flight systems) or shift in the phase of the light wave of the emitted laser beam (phase-shift technology) (Calders et al 2015).

Previous studies combined different types of remote sensing data to quantify important forest variables. For example, Jaakola et al. (2010) detected the heights of individual urban trees with a standard deviation of 30 cm by using an UAV on which they mounted two laser scanners, two cameras, a spectrometer and a GPS system. He et al. (2013) assessed the green biomass of urban forests in Beijing, China using LiDAR data and SPOT5 satellite images. The accuracy of the green biomass estimates based on their analysis was greater than 85% compared to ground truth data. According to Casalegno et al. (2017) the green-space in urban areas is very fragmented and spatially heterogeneous and this creates significant challenges in determining

urban forest cover and structure. However, they developed a method for assessing the urban tree cover and the associated volumetric properties by using waveform airborne LiDAR. Wilkes et al. (2018) suggest the use of multi-scale LiDAR for studying urban carbon densities. They found that TLS-based maximum height and projected crown area explained 93% of the variance in the volume of the trees in their study. Using airborne LiDAR they successfully detected single urban trees but they observed a significant underestimation in aboveground biomass.

1.5.2. Considerations for Terrestrial Laser Scanning of Forest Trees at Plot Scale

Terrestrial laser scanning (TLS) data have been systematically used in forest ecology since the early 2000s (Hackenberg et al. 2015b, Calders et al. 2020). According to Liang et al. (2016) there are three main methods for laser-scanning trees with TLS on plot level: single-scan, multi-scan and multi-single-scan. According to the single-scan method the terrestrial laser scanner is placed at the plot center and it captures only one full field of view scan, and thus trees are detected in a single-scan point cloud. This method is fast and easy but significant occlusion effects in the point clouds can occur because some parts of tree structure (e.g., branches) are shadowed by other tree parts or neighboring trees. The multi-scan method reduces occlusion problems by establishing several scan positions inside and outside the plots. Artificial reference targets are needed for registering the multiple scans. This method significantly decreases the occlusion effects but increases the time cost and complexity of scans. The multi-single-method combines characteristics of the aforementioned methods and several scans are captured inside and outside the plots but reference targets are not used. The multiple scans are registered at feature level, as individual trees are mapped in each scan, and they are used to merge the multiple scans. This method is simpler and faster than the multi-scan method (Liang et al. 2016).

According to Wilkes et al. (2017), the sampling density using TLS depends on the spatial extent that must be scanned, the vegetation density and complexity and the metrics that need to be computed. For example, stem location detection does not require large scan resolution and it can be extracted from less-dense sampling patterns. However, the extraction of metrics related to high order branches require dense sampling patterns. In general, a sampling grid 10x10 m suffices to capture good quality point clouds at plot level.

1.5.3. Studying the Architecture of Individual Trees with the Use of Terrestrial Laser Scanning Technology

TLS data, captured at single-tree scale from multiple directions (minimum three) using reference targets, usually provide the most detailed information needed to study tree architecture, because occlusion effects are significantly reduced, but with increased scanning time (Raumonen et al. 2013, Wilkes et al. 2017). If a large tree is laser scanned under a dense canopy, then six or more scans are needed, while the point cloud quality and the density of points might be significantly reduced when single trees are laser scanned at distances greater than 10 m (Wilkes et al. 2017).

Different types of terrestrial laser scanners may differ in point density and accuracy (Jaakkola et al. 2010). Pueschel (2013) studied the effects of scanner parameters on the extraction of stems, and the estimation of stem diameter and stem volume of individual trees using a FARO Photon 120 terrestrial laser scanner. He found that scan resolution (i.e., angular step size) was the most important scanning parameter and is range dependent. Pueschel (2013) also suggested that we can optimize sampling efficiency by reducing scanning times (low scan resolution and high scan speed) without significant loss of accuracy and he concluded that

multiple scans for a single tree increase the estimation accuracy of diameter at breast height (DBH) and stem volume in the cost of time. Singh et al. (2015), argue that point density reduction through filtering and sub-sampling of point clouds, is a viable strategy for reducing computational costs of tree architecture modeling.

Using TLS data, we can precisely model tree architecture, reduce the uncertainty of above ground biomass estimation, create new allometric equations that apply to large trees, and create distributions of tree characteristics (Calders et al. 2015). There are three main methods to create models of trees from point clouds: the meshing method, the skeletonization approach, and fitting geometric primitives (e.g., cylinders, spheres, cones) in laser point clouds (Bournez et al. 2017). Fitting geometric primitives in point clouds is a common method for creating quantitative structure models (QSM) of trees. Cylinders have the best fit in point clouds and the generated QSMs can be very accurate (Bournez et al. 2017). This method preserves stem and branch topology and it provides information about the size, the location, the hierarchy and the orientation of the branching network of a tree (Raumonen et al. 2013, Kaasalainen et al. 2014, Hackenberg et al. 2015a, Bournez et al. 2017, Disney et al. 2018). There are different algorithms that produce QSMs. *TreeQSM* algorithm (Copyright (C) 2013-2017 Pasi Raumonen) segments the tree point clouds in sections before fitting cylinders (Raumonen et al. 2013) and the SimpleTree algorithm (within the CompuTree platform) employs spheres to detect tree geometry and to extract tree skeleton and thickness before fitting cylinders (Hackenberg et al. 2015a).

Creating QSMs of trees alleviates major challenges associated with the quantification of tree architecture from destructive measurements, such as limited sample sizes, restrictions in protected forests, insufficient spatial and temporal distribution of samples, omission of very large trees (Disney et al. 2018). However, there are also several sources of uncertainty related to tree

laser-scanning, and QSMs generation: occlusion effects, wind effects on point cloud quality, scanner characteristics (e.g., branches of the same or smaller diameter than the scanner footprint at a certain distance cannot be sufficiently captured), errors originating from the operators, and errors in point cloud registration (Disney et al. 2018). There are two components of the uncertainty associated with the QSM method. The stochastic component implies non-deterministic processes for fitting geometric primitives in a point cloud and the systematic component relates to the assumptions inherent to each QSM algorithm e.g., the fitting of cylinders may overestimate woody volumes or woody surface areas due to local tapering of branches, especially as the branch size decreases. Malhi et al. (2018) determine some major challenges in estimating tree mass accurately from TLS data: extraction of high order branches, and the algorithmic classification and separation of woody and non-woody parts of scanned trees because QSMs cannot model foliage (Stovall et al. 2017).

Although QSMs are currently considered to be the most robust method for estimating tree volume and architecture (Disney et al. 2018), there are also other methods to model trees from TLS data. Moskal and Zheng (2011) examined a point cloud slicing algorithm for processing TLS data and they derived allometric variables of urban trees. They demonstrated that some tree allometric variables (e.g., DBH, tree height) can be successfully derived from TLS data, however more research is needed for accurate estimation of tree volume. Hopkinson et al (2004), examined the use of TLS to semi-automatically derive basic allometric variables. They found a systematic underestimation of heights due to canopy shadow and suboptimal distribution of TLS sampling and that timber volume estimates were within 7% of the estimates from conventional allometric models. Maas et al. (2008), developed a fully automatic point cloud processing approach to measure variables like tree height, DBH, and stem profile. Olschofsky et al. (2016),

developed an algorithm that estimates the biomass of branches with complex geometry based on TLS data, giving an accuracy of greater than 95% compared to reference biomass values.

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CHAPTER 2

FRACTAL DIMENSION OF TREE CROWNS EXPLAINS SPECIES FUNCTIONAL-TRAIT RESPONSES TO URBAN ENVIRONMENTS AT DIFFERENT SCALES

Arseniou, G. and MacFarlane, D.W. (2021). Fractal dimension of tree crowns explains species functional-trait responses to urban environments at different scales. Ecological Applications, DOI: 10.1002/EAP.2297.

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 anthropogenicallystructured 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 USA, 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, pre-adapting them to drought-stress in urban ecosystems. Needle-leaved species showed a clear tradeoff between optimizing the fractal dimension of their crowns for drought versus 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.

Keywords: functional traits, fractal dimension, tree physiology, urban ecology

2.1. Introduction

Tree species have inherent traits which 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, so 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 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 which 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 versus slow responses to investments of energy and nutrients in leaves, and the WBE theory (West, Brown and Enquist 1997), which 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-grown form, which might better allow them to express their inherent fractal branching architecture that should be otherwise expected to be disrupted when shaded or crowded by other trees (Mäkelä, A. 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 on 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 studying this, we can inform arborists on 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 USA, to learn more about their responses to urban environments at different scales. Our major questions were:

• How does the fractal dimension of urban tree crowns reflect their life-form and life-history traits, as members of different species?

• How do crown fractional-dimensional traits, expressed at the tree level, relate to functional traits at the leaf level?

• How does the fractal dimension of the crowns of communities of urban trees of many species vary between cities in different climatic regions?

• 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 have lower 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, less developed areas (e.g., parks, vacant areas) should have a positive effect on the fractal dimensionality of urban trees. 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.

2.2. Materials and Methods

2.2.1. Urban Tree Data

The main source of data for this study was an extensive, publicly-available, urban tree dataset, published by McPherson et al. (2016). To produce this dataset, the U.S. was divided into sixteen climatic zones and a reference city was selected within each zone. About twenty of the most abundant species were selected within each reference city. Trees were chosen based on a stratified random sampling design; approximately 5 to 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 trees 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 in the next section). 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 breakdown in Supplemental Files 2.1 and 2.2).

We obtained regional scale climatic data (e.g. mean annual temperature) for different cities from U.S. Climate Data¹ to characterize the climatic region that the trees were growing in, in terms of mean annual precipitation (MAP) and mean annual temperature (MAT). We used cooling degree days (CDD), which is the number of degrees that a day's average temperature is

¹ <u>https://www.usclimatedata.com/climate/united-states/us</u>

above 18.5° Celsius, summed over a year, 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 which had four levels: 1 = 0 to 8 m, 2 = 8.1 to 12 m, 3 = 12.1 to 18 m, 4 = >18.1 m. The second was crown conflicts with utility wires, where 0 = no wires are present in or around the crown and 1 = 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 four levels based on the original factor levels from McPherson et al. 2016).

2.2.2. 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, 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 the fractal dimension. For example, the "path-fraction" method 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" method 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 twosurface-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 which 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 threedimensional 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 Pfeifer 1991, Zeide and Gresham 1991).

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

$$LA = a * Cvol^{\left(\frac{D}{3}\right)} + \varepsilon, \qquad (eq. 2.1)$$

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. 2.1 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. 2.1) 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 towards 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 also fitted to the data and it was found that the second order term was not statistically significant (p= 0.1049; α = 0.05). Only the coefficient of the crown volume to the first power was statistically significant (shown in Fig. 2.1), which enabled us to validate the assumption and use the method for our study population.



Figure 2.1. 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. 2.1 and two theoretical lines for D = 2 (orange, dashed line) and D = 3 (purple, dotted line), respectively, holding coefficient *a* (in eq. 2.1) at the same value estimated from the regression.

2.2.3. 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 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" dataset) for as many study tree species that data were available for (see Supplemental File 2.1).

2.2.4. 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. 2.1, 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. 2.1). 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. 2.1). Thus, the mixed-effects version of eq. 2.1 is written as:

$$LA = a * Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon, \qquad (eq. 2.2)$$

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 Supplemental File 2.1. The random effect of climatic region (R) has 15 levels, given in Supplemental File 2.2. 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 above in Section 2.1.

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. 2.1 and 2.2 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 $\alpha = 5\%$ level of significance.

After the best-fit model (eq. 2.2) 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 sub-population (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" (Supplemental File 2.1), 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).

2.3. Results

2.3.1. 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 2.1) can be found in Supplemental File 2.3. 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 2.1). 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 2.1). 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 2.1) 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.

Table 2.1. Candidate models for eq. 2.2 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. Nested models are characterized by a "/", e.g., Species/Region/LandUse, 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. Best by each statistic in bold.

| Model | Model-Form | $\begin{array}{c} Adjusted \\ R^2 \end{array}$ | AIC values |
|--|--|--|------------|
| Fixed-effects only (eq. 2.1) | $LA = a * Cvol^{\left(\frac{D}{3}\right)} + \varepsilon$ | 0.678 | 113847 |
| Species (eq. 2.2 with S only) | $LA = a * Cvol^{\left(\frac{D+S}{3}\right)} + \varepsilon$ | 0.734 | 112592 |
| Region (eq. 2.2 with R only) | $LA = a * Cvol^{\left(\frac{D+R}{3}\right)} + \varepsilon$ | 0.752 | 111853 |
| Species/Region (eq. 2.2 with S & R) | $LA = a * Cvol^{\left(\frac{D+S+R}{3}\right)} + \varepsilon$ | 0.796 | 110864 |
| Species/Region/Land.Use (eq. 2.2 with S,R, & L) | $LA = a * Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon$ | 0.807 | 99406 |
| Species/Region/Dist.build (eq. 2.2 with S, R, & L) | $LA = a * Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon$ | 0.820 | 97873 |
| Species/Region/Wire.Conf (eq. 2.2 with S, R & L) | $LA = a * Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon$ | 0.808 | 93805 |
| Species/Region/Dist.build/Wire.Conf/ Land.Use (eq. 2.2 with S, R & L) | $LA = a * Cvol^{\left(\frac{D+S+R+L}{3}\right)} + \varepsilon$ | 0.841 | 71963 |

2.3.2. 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 2.2 and Fig. 2.1), 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 2.2), which represents the smallest and largest estimated divergence of a species in that group from the mean trend.

Table 2.2. Estimated fractal dimension of tree crowns (coefficient D) from eq. 2.2, with species-random effects, fitted for all trees and for broad- and needle-leaved trees, separately. The minimum and maximum D value, respectively, come from adding the largest and smallest (most negative) species-random effect to D.mean.

| Tree type | no. species | D.mean | SE of D.mean | 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 |

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. 2.2), 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. 2.2).



Figure 2.2. Mean fractal dimension of tree crowns for species as a function of speciesspecific drought tolerance (1 = very intolerant; 2 = intolerant; 3 = moderately tolerant; 4 = tolerant; 5 = very tolerant). Data fitted to equation 2.2 with S only as a random effect (see Table 2.1).

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. 2.3). For all quantiles of D, the relationship between D and drought tolerance was negative and the strongest relationship was observed for the species at the highest quantile of D.



Figure 2.3. 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 5% quantile is a nonsignificant regression. Fractal dimension was estimated from equation 2.2 with S only as a random effect (see Table 2.1).

A positive relationship was also found between D and the shade tolerance of urban trees (r = 0.22, p = 0.05, Fig. 2.4), 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. 2.4). However, no significant relationship was found between D and shade tolerance of urban broadleaved trees (r = 0.1, p = 0.41, Fig. 2.4). Quantile regressions showed no clear pattern of elasticity in D relative to shade tolerance.



Figure 2.4. Mean fractal dimension of tree crowns for species as a function of speciesspecific shade tolerance (1 = very intolerant; 2 = intolerant; 3 = moderately tolerant; 4 = tolerant; 5 = very tolerant). Data fitted to equation 2.2 with S only as a random effect (see Table 2.1).

A negative relationship was found between D and the LMA of the urban trees (r = -0.5, p = 0.0008, Fig. 2.5). Needle-leaved trees showed a stronger relationship (r = -0.82, p = 0.046, Fig. 2.5) than the corresponding relationship for broadleaved trees (r = -0.41, p = 0.012, Fig. 2.5). Quantile regressions showed no discernible difference in the elasticity of D at low versus high LMA.



Figure 2.5. Mean fractal dimension of tree crowns for species as a function of species-specific leaf mass per unit area (LMA). Data fitted to eq. 2.2 with S only as a random effect (see Table 2.1).

2.3.3. 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 (Supplemental File 2.2). We found D to be strongly related to the mean annual temperature (MAT) of the climatic regions (r = -0.58, p = 0.024, Fig. 2.6). 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.



Figure 2.6. 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 Supplemental File 2.2). Data fitted to equation 2.2 with R only as a random effect (see Table 2.1).

2.3.4. Influence of Local Urban Environments on Fractal Dimension

The local urban environmental effects (L in eq. 2.2) on the fractal dimension of tree crowns were interpreted by looking at the sign of the coefficients influencing D (see Supplemental File 2.3 for full details). Trees that were in the first level of the *Dist.build* factor (0 to 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-thanaverage 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 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.

2.4. Discussion

2.4.1. 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 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 tradeoff for the needle-leaved species we examined, with higher D for shade-tolerant species and lower D for drought-tolerant ones, 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 U.S., 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 towards 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. 2.1), so it was notable that our model predicted a value < 2 for one species, *Juniperus virginiana* (D = 1.843, Table 2.2), a species with very higher 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 showed values consistently lower than D = 2. However, Seidel's method 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 = 0.0000), which were both estimated independently from each other (Niinemets and Valladares 2006 and 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 semi-arid 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 the broadleaved ones, 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. 2.2). 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 2.2) 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 2.2 and above). 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 needleleaved 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.

2.4.2. 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 (Supplemental File 2.2) 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 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. 2.3), 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 broadleaved 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 climate arborists could select drought tolerant species of 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 in urban tree cover in hotter, drier regions.

2.4.3. 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, 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 de-icing 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 CI 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 canyon) 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 (Salim et al. 2015; Mohamed and Wood 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 four hours 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 (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, due to a likely 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.

2.5. 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, 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.

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LITERATURE CITED

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CHAPTER 3

MEASURING THE CONTRIBUTION OF LEAVES TO THE STRUCTURAL COMPLEXITY OF URBAN TREE CROWNS WITH TERRESTRIAL LASER SCANNING

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Abstract

Trees have a fractal-like branching architecture that determines their structural complexity. We used terrestrial laser scanning technology to study the role of foliage in the structural complexity of urban trees. Forty-five trees of three deciduous species, Gleditsia triacanthos L., Quercus macrocarpa Michx., Metasequoia glyptostroboides Hu & W.C. Cheng, were sampled on the Michigan State University campus. We studied their structural complexity by calculating the box-dimension (D_b) metric from point clouds generated for the trees using terrestrial laser scanning, during the leaf-on and -off conditions. Furthermore, we artificially defoliated the leaf-on point clouds by applying an algorithm that separates the foliage from the woody material of the trees, and then recalculated the D_b metric. The D_b of the leaf-on tree point clouds was significantly greater than the D_b of the leaf-off point clouds across all species. Additionally, the leaf-removal algorithm introduced bias to the estimation of the leaf-removed D_b of the G. triacanthos and M. glyptostroboides trees. The index capturing the contribution of leaves to the structural complexity of the study trees (the ratio of the D_b of the leaf-on point clouds divided by the D_b of the leaf-off point clouds minus one), was negatively correlated with branch surface area and different metrics of the length of paths through the branch network of the trees, indicating that the contribution of leaves decreases as branch network complexity increases. Underestimation of the D_b of the G. triacanthos trees after the artificial leaf-removal was related to maximum branch order. These results enhance our understanding of tree structural complexity by disentangling the contribution of leaves from that of the woody structures. The study also highlighted important methodological considerations for studying tree structure, with and without leaves, from laser-derived point clouds.

Keywords: terrestrial laser scanning, fractal dimension, box-dimension, foliage, urban ecology, *Gleditsia triacanthos*, *Quercus macrocarpa*, *Metasequoia glyptostroboides*

3.1. Introduction

Trees have an inherent fractal-like branching architecture (Noordwijk and Mulia 2002, Mäkelä and Valentine 2006) mirroring principles of fractal geometry (Mandelbrot 1983). However, tree branching networks are not perfect fractals, lacking self-similarity across all scales of the branching hierarchy (Halley et al. 2004, Mäkelä and Valentine 2006, Malhi et al. 2018). Nonetheless, major theories linking tree morphology to tree physiology (e.g., pipe-model theory, Shinozaki et al. 1964; metabolic scaling theory, West et al. 1997) and mechanical stability (e.g., resisting wind stress, Eloy 2011) have been advanced by assuming that the fractallike character of trees explains the structural complexity of their crowns (Seidel 2018) and how they grow to occupy space (Silva et al. 2006, Jonckheere et al. 2006). One of the main challenges in testing such theories are reliable ways to accurately measure the structural complexity of trees in a way that reflects the fractal dimension of tree crowns.

The growing environment of a tree affects its crown architecture and competition for light from neighboring trees (Metz et al. 2013) significantly disrupts the inherent fractal-like character of trees growing in forest stands and plantations (MacFarlane et al. 2014, Eloy et al. 2017). According to Seidel (2018) Douglas-fir trees growing in forest gaps had more complex crowns compared to trees of the same species growing in closed canopy conditions, and this implies that light regime significantly affects the fractal dimension of a tree, which negatively relates to competition (Dorji et al. 2019). Therefore, we expect that the typically lower number, or complete absence of, neighboring trees in cities should allow urban trees to better express

their inherent fractal character; this was an important reason to focus on urban open-grown trees in this study. Of course, cities have heterogeneous growing conditions (Moran 1984, Kjelgren and Clark 1992, Iakovoglou et al. 2002, Lu et al. 2010, Jensen et al. 2012, Ferrini et al. 2014, Kostić et al. 2019), characterized by anthropogenic barriers to root and crown expansion (Krizek and Dubik 1987, Rhoades and Stipes 1999, Vogt et al. 2015), systematic tree pruning (Pavlis et al. 2008, Vogt et al. 2015), increased atmospheric temperatures and reduced water infiltration (Kjelgren and Clark 1992, Bourbia and Boucheriba 2010, Nowak and Greenfield 2020), air pollutants (Gregg et al. 2003), and heterogeneous soil properties (Iakovoglou et al. 2001, McHale et al. 2009), which can affect the fractal dimension of tree crowns (Arseniou and MacFarlane 2021). Nonetheless, the inherent fractal-like character of open-grown trees should be more evident compared to trees growing in competition with other trees.

Open-grown trees can be found both in urban and rural forest conditions, but for urban conditions there is a shortage of robust models. This limits our understanding of basic ecological services of urban forests (Tigges and Lakes 2017), despite the fact that urban trees provide a range of significant ecological services e.g., carbon storage (McPherson 1998, Nowak and Crane 2002, MacFarlane 2009, McHale et al. 2009), air pollutant uptake (McPherson et al. 1994, Nowak 1996, Casalegno et al. 2017), water purification, pollination, biodiversity, and energy savings for buildings (Heisler 1986, Jensen et al. 2012, Casalegno et al. 2017, Kostić et al. 2019). In order to optimize the benefits of urban forests, we need to study the structure and function of trees in cities. For example, we know that the fractal dimension of tree crowns relates to their ability to tolerate shade (Zeide and Pfeifer 1991, Zeide and Gresham 1991), which affects the shading benefits of trees, as well as their ability to tolerate the drought and the heat of cities (Arseniou and MacFarlane, 2021).

New advances in terrestrial laser scanning (TLS) technology allow for accurate, direct measurements of the three-dimensional structure of trees (Malhi et al. 2018, Calders et al. 2020) and many studies have utilized TLS to quantify stem profiles and timber volume (Hopkinson et al. 2004, Maas et al. 2008, Moskal and Zheng 2011, Vonderach et al. 2012, Olschofsky et al. 2016), leaf and crown attributes (Moorthy et al. 2010, Jung et al. 2011, Béland et al. 2014), and above-ground tree biomass (Kankare et al. 2013, Calders et al. 2015, Olagoke et al. 2016, Stovall et al. 2017, Tanhuanpää et al. 2017, Zheng et al. 2019). TLS creates "point clouds" of trees by emitting laser pulses and analyzing the returned energy as a function of either time (time-offlight systems) or shift in the phase of the light wave of the emitted laser beam (phase-shift technology) (Calders et al 2015, Liang et al. 2016). One way to generate data for analyzing the fractal-like character of tree branching networks from TLS point clouds is the generation of Quantitative Structure Models (QSMs), by fitting cylinders to a tree's point cloud that preserve branch and stem topology (Raumonen et al. 2013, Kaasalainen et al. 2014, Hackenberg et al. 2015, Bournez et al. 2017, Disney et al. 2018). Lau et al. (2019) generated QSMs of tropical trees to study the theoretical scaling exponents derived from the metabolic scaling theory (West et al. 1997) that describes the fractal-like structure of trees.

Another approach is the "box-counting" method (Silva et al. 2006), which considers the number of boxes that are needed to encapsulate all points of a laser-scanned tree, as box size iteratively reduces. Seidel (2018) showed how the "box-dimension" metric can be calculated from the point cloud of a tree to describe its fractal dimension in terms of structural complexity. The box-dimension metric has no units and its possible values range between one and three. Trees with great crown complexity and "space-filling character" have box-dimension values closer to three, whereas box-dimension equal to one implies a perfectly cylindrical stem with no

branches, e.g., a dead tree (Seidel 2018). Box-dimension values smaller than one imply that the lower "cut-off" has not been properly defined because the mean distance between points is greater than the edge-length of the smallest box. Values of three (or greater) would imply that a tree is a solid cube which is not valid. The box-dimension is a more direct and simple way to measure the fractal-like character of a tree, because it lacks the assumptions and stochasticity inherent in QSMs, using only the raw point cloud data generated by TLS.

Leaves increase uncertainty in the underlying branching architecture, because they occlude underlying branches and move more in the wind (Wilkes et al. 2017, Calders et al. 2020). Davison et al. (2020) for example, showed how leaf phenology affects the estimation uncertainty of metrics of forest structural diversity when laser scanning data are used. "Leaf-off" laser scanning data can provide better estimates of crown architecture of deciduous tree species (Davison et al. 2020), because leaf occlusion effects are avoided.

There are several studies that have explored how leaf-off and leaf-on airborne laser scanning data compare for the estimation of forest volume and other forest inventory attributes (Anderson and Bolstad 2013, Bouvier et al. 2015, Hawbaker et al. 2010, Villikka et al. 2012), but few, if any, have examined the effects of leaves on computation of fractal metrics of tree branching architecture. Perhaps more importantly, we lack a basic understanding regarding the role of foliage in the crown complexity of trees, which is fundamental to understanding how trees position their leaves and branches to maximize light capture and minimize self-shading (Zeide and Gresham 1991, Zeide and Pfeifer 1991, Zeide 1998), optimize crown architecture to improve water transport and resist drought (Arseniou and MacFarlane, 2021), and reduce wind stress (Eloy 2011, MacFarlane and Kane 2017, Jackson et al. 2019), which has been shown to be

affected by both, the increased drag of foliage (Vollsinger et al 2005, Antonarakis et al. 2008) and the uncertain effects of branches.

Artificial leaf separation from the leaf-on point clouds of trees is a promising methodology. There are three main types of algorithms to separate the leaf from the woody material of laser point clouds of trees: (1) algorithms that use the geometry of laser points, (2) algorithms that consider the radiometric properties of the returned laser pulses, and (3) algorithms that combine the previous approaches (Vicari et al. 2019, Wang et al. 2018, Wang et al. 2019, Moorthy et al. 2020). The radiometric-based algorithms assume that the leaves and the woody material of trees have different intensity characteristics at the wavelength of the laser scanner, which depend on the laser scanning distance, the incidence angle and the technical characteristics of each instrument (Wang et al. 2019). However, the geometry-based algorithms consider only the 3D coordinates of the points of a laser-scanned tree based on supervised machine learning (Wang et al. 2017, Moorthy et al. 2020) or unsupervised classification methods (Vicari et al. 2019, Wang et al. 2019). In general, we still need a better understanding of the effect of these classification algorithms for leaf separation when studying tree architecture (Vicari et al. 2019).

In this study, we used the box-dimension metric to quantify the crown complexity of three deciduous tree species in their leaf-on and leaf-off conditions. Furthermore, we artificially removed the leaves from the tree point clouds generated from leaf-on data, using the *TLSeparation* algorithm (Vicari 2017), and we computed the box-dimension metric for the leaf-removed tree point clouds. The questions that we want to answer are the following:

• How do the changes in leaf condition of deciduous tree species with different leaf types affect their crown complexity?

• How do differences in the contribution of leaves to the structural complexity of the study trees relate to the above-ground architecture of the trees?

• What is the effect of artificial leaf-removal from the leaf-on tree point clouds on their estimated fractal dimension? Is there an error in estimating the fractal dimension of the tree point clouds after the artificial leaf- removal compared to the fractal dimension of the leaf-off point clouds of the same trees?

• How does the potential error in estimating the fractal dimension of the tree point clouds due to the artificial leaf-removal relate to the branch architecture of trees?

We hypothesized that the leaves of trees would significantly increase their fractal dimension in terms of crown complexity, because the irregular outline shape of leaves is fractal-like (Borkowski 1999, Hartvigsen 2000, Backes and Bruno 2009), and the presence of foliage implies that more space is occupied by a tree and consequently more laser points are captured in its crown. So, a larger number of boxes is required to encapsulate all points of the laser-scanned tree, which results into greater value of the box-dimension metric (Seidel 2018, Seidel 2019b, Guzmán 2020). Furthermore, we hypothesized that differences in the contribution of leaves to tree structural complexity have ecological importance, because differences should relate to self-shading of tree crowns (Sack et al. 2006), the shade tolerance of the tree species and the type and shape of the leaves (Abrams and Kubiske 1990, Arseniou and MacFarlane, 2021).

We also hypothesized that errors in estimation of the box-dimension resulting from artificial leaf-removal, would relate to the type of leaf (broad vs. needle and compound vs. simple) and the order and the size of the branches of a tree, the latter of which because point cloud density can change across the branching network of a tree and leaf separation algorithms are sensitive to it (Vicari et al. 2019, Moorthy et al. 2020).

3.2. Materials and Methods

3.2.1. Urban Tree Data

Forty-five trees of three species, representing different tree functional types, were sampled on the Michigan State University campus: sixteen *Gleditsia triacanthos* L. (Honey locust) trees, which are compound-leaved, deciduous angiosperms, fifteen *Quercus macrocarpa* Michx. (Bur oak) trees, which are entire-leaved, deciduous angiosperms, and fourteen *Metasequoia glyptostroboides* Hu & W.C. Cheng (Dawn redwood) trees, which are needleleaved, deciduous gymnosperms (Fig. 3.1). The trees were selected to cover a large range of sizes within each species (see Table 3.1).

The *G. triacanthos* and *Q. macrocarpa* trees were laser-scanned with leaves-on in July and August, 2019, and the *M. glyptostroboides* trees were laser-scanned with leaves-on in August, 2020 (see specific methods below). The same trees were also laser-scanned in leaves-off condition between January and March, 2020. Before re-scanning the study trees, we confirmed that none of them were pruned between the leaves-on and leaves-off scans by the Michigan State University arborists. Therefore, pruning did not cause any bias in the quantification of the crown complexity of the trees during the study period. Following this experimental design, any change in the crown complexity of the study urban trees between the leaves-on and leaves-off scans should be attributed only to changes in their foliage, not their branching architecture. Of course, tree-pruning prior to the study should have an effect on the crown architecture of the study trees, but it did not influence the changes in their crown complexity during the study period.



Figure 3.1. Sample of leaves of the species (A) *G. triacanthos* (B) *Q. macrocarpa* (C) *M. glyptostroboides*.

3.2.2. Terrestrial Laser Scanning and Point Cloud Processing

The FARO Focus^{3D} X 330 terrestrial laser scanner was used to scan the trees. This laser scanner operates with laser light of 1550 nm wavelength, typical beam divergence 0.19 mrad, and a range of 0.6 m - 330 m. In order to minimize occlusion effects in the point clouds, each individual tree was scanned at high resolution from a minimum of four different directions at different distances, and six reference target-spheres were placed around a laser-scanned tree to spatially reference all scans and create a single point cloud for each tree, following the field scanning protocols suggested by Wilkes et al. (2017). The first two scans were conducted in opposite directions, from distances that allowed the top of the focal tree to be clearly visible. The other two scans were also conducted in opposite directions (perpendicularly to the first two scans), but from a closer distance to the tree, to better capture its branching architecture and get closer views of the main stem. Two or three additional scans were conducted underneath the

crown of large trees with wide crowns in order to capture more dense point clouds of the branches. All laser scans were conducted when there was little or no wind.

The software SCENE 2019.2 (FARO Technologies Inc., 2019.2) was used to spatially coregister and noise-filter all scans in an automatic way. With the same software each tree was then manually separated from the point cloud of the urban site background. This process has been shown to be an accurate alternative to a fully automatic segmentation process (Seidel, 2019a).

3.3. Leaf and Wood Classification of the Point Clouds

The *TLSeparation* algorithm (Vicari 2017) was applied to the point clouds of the trees with their leaves-on. This algorithm separates points that belong to the woody components of the trees from points that belong to their foliage, based on unsupervised classification of geometric features (leaf and wood materials within the point cloud have different spatial arrangement) and "shortest-path" analysis, which facilitates detection of paths through the branching network (from tree base to branch tip) with high occurrence frequency (Vicari et al. 2019). This approach was used to generate a single point cloud for each tree containing only points classified as woody parts of the tree.

3.4. Quantification of the Structural Complexity of Trees

The box-dimension metric (D_b) , which is derived from fractal geometry principles (Mandelbrot 1983), was used to quantify the above-ground structural complexity (fractal dimension) of the trees (Seidel et al. 2019b) in three conditions: (1) leaf-on, (2) leaf-off and (3) after the leaves were artificially removed from the leaf-on point clouds. The box-dimension

equals the slope of the least-squares line when the logarithm of the number of boxes required to capture all points of a laser-scanned tree is regressed against the logarithm of the inverse of the size of a box relative to the size of the initial box which is the smallest box encapsulating the whole tree i.e. "upper cut-off" (Fig. 3.2, Seidel 2018, Seidel et al. 2019b). The intercept of the regression line describes the size of the crown of a tree (i.e. crown radius, Dorji et al. 2019). The size of the smallest box ("lower cut-off") was 10 cm in this study, and it was selected based on a very liberal estimate of the maximum distance between two neighboring laser points at any given location in the tree, because the "lower cut-off" must ensure that no box is empty due to missing data i.e. it fits in the "unsampled" space of a scanned tree. The algorithm written in Mathematica 12.2 (Wolfram Research, Inc. 2020) for the computation of the D_b metric is available in Supplemental File 3.1.



Figure 3.2. (A) Illustration of the virtual boxes of different sizes that capture the leaf-on point cloud of a *M. glyptostroboides* tree. (B) Exemplary log-log plot for the computation of the box-dimension metric for the same tree. The slope of the regression line equals the box-dimension of the tree i.e. $D_b = 2.05$. The 95% confidence interval has been plotted around the regression line. The number of boxes required to capture all points of the tree point cloud is denoted as *N*, the size of the length of each box is denoted as *s*, and the size of the length of the initial box that encapsulates the whole tree is denoted as *s_initial*.

3.5. The LCC Difference Index and Error Metric Computation

The role of leaves in the above-ground structural complexity of the trees was quantified with the Leaf Complexity Contribution index:

$$LCC = \left[\left(\frac{D_{b}(\text{leaf.on})}{D_{b}(\text{leaf.off})} \right) - 1 \right], \quad (eq. 3.1)$$

where D_b (leaf. on) is the box-dimension of the leaf-on point cloud of each study tree, and D_b (leaf. off) is the box-dimension of the leaf-off point cloud of each study tree. If LCC = 0, the D_b of the leaf-on and leaf-off point clouds of a tree are equal and there is no contribution of the leaves to the structural complexity of the tree. If LCC > 0, it means that the leaf-on D_b of a tree is greater than the leaf-off D_b of the tree, indicating that leaves increase tree structural complexity. Similarly, if LCC < 0, it means that the leaf-off D_b of a tree is greater than the leaf-on D_b of the tree, indicating that leaves increase the structural complexity. Similarly, if LCC < 0, it means that the leaf-off D_b of a tree is greater than the leaf-on D_b of the tree, indicating that leaves reduce structural complexity most likely because they occlude the woody components that are not adequately laser-scanned.

The effect of the artificial leaf-removal using the *TLSeparation* algorithm on the structural complexity of each study tree was quantified with the percent relative error metric (Sileshi 2014, Burt et al. 2021):

$$\% RE = \frac{|D_{b}(lf.off) - D_{b}(lf.rm)|}{D_{b}(lf.off)} *100, \qquad (eq. 3.2)$$

where D_b (leaf. rm) is the D_b of the point cloud of each study tree after the artificial leafremoval.

3.6. Computation of Other Structural Metrics of Trees

We computed some additional metrics that characterize the structure of trees to test our hypotheses regarding how the LCC index and the %RE relate to the above-ground tree architecture. According to major theories of tree structural complexity (i.e. pipe-model theory, Shinozaki et al. 1964; metabolic scaling theory, West et al. 1997), the "pipes" of the vascular system of a tree connect the roots to the leaves, with a surface area that scales with their volume (Enquist 2002). Consequently, the structural complexity of the vascular structure of a tree depends on the length and diameter of its pipes (Enquist 2002, Price and Enquist 2006). Therefore, we expected that the LCC should relate to different metrics of the length of the paths from the base of a tree to each branch tip (e.g., the "path fraction" metric of Smith et al. 2014).

The algorithm *TreeQSM* v.2.3.0 (Copyright (C) 2013-2017 Pasi Raumonen) was used to produce quantitative structure models (QSMs) from the leaf-off point clouds of the trees. *TreeQSM* includes two main steps: (1) the point cloud segmentation into stem and branches based on cover sets and (2) the reconstruction of the volume and the surface area of the segments with cylinders (Calders et al. 2015, Raumonen et al. 2015). The algorithm produced several QSMs for each tree point cloud based on a range of values for the minimum and maximum size of the cover sets and it finally determined the optimal QSM (Raumonen et al. 2013). Based on the parameters of the optimal QSM the algorithm produced 30 additional QSMs in order to estimate the variation of the modeled tree variables (e.g. woody surface area), because of the inherent stochasticity of the *TreeQSM* algorithm (Raumonen et al. 2013). The algorithm separated the main stem from the branches of a tree based on the following criteria: (i) the main stem extends near the top of a tree, (ii) it goes almost straight up, and (iii) it is not too curved which means that the ratio of the stem length to the stem base-tip distance, must be the minimum

among all candidate main stems; the branches were further categorized by branching order based on certain criteria for branch topology, branch length and branch base-tip distance (P. Raumonen, personal communication, June 2, 2020).

From the optimal QSMs of the leaf-off point clouds of the study trees, their total woody surface area (the surface area outside of the bark tissues) was computed as the sum total surface area of the cylinders that were fitted to the point cloud of each tree. The total woody surface area of each tree was also separated into the main stem and the branch woody components.

"Path lengths" (sense Smith et al. 2014) were also used to create alternative structural metrics of the trees. The lengths of all paths from the stem base of a tree to all branch tips were computed from the lengths of the QSM cylinders, whose topological structure is preserved in a QSM. The distribution of the path lengths for each tree was computed i.e. the quantiles of the path lengths (25th, 50th and 75th percentiles), as well as minimum, maximum and mean path lengths. Smith et al. (2014) showed that relative path length variation is an intrinsic element of tree branching architecture relating to tree hydraulic conductance, volume, mechanical stability and light interception.

3.7. 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).

Differences in the mean value of the D_b of the trees for leaves-on versus -off, and leavesartificially removed versus -off, were evaluated with t-tests, for each species separately (*G. triacanthos*, *Q. macrocarpa*, and *M. glyptostroboides*), and for all species combined. T-tests were also used to evaluate differences in the mean value of the LCC index, %RE, and D_b of leafon, leaf-off and leaf-"removed" tree point clouds between the study species. The "sma" function of the standardized major axis regression and testing routines ("smatr") R package (Warton et al. 2012) was used to conduct hypothesis tests regarding the intercepts and the slopes of the species sub-population regression lines. In all statistical tests, significant differences were assessed at $\alpha = 5$ %.

The relationships between the leaf-on, leaf-off, and leaf-artificially removed D_b values, and the relationships of the LCC index and the %RE with the tree structural metrics (see section 3.6) were analyzed using linear regression analysis and relationship strength was quantified with the Pearson correlation coefficient (*r*); statistical significance was assessed at $\alpha = 5$ %.

3.8. Results

3.8.1. Structural Complexity of Leaf-on Versus Leaf-off Tree Point Clouds

The data show that the study trees varied widely in size (DBH and height) and structural complexity (Table 3.1). There was significant difference between the mean D_b of the leaf-on tree point clouds of the *G. triacanthos* (GLTR) and *Q. macrocarpa* (QUMA) species (p = 0.0194). However, no significant difference was found between the mean D_b of the leaf-on tree point clouds of the *G. triacanthos* (GLTR) and *M. glyptostroboides* (MEGL) trees (p > 5%), and also for the MEGL and QUMA trees (p > 5%). Significant differences were found between the mean D_b values of the leaf-off tree point clouds of QUMA and MEGL trees (p = 0.0335), GLTR and QUMA trees (p < 0.001), and MEGL and GLTR trees (p = 0.041).

| Summary Statistics | All trees | Gleditsia triacanthos | Quercus macrocarpa | Metasequoia glyptostroboides |
|---|----------------------------------|------------------------------|----------------------------------|---------------------------------|
| no. trees | 45 | 16 | 15 | 14 |
| DBH (cm) (mean [min, max]) | 54.1 [15, 122.2] | 52.9 [18.4, 72.8] | 58.8 [29, 83.8] | 50.5 [15, 122.2] |
| Height (m) (mean [min, max]) | 13.8 [4.4, 24.1] | 12.5 [10.4, 18.4] | 15.8 [9.1, 21.3] | 13.1 [4.4, 24.1] |
| WSA (m ²) (mean [min, max]) | 204.2 [29.9, 467.0] | 265.4 [65.2, 408.6] | 225.4 [60.4, 467.0] | 111.5 [29.9, 250.2] |
| Stem WSA (m ²) (mean [min, max]) | 13 [2.1, 44.6] | 11.4 [4.1, 20.1] | 16.2 [4.7, 30.3] | 11.4 [2.1, 44.6] |
| Branch WSA (m ²) (mean [min max]) | 191.2 [27.7, 436.7] | 253.9 [61.2, 395.5] | 209.2 [55.7, 436.7] | 100.1 [27.7, 231.8] |
| D _b -leaf.on (mean [min, max]) | 2.06 [1.89, 2.23] | 2.09 [1.89, 2.20] | 2.03 [1.91, 2.11] | 2.07 [1.94, 2.23] |
| D _b -leaf.off (mean [min, max]) | 1.97 [1.82, 2.11] | 2.02 [1.84, 2.11] | 1.92 [1.82, 2.04] | 1.97 [1.84, 2.1] |
| D _b - leaf.rm (mean [min, max]) | 1.9 [1.76, 2.14] | 1.84 [1.76, 2.0] | 1.93 [1.83, 2.03] | 1.93 [1.8, 2.14] |
| LCC index (mean [min, max]) | 0.04633 [0.00064, 0.16394] | 0.03273 [0.01371, 0.0762] | 0.05867 [0.00667, 0.10883] | 0.04864 [0.00064, 0.16394] |
| %RE (mean [min, max]) | 5.55 [0.17, 14.64] | 8.91 [1.07, 14.64] | 2.43 [0.17, 5.46] | 5.06 [0.92, 11.53] |
| Mean Path length (m) (mean [min, max]) | 12.9 [3.7, 23.9] | 14.8 [9.5, 22.0] | 14 [6.9, 23.9] | 9.5 [3.7, 18.6] |
| Max. Path length (m) (mean [min, max]) | 22.8 [6.5, 42.7] | 24.8 [17.3, 37.5] | 24.9 [12.3, 42.7] | 18.3 [6.5, 35.8] |
| 25 th % Path length (mean [min, max]) | 10.9 [3, 20.6] | 13.2 [7.7, 18.1] | 11.7 [5.4, 20.6] | 7.4 [3, 14.9] |
| # of branch orders (median [min, max]) | 5 [1, 11] | 5 [1, 11] | 5 [1, 10] | 4 [1, 9] |

Table 3.1. Summary statistics resulting from different measurements of tree size and structural complexity.

T-tests showed that the mean D_b of the leaf-on tree point clouds was significantly greater than the mean D_b of the leaf-off tree point clouds (Fig. 3.3) across all study tree species combined (p < 0.001), and for each species separately (GLTR: p = 0.0145; QUMA: p < 0.001; MEGL: p = 0.003). Positive relationships were found between the leaf-on and the leaf-off D_b values of the trees across all species combined (Pearson's r = 0.72, p < 0.001) and for the GLTR (Pearson's r = 0.91, p < 0.001) and QUMA species (Pearson's r = 0.6, p = 0.019) (Fig. 3.4). The relationship between the leaf-on and the leaf-off D_b values for the MEGL trees was not significant (Pearson's r = 0.52, p = 0.055), however, all data points were above the 1:1 line indicating that the D_b of the MEGL leaf-on point clouds was clearly greater than the D_b of the MEGL leaf-off point clouds, except one tree with LCC index close to zero (LCC = 0.00064) (Fig. 3.4 D).

The LCC index ranged between 0.00064 and 0.16394 across all trees combined (see Table 3.1), indicating a significant reduction in the structural complexity of deciduous tree crowns when leaves are shed. The mean LCC index value was significantly different between GLTR (mean LCC_{GLTR} = 0.03273) and QUMA (mean LCC_{QUMA} = 0.05867) trees (p = 0.0261). However, the mean LCC index value was not significantly different between QUMA and MEGL (mean LCC_{MEGL} = 0.04864) trees (p = 0.4559), and between GLTR and MEGL trees (p = 0.181).



Figure 3.3. Crown complexity quantified with the box-dimension (D_b) metric of the (A) leaf-on, (B) leaf-off, and (C) leaf-removed point clouds of a *G. triacanthos* tree (first row), a *Q. Macrocarpa* tree (second row), and a *M. glyptostroboides* tree (third row). The leaf-off and leaf-removed tree point clouds have been artificially colored with brown color.



Figure 3.4. Relationship between the leaf-on and leaf-off box-dimension values across all study tree species combined, and for each species separately with 95 % confidence interval around the regression lines. The black dashed line is the 1:1 line.

The LCC index was negatively correlated with the branch woody surface area of the study trees (Pearson's r = -0.4, p = 0.0061), but it was not correlated with their stem woody surface area (p = 0.16) (Fig. 3.5). The "outlier" MEGL data- point in Fig. 3.5 (top-left) did not drive the observed relationship, because the pattern did not change after the removal of this data-point.



Figure 3.5. Relationship between the LCC index and the branch woody surface area of the trees with 95% confidence interval around the regression line. The three species *M. glyptostroboides* (MEGL), *G. triacanthos* (GLTR), and *Q. macrocarpa* (QUMA) have been plotted with different colors and symbols.

Finally, the LCC index was negatively correlated with different path length variables i.e. mean path length (Pearson's r = -0.4, p = 0.0068), maximum path length (Pearson's r = -0.44, p = 0.0025), and the 25th percentile of path lengths (Pearson's r = -0.41, p = 0.0051) (Fig. 3.6). The "outlier" MEGL data-point in Fig. 3.6 (top-left in each graph) did not drive the observed relationships, because the patterns did not change after the removal of this data point.



Figure 3.6. Relationships between the LCC index and different path length variables with 95% confidence interval around the regression lines. The three species *M. glyptostroboides* (MEGL), *G. triacanthos* (GLTR), and *Q. macrocarpa* (QUMA) have been plotted with different colors and symbols.

3.8.2. Box-dimension of Leaf-off Versus Leaf-removed Tree Point Clouds

Significant differences were found between the mean D_b values of the tree point-clouds after the artificial leaf-removal for QUMA and GLTR trees (p = 0.001), and GLTR and MEGL trees (p = 0.0105), but no significant difference was found between the mean D_b of the MEGL and QUMA trees after the artificial leaf-removal (p = 0.9662).

T-tests showed that the mean D_b of the leaf-off tree point clouds was significantly greater than the mean D_b of the leaf-removed tree point clouds across all study tree species combined (*p* < 0.001), and for the GLTR trees (*p* < 0.001). No significant difference was found between the mean D_b of the leaf-off and leaf-removed point clouds for the QUMA trees (*p* = 0.6382), and the MEGL trees (*p* = 0.1622). Furthermore, the leaf-removed and the leaf-off D_b values of the QUMA trees were positively correlated (Pearson's *r* = 0.65, *p* = 0.0082), but no significant relationship was found between the leaf-removed and the leaf-off D_b values across all study tree species combined (p > 5%), and for the GLTR and MEGL trees (p > 5%) (Fig. 3.7). The standardized major axis tests showed that the intercept and the slope of the regression line of the QUMA trees was not statistically different from the 0 and 1 values respectively.

The mean D_b of the leaf-on tree point clouds was significantly greater than the mean D_b of the leaf-removed tree point clouds (Fig. 3.3), across all study tree species combined (p < 0.001), and for each species separately (GLTR, QUMA, MEGL: p < 0.001).



Figure 3.7. Relationship between the leaf-removed and leaf-off box-dimension values across all study tree species combined, and for each species separately with 95% confidence interval around the regression lines. The black dashed line is the 1:1 line.

The mean %RE value was significantly different between GLTR (mean %RE_{GLTR} = 8.91%) and MEGL (mean %RE_{MEGL} = 5.06%) trees (p = 0.0057), and between GLTR and QUMA (mean %RE_{QUMA} = 2.43%) trees (p < 0.001), and also between MEGL and QUMA trees (p = 0.0064).

The %RE was positively correlated with the maximum branch order of the GLTR trees (Pearson's r = 0.53, p = 0.033), but it was not correlated with the maximum branch order of the QUMA and MEGL trees (p > 5%) (Fig. 3.8).



Figure 3.8. Relationship between the % Relative Error (RE) and the maximum branch order of the trees with 95% confidence interval around the regression lines. The species *M. glyptostroboides* (MEGL), *G. triacanthos* (GLTR), and *Q. macrocarpa* (QUMA) have been plotted with different colors and symbols.

3.9. Discussion

3.9.1. Structural Complexity of Urban Trees

This study measured the D_b of the above-ground components of tree architecture (i.e., main stem, branching network and leaves) from TLS point clouds, to determine the aboveground structural complexity of trees growing in urban areas. D_b can help to understand how trees maximize resources uptake for their growth while maintaining their mechanical stability (Seidel 2018, Seidel et al. 2019a, Seidel et al. 2019b). From an evolutionary perspective, trees have had to develop an "adaptive" geometry (Borchert and Slade 1981) to optimize light capture and minimize self-shading (Abrams and Kubiske 1990, Sack et al. 2006, Eloy et al. 2017), while balancing with other competing functions, such as maintaining mechanical stability (MacFarlane and Kane 2017) and resisting drought (Arseniou and MacFarlane 2021). Open-grown trees are relatively free from light competition, due to having fewer tree neighbors (MacFarlane and Kane 2017), so they are more likely to be able to maximize their structural complexity and express their inherent fractal-like architecture than trees growing in forests or plantations (MacFarlane et al. 2014). The urban open-grown trees in this study were not directly influenced by shading from neighboring trees or from the buildings of relatively low height which were nearby to some of the trees. D_b is sensitive to the external shape and the internal structure of trees (Seidel et al. 2019a, Seidel et al. 2019b), so differences in D_b can capture meaningful differences in tree architecture and physiological function. Therefore, it is important to consider what the maximum structural complexity could be.

Seidel et al. (2019b) hypothesized that trees should have D_b values significantly lower than 2.72, which is the D_b of the Menger sponge (a mathematical object with the greatest surface to volume ratio, Menger 1926), assuming a tree would maximize its surface area for light capture and gas exchange, while minimizing building costs, in the absence of competition with other plants. In previous studies that quantified the above-ground complexity of trees growing in dense rural forest stands, leaf-on D_b values were consistently lower than 2 (Seidel 2018, Seidel et al. 2019a, Seidel et al. 2019b, Dorji et al. 2019, Guzmán et al. 2020, Saarinen et al. 2021). In this study, the mean D_b of the leaf-on tree point clouds was greater than 2 across all study tree species (see Table 3.1), indicating a possible structural difference between trees in rural versus

urban areas. However, rural forest trees growing in more open conditions and facing less competition for light (e.g., in forest gaps and in thinned forest stands), also had larger D_b values (Seidel 2018, Dorji et al. 2019, Saarinen et al. 2021), in some cases exceeding 2 (Dorji et al. 2021). This suggests a benefit to increasing D_b with more light and fewer neighbors, but at some level the energy benefits from increased photosynthesis would be minimized due to high level of self-shading (Seidel et al. 2019b). This supports MacFarlane et al.'s (2014) assumption that trees growing in the open, without competition can more closely approach the theoretical maximum D_b (as characterized in Seidel et al. 2019b). In this study, the maximum D_b value observed was 2.23, for a large specimen of *M. glyptostroboides* in the leaf-on condition (Table 3.1). So, even the largest, open-grown, urban trees in this study were well below the theoretical maximum of 2.72.

3.9.2. The Role of Leaves in the Structural Complexity of Deciduous Trees

The urban trees studied here were deciduous species, characterized by distinct leaf phenological changes (i.e., leaf-on and leaf-off periods), which are typically affected by sharp photoperiodic and temperature changes (Lechowicz 1984, Fridley 2012). In general, the outline shape and the texture of leaves can have fractal-like patterns (Vlcek and Cheung 1986, Moraczewski and Borkowski 1997, Borkowski 1999, Hartvigsen 2000, Camarero et al. 2003, Backes and Bruno 2009, Jobin et al. 2012, Gazda 2013, Bayirli et al. 2014, Ianovici and Datcu 2015), and thus, we expected that the presence of leaves can increase the total structural complexity of trees. Indeed, the study trees were shown to have statistically different structural complexity in the leaf-on and leaf-off periods (Fig. 3.4), because the presence of leaves implies greater dispersion of laser points in the leaf-on point clouds compared to the leaf-off point clouds

and more boxes are required to capture them, which results in greater value for the D_b metric and greater structural complexity (Seidel 2018, Seidel et al. 2019b, Guzmán et al. 2020). In a previous study the difference between the D_b of the leaf-on and leaf-off point clouds of forestgrown trees was not significant (Guzmán et al. 2020). However, that study followed a mixed approach to generate leaf-off point clouds. More specifically, from the 76 leaf-off point clouds, only15 point clouds were captured during the leaf-off period and the rest leaf-off point clouds were created after manual segmentation of leaves from the leaf-on point clouds (Guzmán et al. 2020).

The magnitude of change in D_b observed in this study was relatively small; the LCC index, ranged from 0.00064 to 0.16394 across all species combined, indicating that the largest portion of the total above-ground structural complexity of a tree comes from woody components e.g. branches. However, $D_{\rm b}$ is constrained to have values between one and three, so a small change in its value can have significant physiological implications. Seidel et al. (2019b) found that the crown surface area divided by the woody volume of trees increased as a power function of leaf-on D_b, so that, e.g., an increase of 0.2 units in leaf-on D_b resulted in approximately 40 units of increase in crown surface area relative to the woody volume of trees. Similarly, the results here in this study show that a small change in the crown complexity has important structural implications for urban trees. An increase of about 0.05 units in the LCC index was associated with approximately 400 m^2 reduction in the branch woody surface area of the study trees (Fig. 3.5). Such a change could have important implications for the mechanical stability of trees, i.e. the branch woody surface area affects the bending moments due to wind drag (Vollsinger 2005, Pavlis et al. 2008, Gardiner et al. 2016), for the maintenance respiration of trees which relates to their woody surface area (Kinerson, 1975; Kramer and Kozlowski, 1979;

Yoneda, 1993; Bosc et al., 2003; Kim et al., 2007), and for solar radiation and rainfall interception (Weiskittel and McGuire 2006).

Differences in the LCC index were related to other structural metrics of the trees, showing different changes in the D_b value, with and without leaves, for different types of trees. The negative relationships with branch surface area and path length metrics indicate that larger trees, with larger and more "branchy" crowns, have a relatively smaller contribution of leaves to structural complexity (Figs. 3.5 and 3.6). These results can be interpreted within the framework of the pipe model theory (Shinozaki et al. 1964) and the West-Brown-Enquist or WBE model (West et al. 1997, West et al. 1999), which explain the fractal-like architecture of trees by assuming a vascular tree structure consisting from pipes (West et al. 1997). According to these theories as the size (i.e. woody surface area or length) of the pipes of the vascular system of a tree increases, the structural complexity of the woody skeleton of the tree also increases.

Differences in species branching architecture and leaf structure could also explain some of the observed differences in leaf-on versus leaf-off D_b values, because the fractal architecture of urban tree crowns is influenced by both crown and leaf shape (Arseniou and MacFarlane, 2021). *G. triacanthos* trees had the smallest contribution of the leaves to the crown complexity (smallest LCC). According to Niinemets and Valladare (2006), *G. triacanthos* is the least shade tolerant of the three species studied (shade tolerance index for *G. triacanthos* = 1.61, *Q. macrocarpa* = 2.71, and *M. glyptostroboides* = 3). Species which are very shade tolerant distribute their leaves more evenly within their crown volume (Arseniou and MacFarlane 2021), whereas species that are less shade tolerant, e.g. *G. triacanthos*, have their leaves widely spaced mainly in the crown periphery, in order to increase crown porosity and reduce local self-shading (Sack et al. 2006). Furthermore, it has been suggested that inter-canopy variation of leaf traits is
predominantly affected by the exposure of leaves to light, which makes the sun leaves that are distributed in the crown periphery to be smaller, with greater leaf mass per unit area compared to the crown-interior leaves, in order to reduce water loss through transpiration (Abrams and Kubiske 1990, Sack et al. 2006). Therefore, the uneven distribution of leaves in the crown volume of the *G. triacanthos* trees, most of which are small sun leaves in the crown top, could explain why the contribution of leaves in the overall crown complexity was the smallest when compared to *Q. macrocarpa* and *M. glyptostroboides* trees.

3.9.3. The Effect of the Leaf-separation Algorithm on the Structural Complexity of the Trees

Very often, one is unable to laser-scan trees during the leaf-off conditions, either because they are evergreen or due to logistical constraints. Therefore, one of the goals of this study was to explore the effect of artificial leaf-removal from leaf-on point clouds. Separating the woody component from the foliage of tree point clouds using classification algorithms is a challenging task. Zhu et al. (2018), e.g., found a significant overestimation in the leaf area index of trees because of the woody material in tree point clouds.

There are different algorithms and approaches to separate leaves from the woody structure of tree point clouds (Vicari et al. 2019, Wang et al. 2018, Wang et al. 2019, Moorthy et al. 2020), but there is no single best solution that fits for all point classification cases in forests (Moorthy et al. 2020). Some of the factors that influence the classification results are the following: heterogeneity of point cloud density, varying scanner configurations and scanning protocols (Moorthy et al. 2020). The *TLSeparation* algorithm, which was used here, does not depend on a specific scanner (Vicari et al. 2019), and we tried to minimize the occlusion effects

in the point clouds in this study by scanning each tree from multiple directions and distances at high scanning resolution, following the field scanning protocols suggested by Wilkes et al. (2017). The performance of leaf separation algorithms is significantly decreased by occlusion (Vicari et al. 2019), but explicit accounting of this error source is challenging because we don't have a complete control over it, and different types of error can be correlated (Burt et al. 2021).

Errors in characterization of crown architecture should relate to leaf morphology (Moorthy et al. 2020). Wang et al. (2019) suggest that leaves are typically detected as simple, flat structures, and therefore, the oblong-leaf shape or the modular structure of compound leaves might confuse the classification algorithms. Indeed, our results indicate that the TLSeparation algorithm can be more accurate in identifying simple flat leaves, but had more difficulty separating twigs and fine branches from compound leaves. The Q. macrocarpa trees showed no statistical difference in D_b of the leaf-off and leaf-removed point clouds and this species has simple leaves with a single flat and lobbed blade (or lamina) (Efroni et al. 2010), which is associated with important leaf physiological functions e.g. convection-heat dissipation, efficient light interception and reduced leaf hydraulic resistance (Camarero et al. 2003, Sack et al. 2006). The *TLSeparation* algorithm (Vicari 2017) appears to have miss-classified many points of the woody structure as leaves for G. triacanthos, which have compound leaves with a modular architecture because the leaf blade consists from several leaflets stemming from the leaf rachis (Champagne and Sinha 2004, Klingenberg et al. 2012). The *TLSeparation* algorithm added significant noise into characterizations of D_b in *M. glyptostroboides* trees, which are deciduous gymnosperms, have oblong-shaped needles and branches that are either horizontal or curved upward (Ng and Smith 2020). We might expect the accuracy of the *TLSeparation* algorithm for needle-leaved trees to be lower compared to the classification accuracy of broad-leaved trees,

because needles are linear, and it is difficult to resolve an individual needle due to its small size and the dense foliage of conifers (Vicari et al. 2019, Wang et al. 2019). In a previous study, it was found that the artificial leaf-removal using a different leaf-separation algorithm (i.e. *LeWoS* algorithm) resulted into the underestimation of the total woody volume of trees in the generated QSMs, while only the stems and some large branches were detected in coniferous trees (Wang et al. 2019).

As was originally hypothesized, the percent relative error in the estimated crown complexity of the *G. triacanthos* trees, after artificial leaf-removal, was related to the branching architecture of the trees. More specifically, trees of this species with higher maximum branch order had greater %RE values, indicating that the presence of more bifurcations (branching nodes) and smaller branches of higher order can reduce the accuracy of the *TLSeparation* algorithm to classify the leaves and the woody parts. Indeed, increased branch bifurcation and angulation result into increased occlusion in the point clouds of trees that reduces the accuracy of the leaf-classification algorithm (Wang et al. 2018); in a previous study the point density of woody structures decreased for higher branch orders and therefore many points were miss-classified as leaves (Wang et al. 2019). The %RE values of the *M. glyptostroboides*, and *Q. macrocarpa* trees were not related to their maximum branch order, presumably because the leaf-removal algorithm did not significantly affect the accuracy of the D_b of the *Q. macrocarpa* and *M. glyptostroboides* trees on average according to the t-tests, although the D_b of the *M. glyptostroboides* trees after the artificial leaf-removal was imprecise.

3.10. Conclusions

This study used terrestrial laser scanning (TLS) to further refine our understanding of the above-ground structural complexity of urban trees by separating the effect of leaves from the effect of the woody skeleton. Differences in leaf on versus leaf-off structural complexity likely relate to different functional traits of trees for light capture optimization, reduction of selfshading and mechanical stability. As such, this study provides evidence that differences in the contribution of leaves to tree structural complexity could be an important indicator of where the plant lies on a "structural economics spectrum (SES)", which explains species-structural diversity in terms of tree architectural traits along a spectrum balancing light interception, carbon allocation and mechanical stability (Verbeeck et al. 2019). However, more species belonging to different functional groups must be included in future studies in order to further examine differences in the LCC, or a similar index, as part of the SES. This study provided evidence, along with previous studies (Wang et al. 2019, Moorthy et al. 2020), that the accuracy of leafseparation algorithms is affected by the leaf shape and type, but also that bias in the estimation of the above-ground structural complexity of trees after the artificial leaf-removal depends on the branching architecture.

LITERATURE CITED

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CHAPTER 4

WOODY SURFACE AREA MEASUREMENTS WITH TERRESTRIAL LASER SCANNING RELATE TO THE ANATOMICAL AND STRUCTURAL COMPLEXITY OF URBAN TREES

Arseniou, G., MacFarlane, D.W. and Seidel, D. (2021). Woody Surface Area Measurements with

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Abstract

Urban forests are part of the global forest network, providing important benefits to human societies. Advances in remote-sensing technology can create detailed 3D images of trees, giving novel insights into tree structure and function. We used terrestrial laser scanning and quantitative structural models to provide comprehensive characterizations of the woody surface area allometry of urban trees and relate them to urban tree anatomy, physiology and structural complexity. Fifty-six trees of three species (Gleditsia triacanthos L., Quercus macrocarpa Michx., Metasequoia glyptostroboides Hu & W.C. Cheng) were sampled on the Michigan State University campus. Variation in surface area allocation to non-photosynthesizing components (main stem, branches) related to the fractal dimension of tree architecture, in terms of structural complexity (box-dimension metric) and the distribution of "path" lengths from the tree base to every branch tip. Total woody surface area increased with the box-dimension metric, but it was most strongly correlated with the 25th percentile of path lengths. Urban trees mainly allocated woody surface area to branches, which changed with branch order, branch-base diameter, and branch-base height. The branch-to-stem area ratio differed among species and increased with the box-dimension metric. Finally, the woody surface area increased with the crown surface area of the study trees across all species combined and within each species. The results of this study provide novel data and new insights into the surface area properties of urban tree species and the links with structural complexity and constraints on tree morphology.

Keywords: terrestrial laser scanning, woody surface area, crown surface area, urban ecology, *Gleditsia triacanthos, Quercus macrocarpa, Metasequoia glyptostroboides*

4.1. Introduction

Urban trees provide a wide range of important ecosystem services, including temperature regulation, carbon storage, water purification, air pollutants uptake, biodiversity etc. (Heisler 1986, McPherson et al. 1994, McPherson 1998, Nowak and Crane 2002, MacFarlane 2009, Pretzsch et al. 2015, Casalegno et al. 2017, Tigges and Lakes 2017). Trees in urban areas are growing under very different conditions than forest-grown counterparts and it is important to study their architecture and their physiological performance (Calfapierta et al. 2015) to increase our understanding of their adaptability to urban environments (Arseniou and MacFarlane 2021).

The fundamental physiological processes of trees, including urban ones, include rates of respiration and photosynthesis, production efficiency, water balance, energy and gaseous exchange with the atmosphere, and leaching of nutrients from bark and leaves (Lambers et al. 2008, Pallardy 2008); all of these have long been hypothesized to relate to tree surface area (Whittaker and Woodwell 1967). The role of the leaf area and the crown surface area in tree carbon balance, through photosynthesis and respiration, is well known (e.g., Lambers et al. 2008, Pallardy 2008, Lehnebach et al. 2018, Seidel 2019b, Zheng et al. 2019) and tree respiration rates, in particular, are closely related to their woody surface area (Kinerson 1975, Kramer and Kozlowski 1979, Yoneda 1993, Bosc et al. 2003, Kim et al. 2007). Furthermore, the woody surface area of trees and their bark structure create a rich web of bark-using organisms (MacFarlane and Luo 2009). Therefore, the detailed quantification of the surface area of the woody components of trees is necessary for understanding their physiological ecology.

Whitaker and Woodwell (1967) published one of the earliest studies focused on tree surface area and highlighted the need to consider its relationship to tree structural complexity. Urban trees can have a very distinct above-ground architecture which can inform us about the

growth and functional limits of different tree species (Calders et al. 2020). Because competition for light (Metz et al. 2013) significantly reduces the structural complexity (i.e. inherent fractal character) of trees that grow in closed-forest conditions (MacFarlane et al. 2014, Eloy et al. 2017, Seidel 2018, Dorji et al. 2019), we expect that urban trees should better express their fractal character, due to the typically lower number, or complete absence of neighboring trees in cities. Of course, the highly heterogeneous growing environment of urban trees can affect the structural complexity of their crowns (Arseniou and MacFarlane 2021), but, in general, more open-grown, urban trees should have more evident fractal complexity compared to trees growing in forest stands. Therefore, focusing on open-grown urban trees gives us the opportunity to study important aspects of tree allometry, such as the above-ground woody surface area, considering their distinct structural complexity.

Woody surface areas, and particularly branch areas, have long proved difficult to measure (Weiskittel and McGuire 2006). Branch area has often been studied secondarily to leaf area estimation e.g., as a source of noise when trying to estimate leaf area index (e.g., Kucharik et al. 1998). Direct methods of woody surface area quantification are highly laborious, requiring destructive sampling, where trees are cut up into components and the surface areas of various parts are measured (e.g., Weiskittel and McGuire 2006). This has led to the necessity of developing allometric equations to generalize from destructive sampling data (e.g., Halldin 1985, Baldwin et al. 1997, Damesin et al. 2002, Weiskittel and McGuire 2006), to be applied to standing trees via easily measured allometric variables (e.g., diameter at breast height, crown length, crown ratio). However, allometric equations have been previously found to significantly underestimate the total woody surface area of trees (Meir et al. 2017, Malhi et al. 2018). Also,

destructive sampling, which is required to build allometric equations, can be highly problematic in urban areas, due to the additional challenges and costs of safely removing urban trees.

Many indirect methods of woody surface area estimation have been advanced. More specifically, different studies have utilized geometric approximations of stem, branch and crown shapes, branch surface area estimates from vertical photographs, multispectral canopy imaging, woody surface area derivations from principles of the pipe model theory and the branch divarication theory, and combinations of the previous methods (Whittaker and Woodwell 1967, Yoneda et al. 1990, Jennings et al. 1990, Yoneda 1993, Weiskittel and McGuire 2006, Zou et al. 2009, Inoue and Nishizono 2015). A major challenge for any of these methods is dealing with the structural complexity of trees (Whittaker and Woodwell 1967), which exhibits a fractal-like pattern (Seidel 2018) that is very common in ecology (Halley et al. 2004).

According to the pipe model theory (Shinozaki et al. 1964) and the WBE model (West et al. 1997) trees have a fractal-like branching architecture which consists from a network of selfsimilar branching shoots beginning at a central trunk and terminating in leaves at the ends of small twigs (Noordwijk and Mulia 2002, Mäkelä and Valentine 2006). Therefore, simple geometric representations of stem and branches to estimate woody surface areas are likely inadequate and inaccurate because they do not explicitly account for the structural (fractal) complexity of the woody skeleton of trees. However, recent advances in terrestrial laser scanning (TLS) provide new, non-destructive ways for quantifying the structural complexity of trees, including the prospect of directly measuring total tree surface area (Malhi et al. 2018). TLS instruments belong to active remote sensing and they emit laser pulses and capture "point clouds" of the surrounding environment by analyzing the returned energy as a function of either time (time-of-flight systems) or shift in the phase of the light wave of the emitted laser beam

(phase-shift technology), and by using precise angular measurements through optical beam deflection mechanisms (Calders et al. 2015, Liang et al. 2016).

The above-ground structural complexity of trees can be directly quantified from TLS data using the "box-dimension" (D_b) metric, also known as Minkowski - Bouligand dimension (Seidel 2018). The box-dimension metric is derived from fractal geometry principles (Mandelbrot 1983), and it is a measure of plant material density and distribution (Seidel et al. 2019a). The estimation of the total woody surface area of trees from TLS data does not rely on biological assumptions and it is relatively new (Malhi et al. 2018); for example Ma et al. (2016) used terrestrial laser scanning data to compute the woody to total surface area ratio of trees, to estimate their leaf area index. In general, TLS data have been previously used to mainly study other important aspects of tree allometry and ecology e.g. stem density, stem profiles and timber volume (Hopkinson et al. 2004, Maas et al. 2008, Moskal and Zheng 2011, Vonderach et al. 2012, Olschofsky et al. 2016), leaf and canopy properties (Danson et al. 2007, Strahler et al. 2008, Hosoi and Omasa 2009, Polo et al. 2009, Antonarakis et al. 2010, Moorthy et al. 2010, Béland et al. 2011, Jung et al. 2011, Metz et al. 2013, Béland et al. 2014, Li et al. 2017, Hu et al. 2018, Vicari et al. 2019), aboveground tree biomass and carbon stocks (Vonderach et al. 2012, Kankare et al. 2013, Calders et al. 2015, Stovall et al. 2017, Tanhuanpää et al. 2017).

In this study, we used TLS technology to produce novel woody surface area data for urban trees. The objectives of the study are the following: (i) to measure the total above-ground woody surface area of urban trees of different species; (ii) to examine the above-ground woody surface area allocation into stems and branches of different size and position in tree crowns (branch orders, branch base-diameter and branch base-height classes); (iii) to quantify the relationship between tree woody surface area and their fractal-structural complexity (i.e. the box-

dimension metric) and different Euclidean measures of tree architecture (i.e. metrics that account for the length of all paths from the tree base to each branch tip, and crown surface area).

4.2. Materials and Methods

4.2.1. Urban Tree Data

We chose open-grown urban trees as our object of study, because we expected to get better TLS-based measurements of tree attributes without occlusion from neighboring trees, but also because we expected that the low, or complete absence of competition from tree neighbors in cities should allow trees to better express their inherent fractal character in terms of structural complexity (MacFarlane et al. 2014, Eloy et al. 2017, Seidel 2018, Dorji et al. 2019).

Fifty-six trees, of three species, that represent different tree functional types were sampled on the Michigan State University campus: 18 *Gleditsia triacanthos* L. trees (Honey locust; compound-leaved, deciduous angiosperms), 15 *Quercus macrocarpa* Michx. trees (Bur oak; entire-leaved, deciduous angiosperms), and 23 *Metasequoia glyptostroboides* Hu & W.C. Cheng trees (Dawn redwood; needle-leaved, deciduous gymnosperms). The trees were selected to cover a large range of sizes (Table 4.1, from 10.9 cm to 122.2 cm DBH). Since all species were deciduous we were able to study their total woody surface area during the leaf-off period (Fig. 4.1). Of particular interest was *M. glyptostroboides*, which was selected because we wanted to study the structure of an urban-grown, needle-leaved gymnosperm, that could be scanned (alive) in a leaf-off condition; it is difficult to get complete, non-occluded scans of the stems and branches of needle-leaved evergreen species (Stovall et al. 2017).

Laser scanning of the *G. triacanthos* and *Q. macrocarpa* trees was accomplished, with leaves-on, in July and August 2019. The *M. glyptostroboides* trees were scanned, with leaves-on,

in August 2020. The leaf-on tree point clouds allowed the estimation of the crown surface area of the trees (see specific methods below). The same trees were also laser-scanned in leaf-off condition, in January, February and March 2020, in order to estimate their woody surface area (see specific methods below). Before re-scanning the study trees, we confirmed that they were not pruned by the Michigan State University arborists between July 2019 and August 2020. Following this experimental design, pruning did not impose any bias in the estimation of the woody surface area and crown surface area of the study trees, during the study period. Of course, past pruning events could have affected the tree structure observed.



Figure 4.1. Leaf-off images of (A) a *G. triacanthos* tree, (B) a *Q. macrocarpa* tree, (C) a *M. Glyptostroboides* tree. All trees have been flagged with a pink-color tape.

4.2.2. Terrestrial Laser Scanning and Point Cloud Processing

All trees were scanned with the FARO Focus3D X 330 terrestrial laser scanner, which operates with laser light of 1550 nm wavelength, typical beam divergence 0.19 mrad, and range 0.6 m - 330 m. Each individual tree was scanned with high resolution from a minimum of four different directions and distances in order to minimize occlusion effects, and six reference target-spheres were placed around each focal tree to spatially reference all scans and create a single

point cloud for each tree following the field scanning protocols suggested by Wilkes et al. (2017). The first two scans of each tree were conducted in opposite directions from distances that allowed the top of the tree to be clearly visible. The other two scans were conducted in opposite directions (perpendicularly to the first two scans) from a closer distance to the focal tree to better capture its branching architecture and get closer views of the main stem. For large trees with complex crowns two or three additional scans were conducted below the tree crown to capture more dense point clouds of the branches. All laser scans were conducted when there was little or no wind.

Spatial co-registration and noise-filtering of all scans was automatically performed using the software SCENE 2019.2 (FARO Technologies Inc., USA, 2019.2). Using the same software, each tree was manually separated from the point cloud of the urban site background. This process was judged as an accurate alternative to an automatic segmentation process (Seidel 2019a).

4.2.3. Tree Reconstruction from Quantitative Structure Models

Quantitative Structure Models (QSMs; Raumonen et al. 2013, Kaasalainen et al. 2014, Hackenberg et al. 2015, Bournez et al. 2017) describe the three-dimensional architecture of trees by fitting cylinders to a tree's point cloud. QSMs preserve branch and stem topology and provide information about the size, the location, the hierarchy and the orientation of the branching network; they are currently considered to be the most robust method to model tree volume and tree-architecture (Disney et al. 2018).

Quantitative structure models (QSMs) were generated from the leaf-off point clouds of the trees, with the algorithm *TreeQSM* v.2.3.0 (Copyright (C) 2013-2017 Pasi Raumonen) (see

example in Fig. 4.2). There are two main steps for the tree reconstruction from a single point cloud based on this algorithm. The first step is the point cloud segmentation into stem and branches based on cover sets, and the second step includes the reconstruction of the volume and the surface area of the segments with cylinders (Calders et al. 2015, Raumonen et al. 2015). *TreeQSM* generated multiple QSMs for each tree point cloud based on different values for the minimum and maximum size of the cover sets and it finally determined the optimal QSM for each study tree (Raumonen et al. 2013). Based on the optimal QSM parameters the algorithm produced 30 additional QSMs for each study tree in order to quantify the variation of the modeled tree variables, because of the inherent stochastic component of *TreeQSM* (Raumonen et al. 2013).

The definition of the main stem of a tree according to *TreeQSM* is based on three criteria: (1) the main stem extends near the top of a tree, (2) it goes almost straight up, and (3) it is not too curved which means that the ratio of the stem length to the stem base-tip distance, must be the minimum among all candidate main stems (P. Raumonen, personal communication, 2 June 2020). After the main stem has been determined, the first-order branches (i.e. branches attached to the main stem) are defined based on the following criteria: they are the farthest-reaching candidates, with the ratio of the branch length over the branch base-tip distance to be less than 1.2, and the branch base-tip distance to be over 75% of the maximum. The branch length/distance ratio will iteratively increase if no candidates with ratio equal to 1.2 exist. The second-order branches are attached to the first-order branches, and they include the candidates with the longest branch base-tip distance. Branches of higher order are defined following the same rules attached to the second, third, fourth order, etc. (P. Raumonen, personal communication, 2 June 2020).

4.2.4. Tree Woody Surface Area Computation

From the optimal QSMs of the leaf-off scans of the urban trees, their total woody surface area (WSA, m²) was computed as the total surface area of the cylinders that were fitted to the point cloud of each tree (Fig. 4.2). Note: total "woody" surface area in this study is technically the surface area outside of the bark tissues. Next, the total WSA of each tree was separated between the main stem woody component and the branches woody component. The branch WSA was further analyzed by branch order (there was a maximum of eleven branching orders across all species combined), by branch-base diameter classes of 1 cm size from the diameter of the cylinder at the base of a branch (there were 48 classes across all species combined), and by branch-base height classes of 1 m size, based on the height from the base of a tree to the base cylinder of a branch (there were 25 classes across all species combined; described in detail in the results section).



Figure 4.2. (A) The leaf-off point cloud of the *G. triacanthos* tree from Fig. 4.1. (artificially colored with brown color) (B) The QSM of the same tree. (C) A close-up picture of the generated QSM, composed of many cylinders fitted to the point cloud data. The colors denote the different branching orders i.e. the main stem is colored blue, the 1st order branches are colored green, the 2nd order branches are colored red etc. Four facets have been used to visualize the QSM cylinders.

4.2.5. Computation of Other Tree Structural Metrics

We wanted to study how WSA related to other published metrics of tree architectural complexity. Smith et al. (2014) examined a metric called the "path fraction", which is the mean length of all "paths" through the branching network, from the stem base to all branch tips, divided by the maximum path length. Path lengths are Euclidean metrics of tree structure and they can be calculated from a QSM based on the lengths of the cylinders whose topological hierarchy is preserved in a QSM. However, we did not simply use the QSM for each tree to compute Smith et al.'s path fraction, but instead we looked at various statistics from the distribution of path lengths, to take advantage of the rich data provided. This included the quantiles of the path lengths (25th, 50th and 75th percentiles), as well as minimum, maximum, mean and standard deviation of path lengths.

We computed the box-dimension (D_b ; Seidel 2018), as a direct measure of above-ground structural complexity, calculated directly from the leaf-off point cloud of each tree. D_b has the advantage of not having to apply a QSM to the data; it uses only the original tree point cloud. The D_b metric takes into account the number of boxes that are needed to encapsulate all points of a laser-scanned tree, and how the number of boxes varies with the ratio of the box size to the original box size, which is defined as the smallest box that encapsulates the whole tree (Seidel et al. 2019b). The smallest box encapsulating the entire tree point cloud is the so-called "upper cutoff", as it represents the largest box applied to the tree for counting the number of consecutive boxes needed. Consecutive boxes always have half the edge length of the previous box so that eight of them fit exactly in the initial box. The smallest box-size among all boxes is the so-called "lower cut-off", and it was defined to be 10 cm in this study (Fig. 4.3 A). It is a very liberal estimate of the maximum distance between two neighboring laser points at any given location in

the tree. The "lower cut-off" must ensure that no virtual box is considered empty only because it fits in the "unsampled" space that was not reached by any laser beam of the laser scans. This "unsampled" space may be the result of the diverging beams emitted from the scanner leaving unscanned areas at greater distances to the scanner or simply due to occlusion effects in the tree.

 D_b is equal to the slope of the least-squares line when the logarithm of the number of boxes is regressed against the logarithm of the inverse of the size of a box relative to the size of the initial box (Seidel 2018, Seidel et al. 2019b) (Fig. 4.3 B). D_b , which is unitless, takes values between one and three. Values smaller than one are only possible if the "lower cut-off" has not been properly chosen (i.e. mean distance between neighboring points is greater than the edge-length of the smallest box). Values of three (or greater) are not possible in reality, because it would imply that a tree is a solid cube. D_b values close to but smaller than three imply trees with greater crown complexity and "space-filling character", whereas, a perfectly cylindrical stem without branches would have D_b equal to one (Seidel 2018). Both the path fraction (Smith et al. 2014) and the D_b (Seidel 2018) metrics are meant to capture the fractal-like nature of trees (West et al. 1997, Noordwijk and Mulia 2002, Mäkelä and Valentine 2006; metabolic scaling theory), which should explain portion of the variation in their WSA.



Figure 4.3. (A) Illustration of the virtual boxes of different sizes that capture the leaf-off point cloud of a *G. tiacanthos* tree. (B) The log-log plot for the quantification of the box-dimension metric for the same tree. The regression line slope is the box-dimension of the tree i.e. $D_b = 2.05$. *N* is the number of boxes required to capture all points of the tree point cloud, *r* is the size of the length of each box, and *r_initial* is the size of the length of the initial box that encapsulates the whole tree. The 95% confidence interval has been plotted around the regression line.

Finally, the crown surface area of the study trees was computed as the convex hull from the leaf-on laser points of a tree's crown using Heron's formula to quantify the triangles that create the surface of this hull (Metz et al. 2013); in this study it refers to the photosynthetically-active surface area of a tree (Seidel et al. 2019b, Zheng et al. 2019).

4.2.6. 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). Regression analysis was used to relate the total WSA, and the branch to stem WSA, with the metrics of crown complexity and tree architecture (see subsection 4.2.5). Correlation strengths were quantified with the Pearson correlation coefficient (*r*) and the statistical significance of the relationships was assessed at $\alpha = 5$ % level.

The total WSA of the trees was modeled as a power function of the metrics described in the subsection 2.5 in order to explore the relationship between WSA and these metrics. The power function form was selected because it had a better fit to the data compared to the linear model form and because power functions better describe the multiplicative processes of tree allometry (e.g. WSA allometry), and they are scale-invariant (Sileshi 2014). Species was added in the candidate models as a random, grouping variable that influences the exponents of the predictor variables.

The mixed-effects model is of the form:

WSA =
$$b * D_{b}^{(c+S)} * L^{(d+S)} + \varepsilon$$
, (eq. 4.1)

Where WSA is the total woody surface area (m^2) of the trees, b is the normalization constant, D_b is the box-dimension (unitless), L is one of the path length metrics in meters that were described previously, c is the scaling exponent parameter of the box-dimension (fixed effect), d is the scaling exponent parameter of the path length metrics (fixed effect), and S is the species random effect which is added in the candidate models to modify the c and d parameters and it has three levels (i.e. *G. triacanthos*, *Q. macrocarpa*, and *M. glyptostroboides*). The error term (ε) has a multiplicative structure, which is additive on a log-log scale. 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. The "nlme" function of the linear and nonlinear mixed effects models ("nlme") R package (Pinheiro et al. 2021) was used to fit models. The best models were selected considering both the coefficient of determination (adjusted R²) and the Akaike Information Criterion (AIC). A one-way analysis of variance (ANOVA) test, with unequal variances, was used to evaluate differences in the mean value of the branch to stem WSA ratio across the three species combined (i.e. *G. triacanthos*, *Q. macrocarpa*, and *M. glyptostroboides*). A one-way ANOVA test was also used to evaluate differences in mean WSA of branches per branch order, per branch-base diameter class, and per branch-base height class, across and within the abovementioned species. For these tests the WSA of all branches belonging to different classes for every study tree was considered. In all ANOVA tests the normality of the data in each group was checked with Q-Q plots, and significant differences in group means were assessed at $\alpha = 5$ %. Finally, the coefficient of variation was used to quantify the uncertainty in estimating total WSA from the consecutive QSM reconstructions of the same point cloud of a tree.

4.3. Results

4.3.1. Estimated Total and Component Woody Surface Areas

Basic tree measurements and surface areas computed for the study trees are shown in Table 4.1, along with other tree statistics (discussed later). The data show that trees varied widely in their surface areas and other metrics of complexity.

Table 4.1. Summary statistics resulting from different measurements of tree size and structural complexity. DBH = Diameter at Breast Height (cm), WSA = Woody Surface Area (m²), CSA = Crown Surface Area (m²), CV = Coefficient of Variation, $D_b = Box$ -Dimension, SD = Standard Deviation (m), Min = Minimum (m), Max = Maximum (m).

| Summary Statistics | All trees | Gleditsia | Quercus | Metasequoia |
|---|-----------------------|-------------------|-------------------|--------------------|
| - | . | triacanthos | macrocarpa | glyptostroboides |
| no. trees | 56 | 18 | 15 | 23 |
| DBH (cm) (mean [min, max]) | 53.4 [10.9, 122.2] | 53.4 [18.4, 72.8] | 58.8 [29.0, 83.8] | 49.8 [10.9, 122.2] |
| Height (m) (mean [min, max]) | 13.8 [3.8, 24.1] | 12.5 [10.4, 18.4] | 15.8 [9.1, 21.3] | 13.6 [3.8, 24.1] |
| CSA.leaf.on (m^2) | 611.9 [78.3, | 663.9 [203.6, | 747.8 [172.9, | 407 [78.3, |
| (mean [min, max]) | 1238.9] | 1017.4] | 1238.9] | 1217.1] |
| Total WSA (m ²) | 199.3 [13.9, | 267.6 [65.2, | 225.4 [60.4, | 128 0 [12 0 272] |
| (mean [min, max]) | 467.0] | 408.6] | 467.0] | 128.9 [13.9, 372] |
| CV WSA | 0.024 [0.005, | 0.027 [0.007, | 0.024 [0.005, | 0.021 [0.007, |
| (mean [min, max]) | 0.07] | 0.054] | 0.047] | 0.07] |
| Stem WSA (m ²) (mean [min, max]) | 12.5 [1.5, 44.6] | 11.3 [4.1, 20.1] | 16.2 [4.7, 30.3] | 11.0 [1.5, 44.6] |
| Branch WSA (m ²) | 186.8 [12.4, | 256.3 [61.2, | 209.2 [55.7, | 117.9 [12.4, |
| (mean [min max]) | 436.7] | 395.5] | 436.7] | 352.9] |
| # of branch orders | _ | | | |
| (median [min, | 5 [1, 11] | 5 [1, 11] | 5 [1, 10] | 4 [1, 9] |
| max]) | | | | |
| D _b leaf.off (mean | 1.98 [1.82, 2.15] | 2.03 [1.84, 2.11] | 1.92 [1.82, 2.04] | 1.99 [1.84, 2.15] |
| [min, max]) | | | | |
| Mean Path length | | | | |
| (m) (mean [min, | 12.4 [3.7, 23.9] | 14.6 [9.5, 22] | 14.0 [6.9, 23.9] | 9.8 [3.7, 23.8] |
| max]) | | | | |
| Min Path length | | | | |
| (m) (mean [min, | 3.4 [0.8, 7.9] | 4.5 [2.4, 7.0] | 3.7 [2.1, 7.0] | 2.3 [0.8, 7.9] |
| max]) | | | | |
| Max Path length | | | | |
| (m) (mean [min, | 22.1 [6.5, 44.0] | 24.5 [17.3, 37.5] | 24.9 [12.3, 42.7] | 18.5 [6.5, 44.0] |
| max]) | | | | |
| SD Path length (m) | 3.1 [1, 6.9] | 2.8 [2, 5.1] | 3.6 [1.5, 6.1] | 2.9 [1, 6.9] |
| (mean [min, max]) | | | | |
| 25 th % Path length | 10.4 [2.9, 20.6] | 13 [7.7, 18.1] | 11.7 [5.4, 20.6] | 7.7 [2.9, 19.5] |
| (mean [min, max]) | | | | |
| 50 th % Path length | 12.5 [3.6, 24.5] | 14.6 [9.8, 23] | 14.1 [6.6, 24.1] | 9.7 [3.6, 24.5] |
| (mean [min, max]) | | | | |
| 75 th % Path length | 14.4 [4.4, 28.7] | 16.1 [11.4, 25.1] | 165[83 287] | 11 7 [4 / 28] |
| (mean [min, max]) | | | 10.5 [0.5, 20.7] | 11.7 [+.4, 20] |

Branches comprised the greatest portion of WSA of the urban trees studied; the branch to the main stem woody surface area (BMS) ratio ranged between 4.3 and 38.6 with mean value of 16.3 across all study trees. ANOVA showed that mean BMS differed significantly among the three species i.e. *M. glyptostroboides* (MEGL), *G. triacanthos* (GLTR) and *Q. macrocarpa* (QUMA) (p < 0.001). *G. triacanthos* had the highest mean BMS value compared to the trees of the other two species: mean BMS_{GLTR} = 24.1, mean BMS_{QUMA} = 13.4, and mean BMS_{MEGL} = 12.1. Furthermore, a strong positive relationship was found between the BMS ratio and the D_b metric of the trees (r = 0.6, p < 0.001).

The median branch order was five across all study tree species combined (range 1 to 11, Table 4.1), with *M. glyptostroboides* showing fewer branch orders than the two angiosperm species (median 4, range 1 to 9). ANOVA showed that the branch woody surface area (BWSA) significantly differed among the different branch orders across all study tree species combined and within each species (p < 0.001). BWSA was mainly accumulated in lower branch orders and the distribution of surface area was positively skewed (Fig. 4.4). Second and third order branches supplied the greatest amount of BWSA across all study tree species combined, and for *Q. macrocarpa* trees (Fig. 4.4 A, C). BWSA came mainly from second, third and fourth branch orders in *G. triacanthos* trees (Fig. 4.4 B), and from lower order (first, second and third) in *M. glyptostroboides* trees (Fig. 4.4 D).



Figure 4.4. Box-plots of branch woody surface area per branch order across (A) all species combined, (B) for *G. triacanthos* trees, (C) *Q. macrocarpa* trees, and (D) *M. glyptostroboides* trees.

Examination of BWSA by branch basal diameter (Fig. 4.5) indicated that the BWSA followed a positive skewness, but with a somewhat bimodal distribution (except for the *M*. *glyptostroboides* trees). Medium-sized branches (between 4 and 11 cm base diameter approximately) and large branches (more than 35 cm base diameter approximately) accumulated much of the BWSA, while small branches and twigs (less than 4 cm base diameter), though numerous, accumulated a relatively small portion of the BWSA (Fig. 4.5 A - D). ANOVA confirmed that the BWSA differed statistically among the different branch-base diameter classes across all species combined and within each species (p < 0.001).

Some large trees showed very large branches, with a basal diameter greater than 35 cm (Fig. 4.5). These "branches" were actually large forks in the stem, common to large, open-grown, urban trees (see Fig. 4.1), which the *TreeQSM* algorithm defined as branches. At a major fork,

the QSM determines the longest, straightest stem to the top of the tree as main stem (see details in the methods section above), and calls the others branches.



Figure 4.5. Box-plots of branch woody surface area per branch-base diameter class across (A) all species combined, (B) for *G. triacanthos* trees, (C) *Q. macrocarpa* trees, and (D) *M. glyptostroboides* trees. The size of each class is 1 cm.

Because the topology of the trees is captured by the QSM, we were also able to examine how surface area was distributed vertically in the trees (Fig. 4.6). The BWSA differed statistically (as assessed with ANOVA) among the different branch-base height classes across all study tree species combined and within each species (p < 0.001). Graphical analysis (Fig. 4.6) shows a parabolic distribution of relative BWSA for all study tree species combined peaking near the midpoint of the crown (0.5 on the y axis in Fig. 4.6 A). Relative BWSA peaked higher up in the tree for *G. triacanthos* trees (Fig. 4.6 B), about the midpoint for *Q. macrocarpa* trees (Fig. 4.6 C), and below the midpoint for *M. glyptostroboides* trees (Fig. 4.6 D).


Figure 4.6. Relative vertical distribution (branch base height divided by total tree height) of branch woody surface area (proportion of total branch area) for (A) all study trees, (B) *G. triacanthos* trees, (C) *Q. macrocarpa* trees, and (D) *M. glyptostroboides* trees. Horizontal dashed line is halfway up the tree.

4.3.2. Uncertainty Analysis of the Estimated Woody Surface Areas

The coefficient of variation of the WSA of the trees indicated that the uncertainty due to the consecutive QSM reconstructions of the same point cloud of a tree was on average 2.4% of the mean WSA per tree across all study tree species combined, and the *G. triacanthos* trees had the highest uncertainty (on average 2.7% of the mean WSA per tree, Table 4.1). The distribution of the coefficient of variation of the WSA of the trees was positively skewed across all study tree species combined and within each species and bimodal for the *G. triacanthos* and *M. glyptostroboides* species (Fig. 4.7 A-D).



Figure 4.7. Density plots of the coefficient of variation of the woody surface area (CV WSA) for (A) all study trees, (B) *G. triacanthos* trees, (C) *Q. macrocarpa* trees, and (D) *M. glyptostroboides* trees.

4.3.3. Relationships Between Woody Surface Area and Metrics of Tree Architecture and Structural Complexity

Significant, positive relationships were found between the WSA of the urban trees, and the D_b metric, and the different metrics that account for the length of all paths from the tree base to each branch tip (Table 4.2, Fig. 4.8 A-H). The strongest positive relationship was found between the WSA of the trees and the 25th percentile of path lengths (Pearson's r = 0.87, p <0.001, Fig. 4.8 F). However, the relationships between the WSA and the 25th percentile of path lengths, the mean path length, and the 50th percentile of path lengths, were not very different (Fig. 4.8). The best and most parsimonious predictors of WSA (eq. 4.1) were the combination of the D_b metric and the 25th percentile of path lengths with species effects (Table 4.2). The correlation between the D_b metric and the other predictor variables in each model of WSA (Table 4.2) was not statistically significant (i.e. p > 5 %). **Table 4.2.** Woody surface area models with the highest adjusted R^2 and lowest AIC values among all candidate models fitted to the data. Tree woody surface area (WSA) was modeled as a power function of different predictor-combinations (eq. 4.1), including box-dimension (D_b) and various statistics of path length (L), mean and the 25th, 50th, and 75th percentiles of path lengths. The character "| spp" denotes that species was added as a random effect, modifying the exponent of each predictor variable in the model. Best model by each statistic is highlighted in bold.

| Model | Adjusted R ² | AIC |
|---|-------------------------|--------|
| WSA ~ D_b + Mean L spp. + ε | 0.856 | 599.02 |
| WSA ~ $D_b + 25^{th}$ % L spp. + ϵ | 0.863 | 595.49 |
| WSA ~ $D_b + 50^{th} \% L \mid spp. + \epsilon$ | 0.855 | 599.78 |
| WSA ~ $D_b + 75^{th} \% L \mid spp. + \epsilon$ | 0.852 | 601.38 |



Figure 4.8. Relationships between the woody surface area of the study trees (WSA in m²) and (A) the box-dimension metric, (B-H) different path length metrics with 95% confidence interval around the regression lines. The SpCode refers to the three species codes i.e. *M. glyptostroboides* (MEGL), *G. triacanthos* (GLTR), and *Q. macrocarpa* (QUMA). The three species are represented with different symbols and colors.

The WSA was positively correlated with the crown surface area across all study tree species combined, and within each species (Fig. 4.9 A-D, p < 0.001).



Figure 4.9. Relationships of the woody surface area (WSA in m^2) with the crown surface area (CSA in m^2) of (A) all study trees, (B) *G. triacanthos* trees, (C) *Q. macrocarpa* trees, and (D) *M. glyptostroboides* trees. The data points of the three species are represented with different colors. The 95% confidence interval has been plotted around the regression lines.

4.4. Discussion

4.4.1. Advances in Urban Tree Surface Area Measurement

In this study, we used active remote sensing (TLS) to produce detailed WSA data for urban trees. Measuring the total surface area of the woody parts of trees has been challenging in the past with the only direct method via destructive sampling which has been particularly challenging and undesirable for large trees in urban areas. This study provided the first comprehensive measurements of the total above-ground WSA of urban trees with TLS, including the relative surface area of branch versus stem WSA and complete vertical characterizations of BWSAs for branches of different size and order. TLS has become an important tool used to quantify the three-dimensional structure of trees (Disney et al. 2018, Malhi et al. 2018) and more accurate measurements of tree surface area may be the most important new advance in tree measurements associated with this technology. Data from Mobile Laser Scanning (MLS) could also be used to study the WSA of trees covering larger spatial scales if occlusion effects in the point clouds are not significant. According to Dorji et al. (2021) MLS data can be used to study the structural complexity of trees based on fractal analysis and quantified by the D_b metric.

With any new measurement system come new sources of uncertainty. Our field procedure was designed to minimize occlusion effects in the tree point clouds by scanning the study trees from multiple directions and distances (see subsection 4.2.2). This reduced the estimation uncertainty due to cylinder size and cylinder fitting errors in the generated QSMs (Calders et al. 2015). The uncertainty in the estimates due to the consecutive QSM reconstructions of the same point cloud of a tree, comprised only a small portion of the estimated WSA across all study trees combined. This was on average 2.4% of the mean WSA per tree across all species combined (Table 4.1), while very few trees had coefficient of variation of their WSA larger than 5% (Fig. 4.7 A-D). Therefore, the consecutive QSM reconstructions of a tree provide precise WSA estimates. This does not mean that the QSMs do not introduce bias, such as systematically over- or under- estimating surface areas of different parts of the trees, when identifying them from the point clouds.

Some large study trees had large branches with max QSM base-diameter greater than 35 cm. Diameter overestimation of large branches (i.e. larger than 40 cm) is usually quite small in the QSMs generated by the *TreeQSM algorithm* (P. Raumonen, personal communication, 4 March 2021), but parts of forked stems can also be interpreted as branches. In other studies

where branches were destructively sampled, an underestimation of 6% in QSM base-diameter was found for branches, with actual base-diameter greater than 60 cm, while a diameter underestimation of 8% was observed for branches with diameters between 20 cm and 60 cm (Lau et al. 2018, Lau et al. 2019). So, we are confident in the general accuracy of the BWSA values produced in this study.

4.4.2. Relationships of the Woody Surface Area of Trees Explained by Major Theories of Tree Structure (WBE Model and Pipe Model Theory)

It has been suggested that variation in branch area is related to the diameter of a branch and its position in the crown (Baldwin et al. 1997, Weiskittel and McGuire 2006). It was found here that medium and large-sized branches (based on their basal-diameter), of lower branching orders, accumulated the largest portion of the total BWSA. This pattern can be interpreted in the light of the pipe model theory (Shinozaki et al. 1964) and the WBE model (West et al. 1997, West et al. 1999), which connect tree structure with tree physiology. Both theories assume a fractal branching architecture whose vascular structure is an assemblage of tubes that taper from base to tip; so larger, lower-order branches accumulate more conducting and non-conducting tubes over their length, resulting in greater cumulative volume that scales with WSA (Enquist 2002). Similarly, Weiskittel and McGuire (2006), found that on average 82% of the total branch surface area in Douglas-fir (*Pseudotsuga menziesii*) trees was allocated into primary branches (those attached to the main stem). However, Meir et al. (2017) found that small branches significantly contributed to the WSA of trees growing in a tropical rainforest.

According to the models produced in this study, much of the variation in the nonphotosynthetic surface areas of urban trees can be explained by a combination of fractalstructural complexity (quantified by the D_b metric), and "hydraulic" size (quantified by the Euclidean metric of the 25th percentile of the path lengths, see Smith et al. 2014), which are constrained by the genetics of tree species.

Smith et al. (2014) defined the path fraction metric as the ratio of the mean path length to the maximum path length from the tree base to each branch tip, in order to quantify to what extent a real branch network differs from an ideally fractal branch network, such as that described by the WBE theory. In this study, the path fraction was not significantly related to the WSA of the trees, but as expected, significant relationships were found between the WSA and various statistics from the distribution of path lengths. This suggests that the absolute mean, variation and distribution of path lengths may better help to characterize surface area complexity than the mean *relative* path length (a.k.a. the path fraction of Smith et al. 2014). Weiskittel and Maguire (2006) found that the WSA of Douglas-fir (*Pseudotsuga menziesii*) trees increased with crown length, which agrees with the positive relationship that was found in this analysis between the total WSA of the urban trees and the 25th percentile of the path lengths, which is the frequency of the short-path lengths that affects crown length.

The WSA of the studied urban trees was found to increase with their fractal-like architecture, as quantified by the D_b metric (Seidel et al. 2019b). According to the WBE model (West et al. 1997), this pattern implies efficient respiration rates and sufficient supply for energy demanding units, e.g. leaves, chloroplasts (Price and Enquist 2006), because the inherent fractal character of trees allows them to maximize the scaling of their external surface areas for gas exchange with the atmosphere, while minimizing the internal vascular distances for transferring and allocating the available resources to different organs and tissues (West et al. 1999, Enquist 2002, Price and Enquist 2006).

An important issue to consider, when analyzing the relationships between surface areas and metrics of crown fractal complexity, is whether the observed patterns are confounded with tree size (e.g. DBH, total tree height etc.). The D_b metric is reported to be scale and tree-size independent (Seidel et al. 2019a, Seidel et al. 2019b), and therefore, we can use it to compare trees of different size (Seidel et al. 2019b). Further analysis showed that the relationship between the total woody volume of the study urban trees computed from QSMs and the D_b metric was not statistically significant (p > 5%), suggesting that both smaller and larger -volume trees can be structurally complex. This could mean that architectural changes that occur through the ontogeny of trees, e.g. development of higher order branches and altered stem to branch relationships (Seidel et al. 2019a), might explain more complex structures in larger trees, more than their size, *per se*.

4.4.3. Anatomical and Physiological Implications of Surface Area Allocation Patterns

The surface area distribution found for these urban trees and the theories described in the previous sections have implications for understanding the anatomical structure and physiological function of urban trees, and trees in general. This study enabled not only the computation of the total WSA of trees, but also the analysis of its distribution into different components (stem and branches).

As expected, the branch-to-stem surface area ratio of the trees was found to increase with their structural complexity (as captured by the D_b metric), underscoring the contribution of branching to crown complexity (Seidel et al. 2019b). This ratio was found to significantly differ among the studied species, so, in this sense, it describes the resource allocation "decision" of

different species to invest in increasing branch versus stem surface areas, as a functional response to urban environments. The squat form of urban trees (i.e. a wide tree crown with a short trunk) gives them mechanical stability against wind loads in cities (MacFarlane and Kane 2017), and reflects the tendency of trees to allocate less resources to growing a taller main stem as the crowding conditions decrease (Weiner 2004, MacFarlane and Kane 2017). Mäkelä (1997) found that "branchiness" of Scots pine (*Pinus sylvestris*) trees (described as the ratio of total branch cross-sectional area to stem surface area), increased as stand density decreased. So, this pattern appears to hold for trees growing in both rural and urban areas. As such, the branch to stem surface area ratio could be an important component of the plant "structural economics spectrum", which explains species-structural diversity in terms of tree architectural traits along a spectrum balancing light interception, carbon allocation and mechanical stability (Verbeeck et al., 2019).

WSA of trees relates to their respiration rates and captures broad maintenance costs (Kinerson 1975, Kramer and Kozlowski 1979, Yoneda 1993, Bosc et al. 2003, Kim et al. 2007) and crown surface area refers to the photosynthetically active surface of trees and their energy income (Seidel 2019b, Zheng et al. 2019). Therefore, the strong and positive relationship that was observed between the two surface areas (across all study tree species combined and within each species) implies that as the respiration rate of a tree increases, its production efficiency should also increase in order to maintain sustainable growth. Otherwise, trees should lose vigor.

For trees in natural forests and plantations, the distribution of branches and foliage is heavily influenced by shading or sheltering from neighboring trees (MacFarlane and Kane 2017), but particularly the need to maintain a positive carbon balance in the leaves. Weiskittel and McGuire (2006) showed that branch surface area peaked a bit below the middle of the crowns of

Douglas-fir (*Pseudotsuga menziesii*) trees, because smaller branches near the top had considerably less surface area, while large, lower branches, with greater surface area, tended to dieback over time, due to a reduction in sustaining leaves on branches near the base of the crown. Xu and Harrington (1998) found that sub-dominant trees in a plantation of Loblolly pine (*Pinus taeda*) distributed most of their foliage at the top third of their crowns. These patterns might be expected for trees of species which are less tolerant of shade; Niinemets and Valladares (2006) produced numerical tolerance indices ranging from 1 to 5 (1 = very intolerant to 5 = very tolerant) ranking *Pinus taeda* = 1.99 and *Pseudotsuga menziesii* = 2.78.

The three urban tree species studied here showed a branch surface area vertical distribution inversely corresponding to Niinemets and Valladare's (2006) shade tolerance indices, with *Gleditsia triacanthos* = 1.61, *Quercus macrocarpa* = 2.71, and *Metasequoia glyptostroboides* = 3.00, showing patterns of branch area peaking in the upper-mid, middle and lower-mid crowns, respectively (Fig. 4.6). This result was somewhat surprising, since these trees were open-grown and not shaded by other trees. This suggests that self-shading of leaves and branches could be an important element of the branching architecture of open-grown trees (Duursma et al. 2010) along with inherent shade tolerance (Zeide and Pfeifer 1991), but also suggests a mechanism other than maintaining positive carbon balance in leaves might be at play.

Another physiological explanation of this pattern of branch woody surface distribution could be a need to counterbalance optimizing light energy capture with the need to minimize the surface area for heat gain due to incoming solar radiation, and water loss through transpiration. It is well known that warm temperatures and heat islands in cities (Gregg et al. 2003, Bowler et al. 2010, Kostić et al. 2019) cause increased rates of leaf transpiration (Pallardy 2008). Niinemets and Valladare's (2006) also published drought tolerance indices for the study species (drought

tolerance for *Gleditsia triacanthos* = 4.98, *Quercus macrocarpa* = 3.85, and *Metasequoia* glyptostroboides = 2.38), showing that the more drought-tolerant the species, the more it concentrated branch surface area toward the upper crown (see Fig. 4.6).

Niinemets and Valladare (2006) showed, over many species, that inherent traits of shade and drought tolerance of species were often negatively correlated, so the above pattern was expected. However, this study suggests that, at least for the case of open-grown, urban trees, building a branching architecture that optimizes drought tolerance may be a good explanation for branch surface area distribution. It may be that hydraulic limitations are not only an important force limiting the size and hydraulic architecture of tall trees (Ryan and Yoder 1997, Ryan et al. 2006), but also for the branching architecture of any tree whose physiological water stress exceeds their photosynthetic capacity. These findings have important implications for the management of urban forests, particularly the selection of species for urban plantings, given expected, continued increases in global temperatures and urbanization.

While surface area data have long been available for leaves (Lindsey and Bassuk 1992, Nowak 1996, Cutini et al. 1998, Reich 2001, Peper and McPherson 2003, McPherson et al. 2016, Dettman and MacFarlane 2018, Chianucci et al. 2019), TLS, in combination with QSMs, can now be used to quantify the surface area of the "woody skeleton" of trees, which plays a vital role in gas exchange with the atmosphere. Tree respiration rates are closely related to their WSA (Kramer and Kozlowski 1979, Yoneda 1993, Bosc et al. 2003) because respiration of nonphotosynthetic tissues mainly occurs in the cambial sheath and the living annual growing rings around the dead heartwood (Kinerson 1975). Nonetheless, Sprugel (1990) suggested that a forest stand with high bole WSA doesn't necessarily have high rates of respiration, so there is still a need to scale up from tree to stand to forest -level process modeling. Respiration still contributes

a significant portion of uncertainty related to the carbon budget and offset potential of urban forests (Tigges and Lakes 2017). The type of data that was produced in this study could form the basis to develop new process models that describe the carbon balance and growth of urban forests under a changing climate, which has been an important focus of forest process modeling for decades (Mäkelä 1997, Valentine et al. 1999).

4.5. Conclusions

In this study, we demonstrated the use of TLS technology to produce detailed data that quantify the total above-ground WSA of urban trees (first study objective) and we found that the study trees varied widely in their WSA. Furthermore, based on TLS data we studied the allocation patterns of WSA to different components of the woody skeleton of trees i.e. stem and branches of different order, base-diameter and base-height classes (second study objective), and we found that the urban trees allocated their WSA mainly to branches, while branch order, branch-base diameter, and branch-base height influenced the observed allocation pattern.

Measuring the WSA of trees with TLS is a non-destructive method that allows to explicitly account for the above-ground structural-fractal complexity of trees, and it does not rely on any biological assumptions for tree architecture (Malhi et al. 2018) in comparison to previous methods that approximated branch and stem geometry or estimated WSAs from allometric equations (Whittaker and Woodwell 1967, Halldin 1985, Yoneda et al. 1990, Jennings et al. 1990, Yoneda 1993, Baldwin et al. 1997, Weiskittel and McGuire 2006).

This study showed that WSA is a function of the above-ground fractal-structural complexity of trees, and their "hydraulic" size quantified by different Euclidean metrics of path lengths from the tree base to each branch tip (third study objective). The observed positive relationship between the crown surface area and the woody surface area of the trees (third study

objective) implies a physiological mechanism for maintaining a positive carbon balance at tree scale. In general, the type of data produced in this study describes tree surface allometry, and it can be used to develop new or inform existing process models that quantify the growth and productivity of urban forests.

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LITERATURE CITED

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CHAPTER 5

ACCURACY DIFFERENCES IN ABOVE-GROUND WOODY BIOMASS ESTIMATION WITH TERRESTRIAL LASER SCANNING FOR TREES IN URBAN AND RURAL FORESTS IN DIFFERENT LEAF CONDITIONS

Abstract

Forests in both rural and urban areas play a vital role in terrestrial carbon cycling, and tree carbon stocks are directly related to their above-ground biomass (AGB). Traditional allometric models for biomass estimation of trees may have important limitations due to limited sample sizes and an insufficient size range of sampled trees, and destructive sampling to collect data for building these allometric models is time consuming and costly. In this study, thirty-one trees of deciduous and evergreen species were sampled in rural and urban forest conditions. Terrestrial Laser Scanning (TLS) was used to estimate tree volume non-destructively from quantitative structure models, in combination with estimates of tree basic density from sample disks from stems and branches obtained after scanning and felling the trees, but also in combination with published basic density values at the species level. Total woody AGB, main stem and branch biomass were also computed from destructive sampling data, as reference values to compare to TLS-based values. Evergreen and some deciduous trees were scanned in the leaf-on condition, and therefore the effect of artificial leaf-removal using a leaf-separation algorithm on the TLS-based woody biomass estimates was also studied. Strong agreement was found between the TLS-based woody AGB, main stem and branch biomass and the reference biomass data across all study trees using basic density values from destructive measurements and published basic density values to convert the TLS-based volume estimates to biomass. The correlation between the TLS-based branch biomass estimates and reference biomass data was stronger for the urban trees compared to the rural forest trees, most likely because they had fewer tree neighbors to occlude parts of the branches in the laser point clouds. The opposite pattern was found for the TLS-based biomass estimates of the main stem of the urban and rural forest trees. TLS-based biomass estimates from leaf-off and leaf-removed tree point clouds were in strong

agreement with reference biomass data. This study shows that TLS data can be used to produce reliable total and component biomass estimates of trees, however, differences in the quality of the biomass estimates can arise depending on the growing environment, the leaf condition of the laser-scanned trees and the basic density values that are used. These results have important implications for studying the biomass and the carbon stocks of urban and rural forests.

Keywords: terrestrial laser scanning, quantitative structure models, above-ground biomass, components biomass, urban trees, rural forest trees, wood density, leaf- wood classification

5.1. Introduction

The total above-ground biomass (AGB, kg, oven-dry basis) of trees, which is an important element of the decision-making in forest management and policy (MacFarlane 2015), is defined as the total dry mass (i.e., at 0% moisture content) allocated to the live and dead tissues and organs of the above-ground tree structure (Kükenbrink et al. 2021, Burt et al. 2021). Accurate estimation of forest AGB plays a vital role in understanding the wide range of ecological services of rural and urban forests (e.g., biodiversity, pollination, temperature regulation, water purification and infiltration; Casalegno et al. 2017, Baker et al. 2019, Phillips et al. 2019, Nowak and Greenfield 2020), and it is essential for studying terrestrial carbon dynamics at different spatial scales and biomes (Stovall et al. 2017). For example, it has been found that Amazonian forests store large amounts of carbon in above-ground live vegetation (approximately 50-60 Pg of carbon), and this finding is based on the estimation of the above-

ground biomass of the Amazonian forests, considering that approximately 45-50% of live plant biomass is carbon content (Burt et al. 2021). Similarly, it has been found that urban trees store large amounts of carbon in their above-ground biomass which can be comparable to rural forest carbon stocks (McPherson 1998), depending on the level of tree cover and impermeable surfaces (MacFarlane 2009). However, there is still a lot of uncertainty regarding the carbon offsets of rural forests at different spatial scales due to lack of accurate and detailed tree biomass data, over multiple spatial and temporal scales (Weiskittel et al. 2015). There is even more uncertainty for urban forests, due to a paucity of data and models for estimation of urban above-ground mass (Tigges and Lakes 2017, Wilkes et al. 2018). Therefore, it is important to continue to develop new data and models for tree AGB across many different growing environments.

Urban and rural forest trees can have very different growth and biomass allocation patterns, because the lower tree abundance in urban areas compared to rural forests, is associated with less competition for light, water and nutrients (McHale et al. 2009, MacFarlane and Kane 2017). Open-grown trees in cities may grow faster than their rural forest counterparts (Pretzsch et al. 2015) despite the potential negative effects of urban environment (Arseniou and MacFarlane 2021), and they have larger, more complex crowns, and sharper trunk taper in order to resist the strong wind loads which are frequent under urban and open-grown conditions (Telewski et al. 1997, Bang et al. 2010, Mohamed and Wood 2015, Salim et al. 2015, Gardiner et al. 2016). Open-grown, urban trees allocate the largest portion of their AGB to their branches (Zhou et al. 2015, MacFarlane and Kane, 2017), whereas trees in rural forests and plantations are narrower in crown diameter, and they allocate more mass to their stems (Weiner 2004, Lines et al. 2012). Open-grown urban trees and rural forest trees may also have very different woody structure. For example, Zhou et al. (2011) found that the trunk specific gravity of open grown trees was greater than the trunk specific gravity of forest grown trees in the same geographic region. So, the significant allometric and structural differences between urban and rural forest trees should be considered when choosing methods to quantify their AGB.

The AGB of any tree, regardless its growing environment, can be directly measured only by weighing the tree components (i.e., branches, stems and leaves), and measuring the portion of the green biomass that is moisture after a tree has been harvested (Burt et al. 2021, Kükenbrink et al. 2021). However, this method is time consuming and costly, and only a limited number of trees can be destructively sampled (Calders et al. 2015, Weiskittel et al 2015). Therefore, the total AGB of trees and their biomass components (mass of branches, main stem and leaves) are usually estimated indirectly with "allometric models"- statistical models defining relationships between tree biomass and commonly-measured tree variables (e.g., diameter at breast height (DBH), total tree height, and crown dimensions; MacFarlane (2010, 2015), Ver Planck and MacFarlane (2014, 2015), Radtke et al. 2017, Dettman and MacFarlane 2018). However, AGB estimation from allometric models has important challenges and limitations. Existing models are usually limited to certain regions and species, and large trees are usually excluded from the calibration datasets (Calders et al. 2015, Weiskittel et al. 2015, Stovall et al. 2018, Disney et al. 2019, Burt et al. 2021). Harvesting large numbers of sample trees needed to build allometric models (Sileshi et al. 2014, Roxburgh et al. 2015) is particularly impractical in cities (Kükenbrink et al. 2021), and equations that have been created for rural forest trees cannot directly be applied to urban trees (Lefsky and McHale 2008, McHale et al. 2009).

Terrestrial laser scanners (TLS) provide a non-destructive way to quantify the architecture and dimensional properties (e.g., woody volume) of trees growing in rural forests and urban environments, which can then be converted to AGB estimates (Calders et al. 2020).

TLS are active remote sensing instruments that emit laser pulses and capture the threedimensional structure of their surrounding environments by creating "point clouds" based on the returned energy that is analyzed as a function of either time (time-of-flight systems) or shift in the phase of the light wave of the emitted laser beam (phase-shift technology), and by using precise angular measurements through optical beam deflection mechanisms (Calders et al. 2015, Liang et al. 2016). Modeling the architecture of trees based on TLS data can be achieved by generating Quantitative Structure Models (QSMs; Raumonen et al. 2013, Kaasalainen et al. 2014, Hackenberg et al., 2015a). QSMs are created by fitting geometric primitives (i.e., cylinders) to the three-dimensional point-clouds of trees (Bournez et al. 2017), in a way that preserves branch and stem topology and provides information about the size, the location, the hierarchy and the orientation of the branching network. QSMs can provide, accurate direct estimates of the total above-ground volume of trees based on the volume of the fitted cylinders, which can be converted to AGB when multiplied by estimates of tree density, typically wood density (dry woody biomass at 0% moisture content divided by the green woody volume) (Burt et al. 2021, Demol et al. 2021). Estimating tree AGB from TLS data does not rely on any biological assumptions for tree architecture (Malhi et al. 2018) unlike allometric models, but it is a process with its own challenges (Olagoke et al. 2016, Disney et al. (2018, 2020)), whose accuracy depends on (1) generating high-quality point clouds, (2) assumptions and limitations of the QSM and (3) representative estimates of the density of different parts of the trees.

Point cloud registration accuracy and quality depends on having unobstructed views of all parts of the trees and is also affected by weather conditions during laser scanning (e.g., branches swaying due to wind) and the laser scanner technical properties, and any point cloud errors are compounded by factors related to the QSM's quality (e.g. segmentation errors, cylinder fitting problems) (Calders et al. 2015, Disney et al. 2018). Malhi et al. (2018) determine some major challenges in accurately estimating tree biomass from QSMs i.e., extraction of high order branches, and classification of woody and non-woody parts of scanned trees. There are currently no QSM methods that can model foliage volume by fitting cylinders to the point cloud of trees (Stovall et al. 2017) and the inclusion of points from leafy surfaces reduce the accuracy of the reconstruction of the woody skeleton of trees (Burt et al. 2021). Therefore, the artificial leaf-removal from the leaf-on point clouds of trees using leaf-classification algorithms (Vicari et al. 2019, Wang et al. 2019, Moorthy et al. 2020) is required before QSMs generation. However, we need a better understanding of the effect of these classification algorithms on studying tree structure (Vicari et al. 2019, Arseniou et al. 2021a).

Even with a high-quality tree component volume estimate from TLS there is significant variation in wood density between and within species and across different environments (MacFarlane 2020, Demol et al. 2021, Burt et al. 2021), which can create bias in AGB estimates, if the wrong density is applied. Published averaged values of wood density are available for many species (Chave et al. 2009, Miles and Smith 2009), but there haven't been many studies that have tested the consequences of applying these for biomass estimation (e.g., MacFarlane 2015, Demol et al. 2021).

In this study, we used TLS-based volume estimates and estimates of within-tree density (both wood and bark) to model the woody AGB of thirty-one trees of needle-leaf evergreen and broad-leaf deciduous species that grow in rural forest and urban conditions. The objectives of the study were: (i) to evaluate the accuracy of the woody AGB and branch and stem biomass estimates derived from a TLS-based approach by comparing to tree mass measurements from destructively sampled trees; (ii) to assess the effect of wood density (from destructive

measurements versus published values) on the estimation accuracy of the total and components woody biomass of trees from TLS-based woody volumes; (iii) to evaluate the use of TLS for total and components woody biomass estimation of trees that grow in different environments on a continuum of crowding conditions i.e. rural forest and urban growing conditions; (iv) to assess the effect of the artificial leaf-separation from leaf-on point clouds on the total and components woody biomass estimates of trees of broad-leaf deciduous and needle-leaf evergreen tree species.

5.2. Materials and Methods

5.2.1. Tree Data

The basic experimental approach in this study was to identify groups of healthy trees, with undamaged crowns, of different species and sizes, representing different functional groups (broad-leaf deciduous, and needle-leaf evergreen species) in different growing environments (rural and urban settings), that could be destructively sampled after scanning. The rural forest tree dataset consists of ten trees of two broad-leaf deciduous species - *Quercus rubra*, and *Acer rubrum*, and ten trees of two needle-leaf evergreen species - *Tsuga canadensis* and *Pinus strobus*. These trees were all sampled at the Harvard Forest in Petersham, MA, USA. The urban tree dataset consists of ten trees of three broad-leaf deciduous species - *Acer rubrum*, *Acer saccharum, Gleditsia triacathos*, and one tree of a needle-leaf evergreen species - *Pinus nigra*. The urban trees were all sampled on the Michigan State University campus, MI, USA. The trees were selected to cover a large range of sizes (Table 5.1).

Table 5.1. List of the study trees growing in different environments (UF = urban forest; RF = rural forest), belonging to different functional groups (BD = broad-leaf deciduous; NE = needle-leaf evergreen), and having different leaf conditions during laser scanning (Off = leaf-off; On = leaf-on). The variables DBH, Height, Total Woody AGB, Main Stem Biomass and Branch Biomass are based on reference data from destructive measurements.

| Tree | Growing | Functional | Leaf | DBH | Height | Total |
|---------------|-------------|------------|-----------|-------|--------|----------|
| | Environment | Group | Condition | (m) | (m) | Woody |
| | | | | | | AGB (kg) |
| A. rubrum | UF | BD | Off | 0.358 | 7.96 | 364.099 |
| A. saccharum | UF | BD | Off | 0.389 | 12.53 | 901.250 |
| A. saccharum | UF | BD | Off | 0.478 | 13.99 | 1427.948 |
| A. saccharum | UF | BD | Off | 0.523 | 12.66 | 2081.490 |
| P. nigra | UF | NE | On | 0.549 | 14.57 | 2008.654 |
| G.triacanthos | UF | BD | On | 0.577 | 15.79 | 3576.340 |
| G.triacanthos | UF | BD | On | 0.467 | 12.41 | 1538.288 |
| G.triacanthos | UF | BD | On | 0.457 | 12.68 | 1663.478 |
| G.triacanthos | UF | BD | On | 0.432 | 14.05 | 1853.480 |
| G.triacanthos | UF | BD | On | 0.429 | 11.67 | 1524.280 |
| G.triacanthos | UF | BD | On | 0.495 | 11.80 | 1769.792 |
| T. canadensis | RF | NE | On | 0.401 | 24.45 | 708.264 |
| P. strobus | RF | NE | On | 0.137 | 15.64 | 51.457 |
| T. canadensis | RF | NE | On | 0.231 | 17.65 | 181.305 |
| P. strobus | RF | NE | On | 0.216 | 20.39 | 153.642 |
| T. canadensis | RF | NE | On | 0.180 | 16.25 | 120.461 |
| T. canadensis | RF | NE | On | 0.081 | 8.63 | 12.201 |
| P. strobus | RF | NE | On | 0.427 | 25.36 | 752.809 |
| P. strobus | RF | NE | On | 0.257 | 20.54 | 208.891 |
| P. strobus | RF | NE | On | 0.333 | 24.60 | 472.288 |
| Q. rubra | RF | BD | Off | 0.363 | 21.60 | 813.403 |
| A. rubrum | RF | BD | Off | 0.287 | 22.74 | 387.375 |
| T. canadensis | RF | NE | On | 0.345 | 24.45 | 529.965 |
| Q. rubra | RF | BD | Off | 0.193 | 21.15 | 174.977 |
| A. rubrum | RF | BD | Off | 0.076 | 11.00 | 17.721 |
| A. rubrum | RF | BD | Off | 0.218 | 23.13 | 247.392 |
| A. rubrum | RF | BD | Off | 0.119 | 13.44 | 57.312 |
| A. rubrum | RF | BD | Off | 0.107 | 16.86 | 56.248 |

Table 5.1 (cont'd)

| Q. rubra | RF | BD | Off | 0.267 | 23.53 | 401.772 |
|----------|----|----|-----|-------|-------|----------|
| Q. rubra | RF | BD | Off | 0.503 | 24.11 | 1435.951 |
| Q. rubra | RF | BD | Off | 0.323 | 22.16 | 648.207 |

5.2.2. Reference Tree Data

The reference tree data for the rural forest trees were collected during the leaf-on period in August, 2017. The reference tree data for the urban trees of the species *A. rubrum*, *A. saccarhum* and *P. nigra* were collected during the leaf-off period in January, 2018; and the reference tree data for the *G. triacanthos* trees were collected during the leaf-on period in August, 2019. A detailed description of all reference tree measurements is given in the following sub-sections.

5.2.2.1. Standing Tree Measurements

Total standing tree heights were measured with the *TruPulse 360* laser range finder and the diameter at breast height (DBH) of trees (1.37 m above the ground) was measured with a diameter tape to the nearest 0.25 centimeter. Crown width was measured with a *Vertex IV distance measuring* device, first at the tree's approximate widest point and then a second crown width measurement was taken at a 90° angle from the previous measurement.

Each tree was categorized in a canopy class representing crowding conditions in a discrete scale i.e. open grown, dominant, co-dominant, intermediate and overtopped (MacFarlane and Kane, 2017). Furthermore, the DBH of all neighboring trees \geq 10 cm DBH, within a 7.3 m radius, and their distance to the focal study trees were measured to compute a competition index

(see 5.2.2.3) that quantifies the level of crowding that the study trees faced in a continuous scale (MacFarlane and Kane, 2017).

5.2.2.2. Destructive Measurements for Green Weights

After felling, the main stem of the tree was determined from the cut bottom to the tree's top. At any fork in the main stem, the largest and straightest stem was followed; this was repeated all the way to the top of the tree. All other stems connected to the main stem were defined as branches.

After the branches were separated, the main stem was cut at 1.37 meters, 2.44 meters, and then at 1.22 meters intervals. The green (fresh) weight of all sections was then measured with a crane scale. Disks of thickness approximately 5 cm were cut from the top of the 0.15 meters height mark (stump height), at 1.37 meters above the ground (breast height) and the top of every section of 1.22 meters length. The green weight of each disk (including bark) was measured in the field and the diameters inside- and outside- bark were measured in two perpendicular directions on the disks, as well as four measures of disk thickness in four equally-spaced locations on perpendicular directions (all measures to the nearest 0.1 cm). These disks were used to compute the basic density of each section of the tree's main stem (see 5.2.2.3).

Branch measurements followed different protocols for trees of broad-leaf and needle-leaf species. Starting at the base of a tree of a broad-leaf species and working upward, first order branches (branches attached directly to the main stem) were systematically cut from the main stem. Each branch was measured for basal diameter (bd), and it was classified as either a "small" branch (bd < 2.5 cm) or simply a branch (bd \geq 2.5 cm). For every branch with bd \geq 2.5 cm, the basal diameter, the linear length, its status (live or dead) and its position on the main stem were

recorded. Branches were further separated and weighed using the crane scale, with second and higher order portions of a branch with leaves. After weighing the total green weight of a branch, the leaves and the attached twigs were clipped from the branch. The leaves and small twigs were then weighed separately for each branch and their weight was subtracted from the total green weight of a branch. One disk was removed from the mid-section of each branch and weighed green and disk measurements were taken (as above) to compute disk green volume; these were used to compute variation in branch basic density. Small branches with bd < 2.5 cm were counted, their status (live or dead) was recorded, and weighed in a pile. A sample of small branches were weighed green in the field and taken back to the laboratory for further measurements.

For trees of needle-leaf species, the first order branches are generally smaller and more numerous than those in trees of broad-leaf species. So, for these species, the trunk was divided into 1.22 m sections, starting at the base of the tree, and all branches were removed from each section and weighed green in the field. Live and dead branches were weighed separately in each section and a whorl of the three closest branches was selected from the middle of each measurement section to represent branches in that section of the tree. The basal diameter, length and status (live or dead) of all branches in the whorl were measured and one dead and two live branches were selected for laboratory analysis to determine moisture content and basic density.

Regardless of species, "miscellaneous" branches (branches founded on the ground that clearly belonged to the felled tree and whose location on the tree could not be determined) were pooled together and weighed in a third pile. Because the location of these branches in the tree was unknown and they varied in size, it was difficult to subsample this mixed material, and thus,

the dry-weight/green-weight ratio for these branches was calculated as the weighted average of all branches in a tree (see 5.2.2.3).

5.2.2.3. Measurements and Computations in the Laboratory

Disks and samples from the main stem and branches were taken to the laboratory for additional analysis. The bark of each disk was peeled as close to "green" condition as possible and the green-biomass of the wood and bark components was weighed separately. Finally, the bark and wood components of all disks were oven-dried at 105 °C for 48 hours until reaching oven-dry biomass which was weighed and recorded. The following computations include both the wood and the bark components of a disk.

The moisture content of each disk (MC_{disk}) was computed from the following equation:

$$MC_{disk} = \frac{(GW_{disk} - DW_{disk})}{GW_{disk}}, \qquad (eq. 5.1)$$

where GW_{disk} is the green weight of a disk in kg, and DW_{disk} is its dry weight in kg.

The dry biomass of the measurement section of the main stem or branch from which a disk was sampled was computed from the following equation:

$$DW_{section} = (1 - MC_{disk})^* GW_{section}, \qquad (eq. 5.2)$$

where $DW_{section}$ is the dry weight of the section in kg, and $GW_{section}$ is the green weight of the section in kg measured in the field.

The total AGB (excluding the foliage) of a tree was computed by adding together the dry weight of all sections of the main stem and branches of the tree.

The basic density of each sampled disk (BD_{disk} in g/cm³) included both bark and wood tissues and it was computed from the following equation:

$$BD_{disk} = \frac{DW_{disk}}{GV_{disk}},$$
 (eq. 5.3)
where GV_{disk} is the green-volume of the disk (in cm³) computed from the laboratorymeasured dimensions of the disk whose shape was assumed cylindrical. The basic density values of the disks were extrapolated to the section of the main stem or branch from which they were sampled.

The basic density of the main stem of a tree including both bark and wood tissues was computed as the weighted average of the basic density values of the stem sections, and the basic density of all branches of a tree including both bark and wood tissues was computed as the weighted average of the basic density values of the branch sections. Weights were based on the cross-sectional area of the disk.

Finally, the competition that each rural forest- and urban-forest tree in this study faced from its neighboring trees was computed, because we expected that the uncertainty of TLS-based biomass estimates will increase with competition strength due to crowding causing occlusion effects in the laser point clouds. The competition index was computed as follows:

$$CI = \sum_{i=1}^{n} \sum_{j=1}^{s} \frac{\frac{DBH_j}{DBH_i}}{Dist_{ii}}, \qquad (eq. 5.4)$$

where *n* is the number of the study trees, *s* is the number of the tree neighbors ≥ 10 cm DBH around each study tree *i* within a radius of 7.3 m, DBH_j is the diameter at breast height of each tree neighbor *j*, DBH_i is the diameter at breast height of each study tree *i*, and Dist_{ij} is the distance in meters between a study tree *i* and its tree neighbor *j*. This is a distance-dependent competition index which assumes that smaller trees are more sensitive than larger trees to the competition effects from their tree neighbors (Canham et al. 2004).

5.2.3. Terrestrial Laser Scanning of Trees and Point Cloud Processing

All urban trees were laser-scanned with the FARO Focus^{3D} X 330 terrestrial laser scanner (FARO Technologies Inc., Lake Mary, FL, USA). The *G. triacanthos* trees were laser-scanned during the leaf-on period in July, 2019. The rest urban trees of the other species were laser-scanned during the leaf-off period in November, 2017. The FARO Focus^{3D} X 330 terrestrial laser scanner operates with laser light of 1550 nm wavelength, typical beam divergence 0.19 mrad, a range of 0.6 m - 330 m and it captures single return laser scanning data (Calders et al. 2020).

Each individual urban tree was scanned at high resolution from a minimum of four different directions at different distances, in order to minimize occlusion effects in the captured point clouds. The first two scans were conducted in opposite directions, from distances that allowed for a clear sighting of the top of the focal tree. The other two scans were also conducted in opposite directions (at a 90° angle from the first two scans), but from a closer distance to the tree, to better capture its stem and its branching architecture. Two or three additional scans were conducted right below the crown of large trees with wide crowns in order to capture more dense point clouds of the branches. Windy conditions were avoided during the laser scans. For the spatial registration of all scans of a focal urban tree and the generation of a single point cloud, six reference target-spheres were placed around the tree, following the field scanning protocols suggested by Wilkes et al. (2017). The software SCENE 2019.2 (FARO Technologies Inc., Lake Mary, FL, USA, 2019.2) was used to spatially co-register and filter all scans in an automatic way. Finally, using the same software each tree was manually segmented from the point cloud of the background site. This process has been shown to be an accurate alternative to a fully automatic segmentation process (Seidel, 2019).

Rural forest trees were laser-scanned during the leaf-off period in April, 2017 using a RIEGL VZ-400 laser scanner. This laser scanner operates with laser light of 1550 nm wavelength, nominal beam divergence 0.35 mrad, pulse repetition rate 300 kHz, and it captures multiple return laser scanning data (Calders et al. 2015, Calders et al. 2020). The trees in Harvard Forest were scanned across two plots: the 50m x 50m main plot (16 trees, 48 scans) and the 20m x 20m North plot (4 trees, 9 scans). Retroreflective targets were used to guide the co-registration of individual scans in RiSCAN PRO. Trees were extracted with *treeseg* (Burt et al. 2019) followed by visual quality control.

The *TLSeparation* algorithm (Vicari 2017) was used to separate and artificially remove leaves from the point clouds of trees of evergreen species (*T. canadensis*, *P. strobus*, *P. nigra*), and deciduous species that were scanned during the leaf-on period (*G. triacanthos*). The *TLSeparation* algorithm employs unsupervised classification of geometric features because leaf and wood materials within a point cloud have different spatial arrangement, and "shortest-path" analysis to enhance the detection of paths through the branching network of a tree with high occurrence frequency (Vicari et al. 2019). After the laser-points of the woody structure of the trees were separated from the laser-points that belong to their foliage, a single point cloud was created for each tree that consisted only from points classified as belonging to the woody structure.

QSMs were generated from the leaf-off and leaf-removed point clouds of the study trees (Fig. 5.1) using the algorithm *TreeQSM* v.2.3.0 (Copyright (C) 2013-2017 Raumonen P.). There are two main steps in the *TreeQSM* algorithm: (i) the point cloud segmentation into stem and branches based on cover sets, and (ii) the reconstruction of the volume and the surface area of the segments with cylinders (Calders et al. 2015, Raumonen et al. 2015). *TreeQSM* algorithm

generates multiple QSMs for each tree with varying parameter sets for the minimum and maximum size of the cover sets whose generation is random during the point cloud segmentation process and it selects the optimal QSM (Raumonen et al. 2013). Therefore, the generated QSMs can be slightly different even using the same input parameters (Calders et al. 2015). Based on the optimal QSM parameter combination the algorithm produced 30 additional QSMs in order to estimate the variation of the estimated tree variables (e.g. volumes), due to the inherent stochastic component of the algorithm (Raumonen et al. 2013).

In *TreeQSM* the main stem of a tree is separated from its branches following these criteria: (i) the main stem extends near the top of a tree, (ii) it goes straight up, and (iii) it is not too curved (the ratio of the stem length to the stem base-tip distance, must be the minimum among all candidate main stems) (Raumonen P., personal communication, June 2, 2020).

From the optimal QSMs of the leaf-off and leaf-removed point clouds of the study trees, their total woody volume (including bark tissues) was computed as the sum total volume of all cylinders that were fitted to the point cloud of a tree (see close-up in Fig. 5.1 C). The total woody volume of a tree was further separated into the main stem and the branch volume components. These component volumes were converted to biomass by multiplying with the basic density values of the main stem and branches, which were computed from the disks removed during destructive sampling (see 5.2.2.3). Furthermore, published values of bark and wood density at species level (Miles and Smith 2009) were applied to convert the main stem and branches TLS-based volumes to biomass. Miles and Smith (2009) published specific gravity values for the wood and bark tissues (bark and wood density relative to the density of water at temperature 4.0° C) together with percentage of bark volume for several tree species in North America. Finally,

the total woody AGB of a tree was computed by adding together the component biomass values of the tree.



Figure 5.1. (A) The leaf-off point cloud of an urban *A. rubrum* tree. (B) The generated QSM of the tree. (C) A close-up picture of the generated QSM, consisted from several cylinders fitted to the point cloud of the tree. The colors denote the different branching orders i.e. the main stem is colored blue, the 1st order branches are colored green, the 2nd order branches are colored red etc. Four facets have been used to visualize the QSM cylinders.

5.2.4. Comparison between TLS-based Biomass Estimates and Reference Biomass

Measurements

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

The level of agreement between the TLS-based woody AGB and component biomass estimates with the reference biomass values from the destructive measurements was quantified with the concordance correlation coefficient - CCC (Lin 1989), which takes values between -1 (complete discordance) and 1 (complete concordance) (Calders et al. 2015, Gonzalez de Tanago et al. 2018). The Pearson correlation coefficient (r) was used to quantify the relationship between the absolute errors of the TLS-based biomass estimates and the reference biomass values, and to quantify the relationship between the relative errors in TLS-based biomass estimates and the competition index. The statistical significance of all relationships was assessed at $\alpha = 5$ %.

Furthermore, different error metrics were computed to assess the quality of the TLSbased biomass estimates (Calders et al. 2015, Fan et al. 2020, Burt et al. 2021):

• the error for each tree:
$$\varepsilon = \text{Biomass}_{\text{TLS}} - \text{Biomass}_{\text{Ref}}$$
 (eq. 5.5)

• the relative error for each tree:
$$RE = \frac{|\varepsilon|}{Biomass_{Ref}}$$
 (eq. 5.6)

• the mean relative error across all trees (%): MRE% = $\frac{1}{n} \sum_{i=1}^{n} RE_i * 100\%$ (eq. 5.7)

• the root mean square error that refers to the overall accuracy across all trees:

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n} \varepsilon_{i}^{2}} \qquad (eq. 5.8)$$

•
$$CV(RMSE)\% = \frac{RMSE}{Biomass_{Refmean}} *100\% \qquad (eq. 5.9)$$

In the above equations (eqs. 5.5-5.9), $Biomass_{TLS}$ is the TLS-based woody AGB or component biomass of the main stem and branches of a tree, the $Biomass_{Ref}$ is the AGB or component biomass from the reference measurements of a tree, $Biomass_{Ref.mean}$ is the mean value of it, CV(RMSE)% is the % coefficient of variation of the RMSE, n represents the total number of trees and the index i refers to each individual tree.

The accuracy of the TLS-based woody AGB and component biomass estimates was evaluated for the urban versus the rural forest trees, and for the leaf-off versus the leaf-removed point clouds of the studied trees. In order to better understand how the TLS-based woody AGB estimates of the studied trees were affected by the group that a tree belonged to, we fitted the following linear mixed-effects model:

$$AGB_{TLS} = b_0^{(L+H)} + b_1^{(L+H)} * AGB_{Ref} + \varepsilon,$$
 (eq. 5.10)

where AGB_{TLS} is the total above-ground biomass (kg) of the study trees from TLS data, AGB_{Ref} is the total above-ground biomass (kg) of the trees based on reference data from destructive measurements, b₀ is the intercept, b₁ is the slope of the relationship and L and H are the nested random effects that modify the intercept and the slope i.e. L represents the leaf condition of the tree point clouds (leaf-off versus leaf-removed), and H represents the growing environment of the trees (urban versus rural forest growing environment). The error term (ε) has an additive structure and it is normally distributed. 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. Eq. 5.10 without the nested random effects L and H becomes a simple linear function between TLS-based woody AGB and reference AGB values i.e., fixed-effects model : $AGB_{TLS} = b_0 + b_1 * AGB_{Ref} + \varepsilon$, (eq. 5.11)

The accuracy comparisons of the TLS-based biomass estimates of urban and rural forest trees with leaf-off and leaf-removed point clouds were based on the combination of woody volumes from TLS data with reference wood density values from destructive measurements only (i.e. published basic density values were not applied in these comparisons).

Finally, the coefficient of variation was used to quantify the uncertainty in estimating total woody AGB and components biomass from the consecutive QSM reconstructions of the same point cloud of a tree.

5.3. Results

5.3.1. Uncertainty in Estimated Woody Biomass from Multiple QSM Reconstructions

The coefficient of variation of the estimated total woody AGB, main stem biomass, and branch biomass of the study trees indicated that the uncertainty due to the consecutive QSM reconstructions of the same point cloud of a tree was on average 4.3%, 3.1% and 6.3% of the mean woody AGB, mean stem biomass, and mean branch biomass respectively across all study trees combined. The distribution of the coefficient of variation of the woody AGB and main stem biomass of the trees was positively skewed, but it showed a more uniform pattern for the branch biomass of the trees (Fig. 5.2).



Figure 5.2. Density plots of the coefficient of variation of (A) the total woody AGB, (B) the main stem biomass, and (C) the branch biomass of the study trees, based on multiple QSM reconstructions from the same point clouds of the trees.

5.3.2. AGB and Components Biomass Across all Study Trees

Biomass estimates from the TLS-based approach were strongly correlated with the biomass measurements from destructive reference data using both reference and published basic density values for the total woody AGB of the trees, the biomass of their main stem, and the biomass of their branches (see CCC in Table 5.2, and Fig. 5.3).



Figure 5.3. Regression lines between the TLS-based biomass (kg) and the reference biomass (kg) of the study trees for their total woody AGB, their main stem biomass and their branch biomass. The 95% confidence interval has been plotted around the regression lines, and the black dashed line is the 1:1 line. The different colors represent the different sources for basic density values, and the rural forest trees and urban trees are represented with different symbols.

It was also found that the exponential relationship between the total woody AGB of the study trees and their diameter at breast height (DBH) was similar based on reference biomass data and TLS-based biomass data with reference and published basic density values (confidence intervals significantly overlap). Underestimation bias of total woody AGB was greatest for large DBH trees using published basic density values (Fig. 5.4).



Figure 5.4. Relationship between the total woody AGB of the study trees and their diameter at breast height (DBH) based on reference biomass data and TLS-based biomass data with reference and published basic density values. The 95% confidence interval has been plotted around the fitted lines. The different colors represent the different sources for biomass values, and the rural forest trees and urban trees are represented with different symbols.

The statistical metrics that were computed to assess the performance of the TLS-based

biomass estimates across all study trees are given in Table 5.2.

| With | With published basic density values | | | | | |
|-----------|-------------------------------------|-----------|---------|---------|-----------|---------|
| Metric | Total | Main stem | Branch | Total | Main stem | Branch |
| | woody | biomass | biomass | woody | biomass | biomass |
| | AGB | | | AGB | | |
| Mean | | | | | | |
| Relative | 24.5 | 13.8 | 124.1 | 26.3 | 14.1 | 107.7 |
| Error (%) | | | | | | |
| RMSE (kg) | 147.743 | 114.973 | 167.434 | 244.846 | 133.144 | 194.127 |
| _ | | | | | | |
| CV(RMSE)% | 17.52 | 30.92 | 35.52 | 29.04 | 35.8 | 41.19 |
| | | | | | | |
| CCC | 0.982 | 0.909 | 0.961 | 0.947 | 0.878 | 0.941 |

Table 5.2. Statistical metrics to assess the performance of TLS-based biomass estimates across all study trees.

The absolute errors of TLS-based total woody AGB, and branch biomass using the reference basic density values were not significantly related with the reference woody AGB, and branch biomass values (p > 0.05), whereas the absolute errors of TLS-based main stem biomass increased with the reference main stem biomass values (Pearson's r = 0.54, p = 0.0019). The absolute errors of the TLS-based total woody AGB, main stem biomass and branch biomass using published basic density values increased with the reference biomass values (Pearson's r = 0.75, p < 0.001; r = 0.62, p < 0.001; r = 0.61, p < 0.001 respectively).

5.3.3. Growing Environment and Leaf-condition Factors Affecting the Accuracy of TLS-based Biomass Estimates

The results of the fixed-effects model of the TLS-based woody AGB being modeled as a linear function of the reference AGB values (eq. 5.11) showed strong explanation power (adj. $R^2 = 0.927$), and the mixed-effects model (eq. 5.10) which includes the nested random effects L and

H had stronger explanation power (adj. $R^2 = 0.986$). The results of the mixed-effects model (eq. 5.10) showed that L and H were not confounded and they explained about the same portion of the variation in TLS-based woody AGB after they were included compared to the fixed-effects model. More specifically, the random effect L (leaf conditions: leaf-off versus leaf-removed point clouds) explained 45.9% of the 5.9% difference in the explained variation of TLS-based woody AGB between the fixed-effects and mixed-effects models. The random effect H (growing environment: urban versus rural forest conditions) explained 42.4% of the 5.9% difference in the explained variation of TLS-based woody AGB between the fixed-effects and mixed-effects models.

5.3.3.1. AGB and Components Biomass for Urban and Rural Forest Trees

As it was expected the competition strength that the study trees faced affected the accuracy of TLS-based biomass estimates, while urban open-grown trees faced less competition from neighboring trees compared to the rural forest trees of dominant, co-dominant, intermediate and overtopped canopy classes (Table 5.3, and Fig. 5.5). More specifically a positive relationship was observed between the relative error in TLS-based branch woody biomass of the study trees and the competition index (Pearson's r = 0.38, p = 0.033; Fig. 5.5). However, no significant relationship was observed between the competition index and the relative errors in TLS-based woody AGB and main stem biomass of the study trees.



Figure 5.5. Relationship between the relative error (RE) in branch woody biomass from TLS data and the competition index (CI) of the trees. Urban and rural forest trees have been plotted with different colors and symbols. The 95% confidence interval has been plotted around the regression line.

| Tree canopy class | CI (mean [min, max]) | | |
|-------------------|----------------------|--|--|
| Open-grown | 0.03 [0.01, 0.05] | | |
| Dominant | 0.81 [0.62, 0.99] | | |
| Co-dominant | 0.97 [0.39, 1.34] | | |
| Intermediate | 1.54 [0.87, 2.94] | | |
| Overtopped | 3.49 [1.73, 5.61] | | |

Table 5.3. Competition index (CI) values per canopy class of the study trees

Strong positive correlations were found between the biomass estimates from TLS data and the biomass measurements from reference data for the total woody AGB, the main stem biomass, and the branch biomass of the rural forest trees and the urban trees respectively (see CCC in Table 5.4, and Fig. 5.6).



Figure 5.6. Relationship between the TLS-based biomass (kg) and the reference biomass (kg) of the study trees for their total woody AGB, their main stem biomass and their branch biomass. Urban and rural forest trees with leaf-off and leaf-removed point clouds have been plotted with different colors and symbols. The 95% confidence interval has been plotted around the regression lines, and the black dashed line is the 1:1 line.

The statistical metrics that were computed to assess the performance of the TLS-based biomass estimates for rural forest and urban trees are given in Table 5.4.

| | Urban trees | | | | | |
|-----------|--------------------------------------|---------|---------|---------|---------|---------|
| Metric | Total | Main | Branch | Total | Main | Branch |
| | woody | stem | biomass | woody | stem | biomass |
| | AGB | biomass | | AGB | biomass | |
| Mean | | | | | | |
| Relative | 36.2 | 8.7 | 184.7 | 3.2 | 23 | 14.1 |
| Error (%) | | | | | | |
| RMSE (kg) | 109.02 | 43.741 | 99.147 | 199.764 | 183.777 | 247.250 |
| CV(RMSE)% | 29.34 | 15.38 | 113.77 | 11.75 | 34.61 | 21.13 |
| CCC | 0.953 | 0.987 | 0.623 | 0.959 | 0.62 | 0.891 |
| Trees | Trees with leaf-removed point clouds | | | | | |
| Metric | Total | Main | Branch | Total | Main | Branch |
| | woody | stem | biomass | woody | stem | biomass |
| | AGB | biomass | | AGB | biomass | |
| Mean | | | | | | |
| Relative | 14.9 | 14.4 | 93.1 | 32.4 | 13.2 | 149.7 |
| Error (%) | | | | | | |
| RMSE (kg) | 47.26 | 111.693 | 108.349 | 194.846 | 117.605 | 203.601 |
| CV(RMSE)% | 7.34 | 31.3 | 37.73 | 19.34 | 30.6 | 32.68 |
| CCC | 0.997 | 0.926 | 0.968 | 0.976 | 0.892 | 0.955 |

Table 5.4. Statistical metrics to assess the performance of TLS-based biomass estimates for rural forest and urban trees, and trees with leaf-off and leaf-removed point clouds.

It was also found based on both TLS and reference data that the rural forest trees

allocated more biomass to their main stem compared to their branches, whereas, the urban trees showed the opposite biomass allocation pattern.

5.3.3.2. AGB and Components Biomass of Leaf-off and Leaf-removed Tree Point Clouds

Strong positive correlations were found between the biomass estimates from TLS data and the biomass measurements from reference data for the total woody AGB, the main stem biomass, and the branch biomass of trees with leaf-off and leaf-removed point clouds respectively (see CCC in Table 5.4, and Fig. 5.7).



Figure 5.7. Relationship between the TLS-based biomass (kg) and the reference biomass (kg) of the study trees for their total woody AGB, their main stem biomass and their branch biomass. Trees with leaf-off and leaf-removed point clouds that grow in urban and rural forest conditions have been plotted with different colors and symbols. The 95% confidence interval has been plotted around the regression lines, and the black dashed line is the 1:1 line.

The statistical metrics that were computed to assess the performance of the TLS-based biomass estimates for trees with leaf-off and leaf-removed point clouds are given in Table 5.4.

5.4. Discussion

Terrestrial laser scanning (TLS) data have been systematically used in forest ecology since the early 2000s (Hopkinson et al. 2004, Hackenberg et al. 2015b, Calders et al. 2020). To the best of our knowledge, this is one of the few studies that aims to evaluate and compare the total TLS-based woody AGB and components biomass estimates accuracy for trees growing in fundamentally different environments reflecting different crowding conditions (urban and rural forest conditions), and in different leaf conditions (leaf-on and leaf-off). Previous studies have mostly focused in studying the total AGB and woody volume of trees growing either in rural forest or in urban conditions (Polo et al. 2009, Moskal and Zheng 2011, Holopainen et al. 2011, Vonderach et al. 2012, Kankare et al. 2013, Calders et al. 2015, Olschofsky et al. 2016, Rahman et al. 2017, Stovall et al. 2017, Tanhuanpää et al. 2017, Burt et al. 2021), while other studies focused in studying the crown architecture (Moorthy et al. 2010, Jung et al. 2011, Metz et al. 2013), the stem profile (Maas et al. 2008), and the woody surface area of trees (Arseniou et al. 2021b).

The main results of the study are discussed in the following subsections according to the different factors affecting the accuracy of TLS-based biomass estimates that were revealed in this study i.e., overall accuracy of TLS-based biomass estimates, the influence of the type of basic density that is used, influence of inherent QSM stochasticity, influence of growing

environment (urban versus rural forest environments), influence of leaf conditions (leaf-off versus leaf-on which requires artificial leaf-removal).

5.4.1 Overall Accuracy of TLS-based Biomass Estimates

The overall accuracy of AGB across all study trees with the use of reference basic density values (see CV(RMSE)%, Table 5.2), was comparable to the overall AGB accuracy that has been reported by Calders et al. (2015) i.e. CV(RMSE) = 16.1%, and Olagoke et al. (2016) i.e. %RMSE = 13.5%. AGB estimation from QSMs can be within 10% of the measured biomass from destructive sampling data (Wilkes et al. 2018). The error analysis across all study trees showed that the overall accuracy of the TLS-based main stem biomass estimates was higher compared to the overall accuracy of the branch biomass estimates (see error metrics in Table 5.2). This result was expected because the reconstruction of branches in QSMs is challenging (Disney et al. 2018). The size of smaller branches is usually overestimated from TLS data (Momo Takoudjou et al. 2018, Disney 2019), while branch-size underestimation of 8% from QSMs has been found for branches with base diameters between 20 cm and 60 cm, and an underestimation of 6% has been found for branches with base-diameter greater than 60 cm (Lau et al. 2018, Lau et al. 2019a)

5.4.2. Influence of Measured Versus Published Values of Basic Tree Density

The wood density of trees is very variable because it relates to their mechanical properties (Telewski 2012), their hydraulic conductance (Markesteijn et al. 2011) and their

environmental and evolutionary strategies (Disney et al. 2018). However, published averagedvalues of wood density for different tree species (Chave et al. 2009, Miles and Smith 2009) are also available because wood density is phylogenetically preserved (MacFarlane 2020). Therefore, it is important to account for the uncertainty in TLS-based biomass estimates due to the type of basic density that is used, which combines the density of the wood and bark tissues of trees.

The strong agreement between the TLS-based estimates of total woody AGB, main stem biomass, branch biomass and the reference biomass data from destructive measurements across all study trees using both reference and published basic density values indicates that TLS technology provides a precise method for estimating tree woody biomass. This result was also supported by the relationship between the total woody AGB of the study trees and their diameter at breast height (DBH) which was very similar whether the AGB values came from QSM estimates (with reference and published basic density values) or reference biomass data because the fitted lines and their confidence intervals significantly overlapped.

The regression lines of TLS-based woody AGB, main stem biomass and branch biomass were mainly below the 1:1 line using both reference and published basic density values. The reference basic density values should be unbiased, which implies that the observed underestimation in TLS-based AGB and branch biomass of large trees is most likely due to underestimation of their volume from the QSMs. Furthermore, all TLS-based biomass estimates using published basic density values were less accurate compared to the TLS-based estimates using reference basic density estimates (see CV(RMSE)%, Table 5.2). Similarly previous studies have showed that TLS-based woody AGB estimates using published species-average wood density values were less accurate compared to TLS-based woody AGB estimates using direct

wood density measurements at tree scale (Burt et al. 2021, Demol et al. 2021), and Takoudjou et al. (2020) reported 10% bias in TLS-based woody AGB estimates with the use of published wood density values due to the vertical gradients in wood density at tree scale.

According to MacFarlane (2020) the branch to stem wood density ratio significantly varied among trees of different canopy positions and with less competition for light the branch wood density was relatively higher. This could explain the observed underestimation in the TLSbased AGB and branch biomass mostly for large urban trees when published basic density values were used (Figs. 5.3 A, 5.3 C, and 5.4) i.e., the large open-grown urban trees had denser branches compared to the published basic density values which are based on wood and bark density measurements of the main stem of trees of different species (Miles and Smith 2009).

When evaluating the uncertainty in TLS-based biomass estimates considering the basic density values that are used it is important to understand how the biomass estimation errors change with tree size. The absolute errors of TLS-based AGB, and branch biomass using reference basic density values did not relate with the reference AGB and branch biomass values, which indicates that the overall error in the TLS-based woody AGB and branch biomass using reference basic density values is independent of tree size and it is mainly random error. Similarly, the error of TLS-based total woody AGB using basic density values from destructive measurements was independent of tree size in previous studies (Calders et al. 2015, Burt et al. 2021). However, the combination of TLS-based woody volumes with published basic density values generated absolute errors of woody AGB, main stem and branch biomass, which increased with tree size. Gonzalez de Tanago et al. (2018) also found that the error in TLS-based woody AGB increased with tree size when published basic wood density values were used.

Similarly, Burt et al. (2021) showed that the error in woody AGB estimates from allometric models that included published basic wood density values increased with tree size.

In general, the use of reliable non-destructive estimates of tree basic density at species or tree level is important for obtaining accurate TLS-based biomass estimates. In previous studies corrective models were created based on literature-based wood specific gravity values and variables of the size and structure of trees to estimate tree-level volume average-weighted wood specific gravity (Sagang et al. 2018, Takoudjou et al. 2020), which is an approach that can be followed for calibrating species-average basic density values for trees in various regions. Future advances in x-ray tomography (Van den Bulcke et al. 2019) are expected to significantly contribute in the non-destructive estimation of accurate basic density values at tree level. Therefore, reliable TLS-based biomass estimates of individual trees may still be possible when reference basic density values from destructive measurements are not available depending the quality of the produced QSMs, and the size of the trees. This is important for studying the AGB of trees in urban areas and protected forests where tree harvesting to build allometric models is not applicable (Lefsky and McHale 2008, Calders et al. 2020, Kükenbrink et al. 2021). In previous studies, AGB estimates from allometric models based on TLS data were more accurate compared to biomass estimates from traditional and regional allometric models (Holopainen et al. 2011, Kankare et al. 2013, Zheng et al. 2019, Stovall et al. 2018, Wilkes et al. 2018, Lau et al. 2019b, Kükenbrink et al. 2021).

5.4.3. Influence of QSM Stochasticity

According to Disney et al. (2018) there is an inherent stochastic component in tree volume estimation from QSMs due to some non-deterministic procedures for fitting geometric primitives (e.g. cylinders) to the point cloud of a tree. Here, only a relatively small portion of the total uncertainty of the mean woody AGB, main stem and branch biomass of the study trees was due to the multiple QSM reconstructions, which implies that the reconstruction method of the *TreeQSM* algorithm is robust. The coefficient of variation of the branch biomass of the trees was the largest compared to the woody AGB and main stem biomass, indicating that the reconstruction of the branches of a tree is relatively more variable compared to the main stem reconstruction; this is most likely related to the size of the branches (Disney et al. 2018).

5.4.4. Influence of Urban Versus Rural Environments on TLS-based Biomass Accuracy

Strong agreement was found between the TLS-based estimates of total woody AGB, main stem biomass, branch biomass and the reference biomass data from destructive measurements for both urban and rural forest trees. Calders et al. (2015) and Gonzalez de Tanago et al. (2018) also found strong correlations between the total woody AGB of rural forest trees from TLS and reference data (concordance correlation coefficients were 0.98 and 0.95, respectively). Momo Takoudjou et al. (2018) compared the total woody volume and the component volumes of stumps, stems and crowns of rural forest trees from TLS data with reference woody volume data and they found that the TLS-based volume estimates were very precise and accurate (adj. R^2 values greater than 0.98) and the they also reported adj. R^2 value equal to 0.97 for tree AGB. Fewer studies have focused on TLS-based biomass estimation for urban trees. A recent study by Kükenbrink et al. (2021) reported adj. R² value equal to 0.95 for the TLS-based woody AGB of urban trees compared to reference AGB data.

The error analysis revealed that the TLS-based woody AGB of the rural forest trees was less accurate and had a greater CV(RMSE)% compared to the urban trees; and it was comparable to the coefficient of variation of the root mean square error for the AGB of tropical trees (CV(RMSE) = 28%) that was reported by Gonzalez de Tanago et al. (2018). However, Calders et al. (2015) studied the AGB of rural forest trees form TLS data and they reported CV(RMSE)% equal to 16.1%, which is more comparable to the CV(RMSE)% of the TLS-based woody AGB of the urban trees in this study. Momo Takoudjou et al. (2018) found that the % mean relative error of the TLS-based woody AGB of rural forest trees was 23%, which is comparable to the mean relative error of the TLS-based woody AGB of the rural trees in this study. According to Kükenbrink et al. (2021) the RMSE of the TLS-based woody AGB of urban trees was 556 kg, which is larger than the RMSE of the TLS-based woody AGB of the urban trees here, however the CV(RMSE)% of the AGB which accounts for different tree sizes was not provided in their study. Vonderach et al. (2012) reported a bias in the total tree volume of urban trees ranging between -5.1% and +14.3% based on a voxel-based method for tree volume estimation from TLS data. The CV(RMSE)% value of the TLS-based branch biomass of the rural forest trees was substantially larger compared to the urban trees, and it was mainly based on three trees of needle-leaf evergreen species (i.e. T. canadensis and P. strobus) whose leaves were artificially removed before the QSMs generation. Without these three trees, the CV(RMSE)% of the TLSbased branch biomass of the rural forest trees reduced to 60%.

The correlation between the TLS-based branch biomass and the reference biomass values was stronger for the urban trees compared to the rural forest trees. This pattern may be related to less occlusion effects in the crown of the point clouds of the urban trees due to less tree density compared to the study trees growing in forest conditions where the view of the laser scanner can be obstructed by the foreground vegetation (Wilkes et al. 2017). Indeed, it was found that the relative error in TLS-based branch biomass of the study trees increased with the competition strength that they faced from their tree neighbors, while the urban open-grown trees faced significantly less competition compared to the rural forest trees of different canopy classes. Furthermore, the two groups of trees were scanned following different scanning patterns and using different laser scanning systems, which both can affect the quality of the TLS data (Wilkes et al. 2017). More specifically, the rural forest trees were scanned based on a scanning grid on plot level, whereas, the urban trees were individually scanned at tree scale in order to further reduce the occlusion effects in the tree crowns. We also need to notice that the performance of the TLS-based branch biomass estimates of the urban trees was better, although the trees in Harvard Forest were scanned with the Riegl VZ-400 laser scanner which typically captures good quality point clouds of trees (with less noise) in dense forests, as it has greater maximum range and it better resolves small branches compared to the FARO Focus^{3D} X 330 terrestrial laser scanner (Calders et al. 2020) that was used to scan the urban trees.

The results also showed that the TLS-based stem biomass estimates of the urban trees were less accurate compared to the main stem biomass estimates of the rural forest trees. In general, urban trees tend to have wider crowns and less discrete main stem compared to rural forest trees which typically have a spindly main stem (MacFarlane and Kane, 2017). Therefore, the detection of the main stem in the QSMs might have not aligned well with the "main" stem of

the urban trees based on the reference data from destructive measurements, which can explain the observed lower accuracy of the TLS-based main stem biomass estimates for the urban trees. This explanation is further supported by the opposite biomass allocation patterns of urban and rural forest trees that was found in this study. More specifically, the urban trees allocated more biomass to their branches versus their main stem compared to the rural forest trees. This biomass allocation "decision" of open-grown urban trees enhances their mechanical stability against strong wind loads in the complete absence or reduced competition for light from neighboring trees (MacFarlane and Kane 2017). In a previous study, Tanhuanpää et al. (2017) reported -5.5% underestimation in stem biomass of urban trees from TLS data.

5.4.5. Influence of the Leaf-removal Algorithm on TLS-based Biomass Accuracy

According to the model results the fixed effects model (eq. 5.11) explained most of the variation in the TLS-based woody AGB of the study trees and the leaf conditions (leaf-off versus leaf-removed point clouds; eq. 5.10) explained a substantial portion of the relatively small residual variation. This explains the strong agreement between the leaf-off and leaf-removed TLS-based biomass estimates and the reference biomass data. However, the total woody AGB estimates from the leaf-off point clouds were more accurate (see CV(RMSE)%, Table 5.4). The overall accuracy of the woody AGB estimates based on the leaf-removed point clouds was comparable to the woody AGB accuracy based on leaf-off point clouds in previous studies e.g. CV(RMSE)% = 16.1% according to Calders et al. (2015). Momo Takoudjou et al. (2018) performed a manual but still artificial leaf-removal from the leaf-on point clouds in their study and they reported an agreement between TLS-based woody AGB and reference biomass data (R²

= 0.97) which aligns with the agreement between the TLS-based woody AGB after the algorithmic leaf-removal and the reference woody AGB in this study (Fig. 5.7 A). However, Momo Takoudjou et al. (2018) did not examine how the manual-artificial leaf-removal process affected the estimation of the main stem and the branch biomass of the trees. Our study also showed that the overall accuracy of the TLS-based biomass of the main stem from the leaf-off point clouds was very similar to the overall accuracy of the main stem biomass from the leaf-removed point clouds, which was expected because the leaf-separation algorithm should not affect the main stem of the trees. Similarly, the accuracy of the TLS-based branch biomass estimates from the leaf-off point clouds (see CV(RMSE)%, Table 5.4).

The tree with the largest absolute error and underestimation in TLS-based AGB and branch biomass was an urban tree of *G. triacanthos* species which had the largest woody AGB and branch biomass and whose leaves were artificially removed (see Figs. 5.7 A and 5.7 C). *G. triacanthos* trees have compound leaves with modular architecture i.e. the leaf blade consists from several leaflets stemming from the leaf rachis (Champagne and Sinha 2004, Klingenberg et al. 2012). According to Wang et al. (2019) leaf-separation algorithms typically detect leaves as simple flat structures, which implies that the modular structure of compound leaves of the *G. triacanthos* trees may confuse the leaf-separation algorithms. Therefore, the leaf type of a tree species can affect the quality of the artificial leaf-removal results (Moorthy et al. 2020). However, the TLS-based biomass estimates of the rest *G. triacanthos* trees which were of smaller size in terms of AGB and branch biomass were not significantly underestimated after the artificial leaf-removal. This could imply that the effect of leaf type on the performance of the *TLSeparation* algorithm may also depend on tree size in terms of branching complexity.

Similarly, Arseniou et al. (2021a) found that the artificial leaf-removal using the *TLSeparation* algorithm introduced an underestimation of the fractal-structural complexity of urban trees of *G*. *triacanthos* species which increased with maximum branch order, while larger trees tend to have higher branch orders (Seidel et al. 2019). In general, despite the existence of different algorithms to separate leaves from the leaf-on point clouds of trees of needle-leaf and broad-leaf species (Stovall et al. 2017, Vicari et al. 2019, Wang et al. 2019, Moorthy et al. 2020), there is no best approach that fits for all leaf-wood classification cases in forest conditions (Moorthy et al. 2020).

5.5. Conclusions

The above-ground biomass of urban and rural forest trees is directly related to important ecological and economic services of forests e.g. atmospheric carbon dioxide sequestration, bio-fuels etc. Therefore, the accurate monitoring of the biomass of trees is essential. Terrestrial laser scanning (TLS) is an active remote sensing technology which has been used to study the architecture and biomass allocation patterns of trees (Liang et al. 2018) and it has been recently added to the IPCC guidelines for national greenhouse gas inventories (Kükenbrink et al. 2021). Furthermore, TLS allows to study the above-ground biomass in areas where tree harvesting is not applicable or preferable i.e. protected forest areas and urban sites; while studying the biomass allocation patterns of urban trees can inform us about the growth limits of different species (Calders et al. 2020). This study demonstrates that TLS data provide reliable above-ground biomass estimates of trees, whose quality can vary depending the basic density values that are used, the growing environment of trees (i.e. urban versus rural forest growing conditions), and their leaf conditions (i.e. leaf-off versus leaf-on which requires artificial leaf-removal). The study results have important implications for studying the biomass and the carbon stocks of forests,

especially for trees in urban areas where there is a paucity of allometric models for tree biomass estimation (Tigges and Lakes 2017).

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CHAPTER 6

DISCUSSION

6.1. Synthesis

6.1.1. Differences in Fractal Metrics for Characterizing Tree Architecture

The previous chapters have produced new knowledge about the architecture and the fractal-structural complexity of trees in urban areas, which gives us a deeper understanding of their physiological responses to their growing environment. Fractal analysis (Mandelbrot 1983) provides the fundamental theory and principles for analyzing tree architecture; however, there is significant ambiguity regarding the methods and the metrics used to quantify the inherent fractal-like architecture of trees and their biological/ecological interpretation. More specifically, Halley et al. (2004) noted that applying fractal values to natural objects is, in general, dependent on the method used, and Mandelbrot (1983) warned against the underlying ambiguity of a precise mathematical interpretation of fractal dimension (Halley et al. 2004).

The study of the self-similar character of trees depends on the theoretical models that are used to quantify and interpret the fractal dimension of trees. Niklas (1994) explained three models following engineering design principles that dictate different scaling relations among stem length, diameter and mass: (1) elastic self-similarity, (2) stress self-similarity for selfloading of trees, and (3) geometric self-similarity, when wind-loads are the main factor of tree mechanics. In this dissertation, the fractal dimension of urban trees was quantified with the twosurface method and the "box-dimension" metric (D_b) and interpreted based on the metabolic scaling theory (West et al. 1997, West et al. 1999) and the pipe-model theory (Shinozaki et al. 1964, Chiba 1998), considering the biological scaling of the volume and surface area of the different components of tree structure. The two-surface method and the D_b metric are based on different theoretical assumptions and they require different types of data to quantify the fractal dimension of trees.

The study presented in the first chapter used a variant of the "two-surface" method (Zeide and Gresham 1991, Zeide and Pfeifer 1991, Zeide 1998) to quantify the fractal dimension of the crowns of thousands of trees of several species across different climatic regions in the United States. The fractal dimension based on this method refers to the distribution of leaf surface area within a crown volume occupied by the leaves and branches. This measure of fractal dimension takes values between two and three (Zeide and Gresham 1991). The two-surface method essentially includes the foliage of tree crowns, but it doesn't allow to explicitly account for the contribution of the two main components of a tree's crown to its fractal dimension, the branches and the leaves. Therefore, in the third chapter of the dissertation TLS data of urban trees were used to compute the D_b metric which quantifies their above-ground structural complexity (Silva et al. 2006, Seidel 2018), in order to disentangle the contribution of leaves and the woody skeleton of trees.

The D_b metric has no units and, in contrast to the two-surface method, its possible values range between one and three. These two methods not only provide metrics on different scales but their interpretation is also different. More specifically, trees with greater crown complexity and "space-filling character" have D_b values closer to three, and D_b equal to one implies a perfectly cylindrical stem with no branches, e.g., a dead tree (Seidel 2018). However, the two-surface method focuses on the distribution of foliage within crown volume and fractal dimension equal to two means that the foliage is distributed on the crown's periphery and the crown surface is a classic, flat Euclidean surface. According to the same method, as the fractal dimension increases the crown surface becomes more fractal until the fractal dimension is equal to three, when the foliar surface is evenly distributed within a given crown volume (Zeide and Pfeifer 1991, Zeide and Gresham 1991). Benefiting from the inherent differences of the two methods, which requires

more research to better understand why and how they differ (see 6.3), it was possible to answer two important research questions of the dissertation: (1) How the urban growing environment and species-specific effects affect the structure and function of trees at different scales?, and (2) what is the role of the photosynthesizing and non-photosynthesizing components of trees in their fractal-structural complexity?

6.1.2. Urban Environmental Effects Versus Species-specific Effects on Tree Architecture and Physiology

Tree architecture is genetically controlled and environmentally altered (Seidel et al. 2019a), and it is important to understand how the built-up environment in cities affects tree architecture. The study results in the second chapter indicated that trees exhibit reduced crown fractal dimension mainly to reduce water loss through transpiration in hotter cities. Trees of different species with different drought tolerance reduced their surface to volume ratios at both whole-crown and leaf scales, pre-adapting them to drought-stress in urban ecosystems; while adjusting for the temperature of cities and intrinsic species effects, it was found that more heavily urbanized areas had a negative effect on trees' fractal dimension. Another important result was that urban trees followed different patterns of structuring their fractal-like crowns based on their life-history traits. More specifically, needle-leaved species showed a clear tradeoff between optimizing the fractal dimension of their crowns for drought versus shade tolerance, whereas broad-leaved species showed a fractal crown architecture that responded principally to inherent drought tolerance. These results have significant management implications for urban forests, because we can inform arborists how to better manage urban trees for optimizing their several socio-ecological benefits, e.g., shading, air pollutant uptake, energy saving for buildings,

temperature regulation, carbon dioxide sequestration (Heisler 1986, McPherson et al. 1994, McPherson 1998, Nowak and Crane 2002, MacFarlane 2007, Casalegno et al. 2017, Tigges and Lakes 2017), which all depend on the crown architecture of trees. More specifically, in regions with arid and warm climate, arborists could plant drought tolerant species of lower fractal dimension or they could select less drought tolerant species with larger fractal dimension that can cast deeper shade. The latter would require more frequent watering, which implies higher water maintenance costs.

A common pattern revealed in the second, third and fourth chapters of the dissertation is the relationship between the fractal-structural complexity of trees growing in urban areas and their inherent functional traits, specifically drought and shade tolerance. Chapter two showed that very shade tolerant (and less drought tolerant) species distribute their leaves more evenly within their crown volume, which helps to explain why the trees of *Gleditsia triacanthos* species in the third chapter had the smallest contribution of leaves in their crown complexity compared to the trees of the other two studied species (Quercus macrocarpa, Metasequoia glyptostroboides). According to Niinemets and Valladares (2006), G. triacanthos is the least shade tolerant of all studied species, which implies that their leaves are widely spaced mainly in the crown top, in order to increase crown porosity and reduce local self-shading (Sack et al. 2006). The leaves distributed in the crown periphery are "sun" leaves and they have greater leaf mass per unit area, in order to reduce water loss through transpiration (Abrams and Kubiske 1990, Sack et al. 2006). The the study in the second chapter showed a negative relationship between leaf mass per unit area and crown fractal dimension. Finally, chapter four showed that self-shading of leaves and branches and inherent shade tolerance could be an important element of the branching architecture of open-grown trees (Duursma et al., 2010), because the three studied urban tree

species indicated a branch surface area vertical distribution inversely corresponding to Niinemets and Valladare's (2006) shade tolerance indices.

6.1.3. Photosynthetic Versus Non-photosynthetic Components of Urban Tree Architecture

The contribution of photosynthesizing and non-photosynthesizing components of trees to their above-ground structural complexity has implications for their carbon-balance through photosynthetic and respiration efficiency (Kinerson 1975, Kim et al. 2007, Seidel 2019b, Zheng et al. 2019). The D_b metric computed from leaf-on and leaf-off point clouds of deciduous urban trees on Michigan State University campus helped disentangle the different components of the structural complexity of trees. Open-grown urban trees were chosen as objects of study, because it was expected better quality of TLS-based measurements of tree attributes without occlusion from neighboring trees, but also because the low, or complete absence of competition from tree neighbors in cities should allow trees to better express their inherent fractal character in terms of structural complexity (MacFarlane et al. 2014, Eloy et al. 2017, Seidel 2018, Dorji et al. 2019). The study presented in the third chapter showed that the D_b of the leaf-on tree point clouds was significantly greater than the D_b of the leaf-off point clouds across all species. The index capturing the contribution of leaves to the structural complexity of the study trees was negatively correlated with branch woody surface area and different metrics of the length of paths through the branch network of the trees, indicating that the contribution of leaves decreases as branch network complexity increases. These results have important implications for studying the fractalstructural complexity of trees in leaf-on and leaf-off conditions, because the presence of leaves influences the modeled patterns of the fractal-like architecture of trees.

6.1.4. Studying the Above-ground Allometry of the Woody Surface Area and Woody Biomass of Urban Trees with TLS

The observed relationship between the woody surface area of the branches of the study trees and the contribution of leaves to their above-ground structural complexity, indicated a potential connection between the above-ground woody surface area of trees and their structural complexity, which aligns with research hypotheses in previous studies (Whitaker and Woodwell 1967); this was thoroughly studied in chapter four. More specifically, it was found that the total woody surface area of the studied urban trees increased with the D_b metric of their leaf-off point clouds, but it was most strongly correlated with the 25^{th} percentile of path lengths from the tree base to every branch tip. Furthermore, the sampled urban trees mainly allocated woody surface area to branches, which changed with branch order, branch-base diameter, and branch-base height, and the branch-to-stem area ratio differed among the studied species and increased with their crown surface area across all species combined and within each species, which implies a physiological mechanism for maintaining a positive carbon balance at tree scale.

According to Weiskittel et al. (2015) there is still a lot of uncertainty regarding the carbon offsets of rural forests at different spatial scales, due to lack of accurate and detailed tree biomass data, over multiple spatial and temporal scales (Weiskittel et al. 2015). This uncertainty becomes stronger for trees growing in urban areas (Tigges and Lakes 2017, Wilkes et al. 2018). Therefore, the study presented in the fifth chapter of the dissertation evaluated the accuracy of TLS-based estimates of the above-ground biomass of trees in different growing and leaf conditions. The results of the study showed that TLS-based total and component biomass estimates of trees are reliable, and differences in the quality estimates are affected by the growing environment, the leaf condition of the laser-scanned trees and the basic density values that are used. These results are important for studying the biomass of trees in urban areas and protected forests, where tree harvesting to build allometric models is difficult to be justified (Lefsky and McHale 2008, Calders et al. 2020, Kükenbrink et al. 2021). The hypothesis of TLS-based tree measurements of better quality in urban areas due to absent or reduced occlusion from neighboring trees, which was integral of the experimental design in chapters three and four, was validated in the fifth chapter. It was shown that the TLS-based branch biomass estimates correlated more strongly with reference biomass data for the urban trees compared to the rural forest trees, and the relative error in TLS-based branch woody biomass of the study trees increased with the competition they faced.

6.1.5. Methodological Considerations for Studying Tree Architecture from Leaf-on TLS Data

In chapters three and five the effect of the artificial leaf-removal on estimating the structural complexity and the biomass of trees was studied. In both chapters the *TLSeparation* algorithm (Vicari 2017) was used to algorithmically remove the leaves from leaf-on tree point clouds and subsequently for each tree the D_b metric and the total and components biomass were estimated. In chapter three, it was found that the artificial leaf-removal introduced bias to the leaf-removed D_b of the *G. triacanthos* and *M. glyptostroboides* trees compared to the D_b of the leaf-off point clouds. Chapter five showed that the accuracy of the TLS-based branch and stem biomass estimates after the artificial leaf-removal was comparable to the branch and stem biomass estimates for trees that were scanned in leaf-off conditions, despite the lower accuracy (underestimation) of the TLS-based woody AGB from leaf-removed point clouds. The results of

these two studies imply that the potential bias due to artificial leaf-removal can be stronger when the fractal-structural complexity of leaf-removed point clouds is studied compared to their TLSbased biomass. The D_b metric is computed directly from point clouds of trees, and therefore, the miss-classification of laser-points as leaves due to the shape of leaves (Vicari et al. 2019, Wang et al. 2019) and the branching architecture of trees can introduce a significant bias to the $D_{\rm b}$ computation (see the results in chapter three). However, the accuracy of TLS-based biomass estimates also depends on the quality of the QSM volumes and the use of appropriate basic density values. An explicit accounting of the error sources is challenging because we don't have a complete control over them, and different types of errors can be correlated (Burt et al. 2021). A previous study the artificial leaf-removal using the *LeWoS* algorithm resulted in the underestimation of the total woody volume of trees in the generated QSMs, while only the stems and some large branches were detected in coniferous trees (Wang et al. 2019). In general, the results of the artificial leaf-removal should be carefully examined and the effects on estimated tree attributes should be further studied. We still need a better understanding of the effect of classification algorithms for leaf separation when studying tree architecture (Vicari et al. 2019).

6.2. Accounting for Different Sources of Uncertainty in Studying Tree Architecture from TLS

It is important to account for the technical parameters of different laser scanners when we analyze tree architecture from TLS data. Terrestrial laser scanners scan the surrounding environment stepwise using a fast vertical mirror rotation and a slower horizontal instrument rotation and systematic errors can occur due to imperfections in instrument manufacture and assemble. Rotation axes are supposed to be mutually orthogonal and they should intersect at a specific common point. However, these assumptions do not always hold true (Liang et al. 2016).

Pueschel (2013) studied the effect of different technical characteristics of the FARO Photon 120 laser scanner on the quality of scanned trees. More specifically he focused on the effects of scanner resolution (the angular step size), scan speed (the number of laser pulses per second), and pulse duration (signal to noise ratio) on the detection of tree stems, and the estimation of tree diameter and total tree volume. He found that the accuracy of stem detection, and the quality of tree diameter and volume estimates were not significantly affected by the scan speed, and the pulse duration. However, the scan resolution had a significant effect and its magnitude depended on the range. Therefore, Pueschel (2012) concludes that higher scanning resolution is required at larger distances from a focal tree.

According to Wilkes et al. (2017), the recommended distance for scanning individual trees is less than 10 m and the recommended scan resolution is 0.04 degrees. The footprint size of the scanner significantly affects the quality of the data. Branches of similar or smaller diameter than the TLS footprint size at a given distance are not sufficiently captured in a point cloud (Disney et al. 2018). This issue becomes more pronounced at the upper parts of tree crowns due to larger occlusion, and due to larger distance from the scanner. The pulses that reach the upper parts of the crowns have larger footprint due the laser beam deflection (Disney et al. 2018). The current commercial laser scanners have footprint size 2-5 cm at 100 m range and branches less than 5 cm diameter cannot be effectively captured at large distances (Disney et al. 2018). Due to this issue, there is more uncertainty in volume estimation of smaller branches, but this affects only a small portion of the total aboveground tree volume (Disney et al. 2018). In the studies compiled in this dissertation, the FARO Focus^{3D} X 330 terrestrial laser scanner was used to scan the study trees, and according to Calders et al. (2020) the technical characteristics of this scanner allow for resolving small branches. All study trees were laser scanned from multiple

directions and distances at high scanning resolution, following the field scanning protocols suggested by Wilkes et al. (2017).

Another source of uncertainty originates from QSMs that has a stochastic and a deterministic component (Disney et al. 2018, Malhi et al. 2018). The stochastic component refers to non-deterministic processes for fitting geometric primitives in a point cloud and the systematic component relates to the assumptions inherent to each QSM algorithm (Disney et al. 2018). In chapters four and five it was found that the uncertainty due to the consecutive QSM reconstructions of the same point cloud of a tree was a relatively small portion of the mean aboveground woody surface area and woody biomass per tree across all study tree species combined. This does not mean that the QSMs do not introduce bias, such as systematically overor under- estimating surface areas and biomass of different parts of the trees. Finally, the algorithmic leaf separation introduces an additional source of uncertainty (Malhi et al. 2018). The results in chapter three provided new insights into the effects of the algorithmic leaf separation on studying tree architecture (also see 6.1.5). According to Burt et al. (2021) an explicit accounting of all different error sources is challenging because we don't have a complete control over them, and different types of error can be correlated.

6.3. Evaluation of the Analysis Methods and Further Research Opportunities

The underlying ambiguity inherent in the methods used to study the fractal-like architecture of trees (Halley et al. 2004), makes it essential to reflect on the analysis methods in a critical way to identify opportunities for future research that will deepen our understanding of the structural complexity and architecture of trees. The variant of the two-surface method that was used in the second chapter provided significant results and new insights into the fractal dimension of the crowns of thousands of trees of different species in relation to their functional

traits and stress tolerance. The publicly available dataset that was used in chapter two (McPherson et al. 2016) has independent measurements of leaf area and crown volume of the trees, and the leaf area was estimated for every tree using a novel photographic method developed by Peper and McPherson (2003). The occluded portions of foliage when a photographic method is used could imply conservative leaf area estimates. This hypothesis was tested here by comparing leaf area estimates from digital image analysis and destructive measurements for five *G. triacanthos* trees sampled on the Michigan State University campus, and the analysis showed an underestimation of leaf area using the photographic method (see Supplemental File 6.1). However, this comparison was based only on few trees of the same species and similar crown structure and crown porosity. Therefore, further analysis is needed to evaluate the accuracy of the photographic method (Peper and McPherson 2003) based on a large sample of destructive measurements of trees of several species.

A different way to obtain leaf area estimates is from TLS data (Hosoi and Omasa 2009, Béland et al. 2011, Béland et al. 2014), which is a more precise methodology. Future work can focus on studying the leaf surface area and the leaf angle distribution (Stovall et al. 2021) of urban trees from TLS data in order to better understand how different leaf properties affect the structural complexity of the crown of open-grown trees. One of the main findings in the first chapter was that 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. Data describing in more detail the eco-physiological local growing environment of trees (e.g. soil properties, seasonal variation of the amount of light transmitted through a tree's crown) can deepen our understanding of the crown fractal dimension dependency on the local growing environment of urban trees.

The D_b metric (leaf-on and -off) that was used in chapters three and four included both the trunk and the crown of the study trees, and therefore it computes the total above-ground structural complexity of trees compared to the two-surface method that includes only the crown of trees. However, it has been noted that trunk length does not scale with crown fractal dimensions (Mäkelä and Valentine 2006). Therefore, a next research step is to examine how the removal of a tree's trunk below its crown affects the computation of the D_b metric i.e., what is the scale and the magnitude of the computed values and what is their biological interpretation.

As it was explained in section 6.1., the two-surface method and the D_b metric derived from the box-counting method make different assumptions and they produce values of different scales. Further research is needed to explicitly compare fractal-dimension values produced by the two-surface method and the D_b metric (leaf-on and -off) considering the functional traits of different tree species. More specifically, a research question that remains to be answered is what method of fractal analysis is more appropriate to be used to study different aspects of the fractallike character of trees; how the fractal dimension values from different methods compare each other and how they relate to the functional traits of different species, e.g., drought and shade tolerance, and the life-history strategies of different species, e.g., broad-leaved deciduous and needle-leaved evergreen species.

Another question that remains to be answered is: what can be the maximum realized fractal-dimension of a tree considering not only the inherent differences of fractal-analysis methods but also the metabolic, hydraulic and mechanical constraints of tree architecture (Abrams and Kubiske 1990, Sack et al. 2006, Eloy et al. 2017, MacFarlane and Kane 2017, Seidel et al. 2019a). A small change in the fractal dimension of a tree can have important physiological implications; for example in chapter three it was found that an increase of about

0.05 units in the LCC index was associated with approximately 400 m^2 reduction in the branch woody surface area of the study trees. According to Seidel et al. (2019b) trees should have D_b values significantly lower than 2.72, which is the D_b of the Menger sponge (Menger 1926), assuming a tree would maximize its surface area for light capture and gas exchange, while minimizing building costs, in the absence of competition with other plants. In chapter three the maximum D_b value that was observed was 2.23, for a large *M. glyptostroboides* tree in the leafon condition and the study also showed that the mean D_b of the leaf-on tree point clouds was greater than 2 across all study urban tree species, while previous studies reported leaf-on D_b values of trees growing in dense rural forest stands consistently lower than 2 (Seidel 2018, Seidel et al. 2019a, Seidel et al. 2019b, Dorji et al. 2019, Guzmán et al. 2020, Saarinen et al. 2021), supporting the assumption that trees growing in the open, without competition can more closely approach the theoretical maximum fractal complexity (MacFarlane et al. 2014). TLS data can be used to further examine this assumption by comparing the allometric scaling exponents of urbanopen grown trees against the theoretical expectations from the metabolic scaling theory (West et al. 1997), while a previous study showed that trees growing in dense tropical forests might not follow the theoretical expectations for self-similar branching architecture according to the metabolic scaling theory (Lau et al. 2019).

Chapters four and five showed important patterns of the woody surface area and biomass allometry of trees. Some additional analysis in chapter four that included photographic-based one-side leaf area estimates (Peper and McPherson 2003) and woody volumes from the QSMs of the study trees showed negative relationships between the ratio of the woody surface area, leaf surface area and total surface area to the total woody volume of the trees, and different Euclidean metrics of tree architecture (e.g., maximum path length), but no statistically significant

relationships were observed with the D_b metric of fractal complexity (see Supplemental File 6.2). These results imply that as trees increase the average distance from the ground to leaves (longer hydraulic pathways), their total woody volume increases faster than the surface areas of their woody organs and their leaves.

According to Smith et al. (2014) the hydraulic conductance of trees should reduce with mean path length and the WBE model (West et al. 1997), which suggests that greater woody volume implies more conducting elements, but also proportional surface area. These dissertation results suggest that reduced hydraulic conductivity over a longer branching network might come from reduced evaporative surfaces (leaf stomata and stem lenticels) relative to the addition of woody volume. However, pipe-model theory would suggest that much of the volume in larger trees is dead and not conductive (Shinozaki et al. 1964). It has been found that the foliage mass of a tree scales with its sapwood mass (Valentine 1985, Mäkelä and Valentine 2006, Peng et al. 2010, Lehnebach et al. 2018), but the QSM woody volume estimates include both sapwood and heartwood tissues, because the laser scanning method cannot see beyond the tree's surface. Therefore, it is also possible that the leaf area and living, conductive (sapwood) volume remain in balance as the tree expands its branching network. Further research is needed to partition the active and non-active components of the woody volumes of trees generated from QSMs through new allometric models; and more precise estimates of leaf surface area can be derived from TLS data (Béland et al. 2014).

The surface area data that were produced in chapter four can be used to develop new or inform existing process models that quantify the growth and productivity of urban forests. Similarly, one of the most promising findings in chapter five is that TLS data can be used to produce reliable total and component biomass estimates of trees, which is important for studying

the AGB of trees in urban areas and protected forests where tree harvesting to build allometric models is not applicable (Lefsky and McHale 2008, Calders et al. 2020, Kükenbrink et al. 2021). Considering the current paucity of data and allometric models of the AGB of urban trees (Tigges and Lakes 2017), further research is needed to produce new allometric models from TLS data that predict the biomass of urban trees at different spatial scales which will enhance our understanding of urban forest carbon budgets.

6.4. Conclusions

Studying the aboveground fractal-structural complexity and architecture of trees is an important element of the decision-making in forest management and policy. Open-grown urban trees are ideal objects for studying the fractal-like architecture of trees because of the reduced or absent crowding conditions. This dissertation research showed that the fractal-like character of urban trees is affected by their growing environment at regional and local spatial scales, and it relates to their functional and life-history traits. Terrestrial laser scanning (TLS) data of urban trees provided a deeper understanding of the architecture of trees in general i.e., the role of the different structural components of trees in their fractal-structural complexity, and the allometry of their aboveground woody surface area and woody biomass. Challenges and opportunities for further research arise from the inherent ambiguity of fractal analysis methods, the different metrics that are used, and their biological interpretation. The quality of the TLS data and the algorithms that are used to process them (e.g., artificial leaf-removal) can significantly affect the quality of tree models depending on the aspect of tree architecture that is studied (e.g., fractal dimension, woody surface area and biomass). TLS data collected on trees of several species growing in different environments (urban versus rural forests), in combination with the

anticipated future progress of TLS systems and algorithms will further enhance our understanding of tree architecture.

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