



A new approach for quantification of total above-ground heartwood and sapwood volume of trees

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Abstract

Key message Terrestrial laser scanning data of trees combined with models of heartwood content proportion of woody disks can provide precise characterization of total aboveground tree sapwood and heartwood volume.

Abstract Quantifying sapwood and heartwood content of trees is challenging. Previous studies have primarily characterized main stem wood composition, while branches have rarely been studied. Terrestrial Laser Scanning (TLS) can provide precise representations of the entire above-ground tree structure, non-destructively, to help estimate total tree sapwood and heartwood volume. In this study, we used TLS to scan above-ground portions of twenty-four open-grown, urban *Gleditsia triacanthos* trees on Michigan State University campus. TLS data were used to generate quantitative structure models that provided comprehensive characterizations of the total tree woody surface area (WSA) and volume. A subsample of trees was harvested (after scanning) and main stem and branch woody disks were collected to build models of heartwood content proportion. Models were applied to measurements from TLS to quantify complete heartwood and sapwood volume of each tree, including main stem and branches. From the base to the top of the trees, the largest portion of stem vertical cumulative volume was heartwood, whereas vertical cumulative volume of branches showed the opposite pattern. Absolute heartwood volume declined monotonically toward zero from stem base to stem top, while absolute sapwood volume declined sharply from stem base up to near the crown base and then remained relatively constant within crown. We also found that tree WSA increased with sapwood volume for both branches and main stem. This study developed a novel, general method for quantifying total aboveground sapwood and heartwood volume of trees and provided new insights into urban tree growth and structure.

Keywords Branches · Heartwood · Main stem · Sapwood · Terrestrial laser scanning · Urban trees

Introduction

Wood is the secondary xylem of trees, accounting for approximately 95% of total tree biomass (Celedon and Bohlmann 2017). Heartwood is the inner dark-colored core of wood, which is metabolically inactive and considered to be dead tissue. Sapwood consists of the outer, paler layers of

wood, which contain living tissues, though most sapwood cells are also dead (Celedon and Bohlmann 2017). Sapwood is the conducting portion of xylem, and it contains reserves of sugar and starch (Wilkins 1991), whereas heartwood has an important role in tree mechanical stability and health, because it has greater resistance to pathogens and insects (Celedon and Bohlmann 2017). During tree ontogeny, inner layers of sapwood progressively transform to heartwood in the transition zone (Climent et al. 2003). The process of sapwood to heartwood transformation is not completely understood yet, but it is genetically and environmentally controlled, and it includes the death of ray parenchyma cells (Taylor et al. 2002; Kampe and Magel 2013; Cruickshank et al. 2015; Celdon and Bohlmann 2017).

Both sapwood and heartwood components have important implications for wood utilization, as well as tree physiology. Accurate measurements of heartwood and sapwood volumes

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are fundamental to understanding the functional ecology and evolution of woody plant species, and testing major theories of plant biology, including the ‘pipe model’ theory and ‘WBE’ metabolic scaling theory (Shinozaki et al. 1964; West et al. 1997; Mäkelä and Valentine 2006). Accurate quantification of sapwood and heartwood volume can also enhance our mechanistic understanding of the aboveground biomass and carbon dynamics of forests at different scales, because of wood density differences between heartwood and sapwood tissues affecting biomass and carbon accumulation (Climent et al. 2003). So, a better understanding of how trees accumulate heartwood and sapwood volume can provide new insights into the growth, carbon balance and value of forests.

Accumulation of tree sapwood and heartwood is challenging to quantify and wood branch composition has rarely been quantified relative to the main stem (Kyker-Snowman and Wilson 1988). Due to the lack of internal tree visibility, a model is required to estimate heartwood and sapwood proportions based on a calibration of destructive samples, typically from extracted tree cores or disks. Previous studies utilized geometric approximations (i.e., cone shape) (Climent et al. 2003; Pinto et al. 2004; Cardoso and Pereira 2017) or taper functions for estimating sapwood and heartwood volumes in vertical profiles of main stem (Ojansuu and Maltamo 1995; Maguire and Batista 1996; Knapic et al. 2006; Debell and Lachenbruch 2009). Other studies have modeled sapwood and heartwood volume accumulation as a function of species functional traits and tree allometry (e.g., wood density, height to live crown base, tree vigor, tree age and mean annual growth; Wilkes 1991; Sellin 1994; Cruickshank et al. 2015). Currently, available methods are mostly limited due to exclusion of branches and a priori assumptions of stem form and growth. A more useful approach would directly measure the actual tree form and include sapwood and heartwood formation in both stems and branches.

Terrestrial Laser Scanning (TLS), which is an active remote sensing technology, provides precise representations of the entire aboveground tree structure by emitting laser pulses and generating ‘point clouds’ of trees (Malhi et al. 2018). Main stem and branches can be modeled by fitting geometric primitives (cylinders) in point clouds to create quantitative structure models (QSM) of trees (Raumonen et al. 2013). Several studies have showed that QSMs provide precise non-destructive estimates of aboveground woody volume, biomass and woody surface area of trees preserving stem and branch topology (Raumonen et al. 2013; Calders et al. 2015; Disney et al. 2018; Arseniou et al. 2021b; Burt et al. 2021). TLS-based estimates of total aboveground woody volume of trees cannot directly quantify heartwood and sapwood volumes, but could be combined with models of heartwood and sapwood proportions, calibrated with destructive sampling data.

Including branches explicitly in characterizations of tree sapwood and heartwood formation should allow for more biologically meaningful interpretations. According to pipe model theory (Shinozaki et al. 1964), which suggests that trees have an inherent fractal-like architecture (Noordwijk and Mulia 2002; Mäkelä and Valentine 2006), based on fractal geometry principles (Mandelbrot 1983), the cross-sectional area of stems is preserved when they bifurcate into branches and tree vascular system consists of active and inactive woody ‘pipes’ and each woody ‘pipe’ transfers water from roots to a unit of foliage providing mechanical support (Shinozaki et al. 1964; Lehnebach et al. 2018). Therefore, sapwood area of active woody ‘pipes’ scales with foliage area or biomass (Dean and Long 1986; Mäkelä 2002; Cruickshank et al. 2015; Ogawa 2022). The theory assumes that heartwood is formed through branch or twig senescence and death as woody ‘pipes’ of tree vascular system disconnect from leaves and they become inactive (Mäkelä and Valentine 2006).

In this study, we used TLS technology combined with measured heartwood and sapwood proportions of woody disks sampled from branches and stems of open-grown trees. Open-grown trees typically have few or no neighboring trees, which should allow them to better demonstrate their fractal-like character, as competition for light disrupts the inherent self-similar structure of trees (MacFarlane 2014; Arseniou et al. 2021a). Therefore, heartwood and sapwood accumulation of such trees may be better described within the pipe model theory framework. The objectives of the study are: (1) develop new models of sapwood and heartwood proportions of stem and branch disks; (2) produce novel estimates of whole tree vertical accumulation of sapwood and heartwood volume; (3) examine how woody surface area (surface area outside of the bark tissues) of trees, which relates to their growth respiration (Kim et al. 2007), changes with their sapwood volume, which relates to maintenance respiration and the hydraulic conductance of active root-to-foliage unit ‘pipes’ according to pipe model theory (Shinozaki et al. 1964; Sprugel 1990).

Materials and methods

Tree data

Twenty-four open-grown *Gleditsia triacanthos* trees (a broad-leaf deciduous species), were sampled on Michigan State University campus, USA. The basic experimental approach was to identify healthy trees with undamaged crowns covering different sizes (stem diameter at breast height, DBH (cm): mean = 51.9, minimum = 18.4, maximum = 72.8; Height (m): mean = 12.11, minimum = 9.45,

maximum = 18.44). A complete list of all their measured/estimated properties is given as Supporting Information.

Reference field and laboratory measurements

Six *G. triacanthos* trees were harvested in July 2019. Before felling, total standing height of trees was recorded with a *TruPulse 360* laser range finder and their DBH (at 1.37 m from the ground) was measured with a diameter tape to the nearest 0.25 cm. After felling, the ‘dominant’ main stem was determined following the largest and straightest stem at any fork in main stem all the way to tree top. All other stems connected to the dominant main stem (hereafter ‘main stem’) are defined as branches. After branches were separated, the main stem was cut at 1.37 m, 2.44 m, and then at 1.22 m intervals. Disks of thickness approximately 5 cm were cut from the top of the 0.15 m height mark (stump height), at 1.37 m above the ground (breast height), at the middle of the stem, and at the top of the last stem section. Starting at tree base and working upward, first-order branches (attached directly to the main stem) were systematically removed. 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 ≥ 2.5 cm). Disk samples from the base of the largest branch and the highest branch in tree (with bd ≥ 2.5 cm) were collected.

Bark of sampled stem and branch disks was removed. Then, the woody surface was sanded and scanned using an Epson Perfection V39 color scanner at a 600 DPI resolution. Disk images were processed with *ImageJ* 1.46r software (Schneider et al. 2012), using a pixel-based approach to quantify the total surface area of each disk, and the surface areas of heartwood and sapwood, after they were separated based on their strong color difference (which is typical for *G. triacanthos* trees, Fig. 1). The scanning method was selected to avoid bias in surface area measurements due to irregular disks shape (Cruickshank et al. 2015).

Terrestrial laser scanning of trees and point cloud processing

All trees were laser-scanned with the FARO Focus^{3D} X 330 terrestrial laser scanner, which has wavelength of 1550 nm, beam divergence 0.011°, maximum angular resolution 0.009°, horizontal/vertical field of view (FOV) 300°/360°, exit beam diameter 2.25 mm, and ranging error ± 2 mm (FARO Technologies Inc., Lake Mary, FL, USA). Harvested trees were laser-scanned with their leaves-on before felling in July 2019, and the remaining trees were laser-scanned without their leaves in January 2020. Each tree was scanned with high resolution from a minimum of four different directions and distances to minimize occlusion effects. Six reference target-spheres were placed around each focal tree to spatially-reference each scan, then combined to create a single point cloud for each tree (following field scanning protocols suggested by Wilkes et al. 2017). All scans for each tree were spatially co-registered and filtered using the software SCENE 2019.2 (FARO Technologies Inc., 2019.2). The same software was used to manually segment a tree from the point cloud of the background site.

QSMs were generated from leaf-off point clouds of the trees (Fig. 2) using the algorithm *TreeQSM* v.2.3.0 (Raumonen and Åkerblom 2022), which includes two main steps: (1) segmentation of stem and branches (2) reconstruction of volume and surface area of segments with cylinders (Calders et al. 2015). *TreeQSM* simultaneously generates multiple QSMs for each tree with varying input parameter values and then selects the optimal QSM (Raumonen et al. 2013). In *TreeQSM* the main stem is determined following these criteria: (1) main stem extends near the tree top, (2) it goes straight up, and (3) 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). This definition of tree main stem in *TreeQSM* is very similar to the definition used to identify the “dominant” main stem in the field during destructive sampling (described previously).

Due to the inherent stochasticity of the *TreeQSM* algorithm, multiple slightly different QSMs are generated for each tree based on the same input parameters and the algorithm finally selects the optimal QSM (Raumonen et al.

Fig. 1 **a** Part of a scanned DBH disk of a harvested *G. triacanthos* tree after bark removal, **b** Separated heartwood surface area of the same part of the disk, **c** Separated sapwood surface area of the same part of the disk

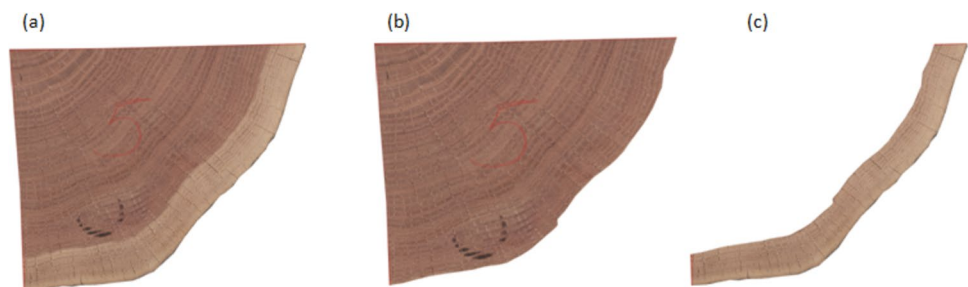
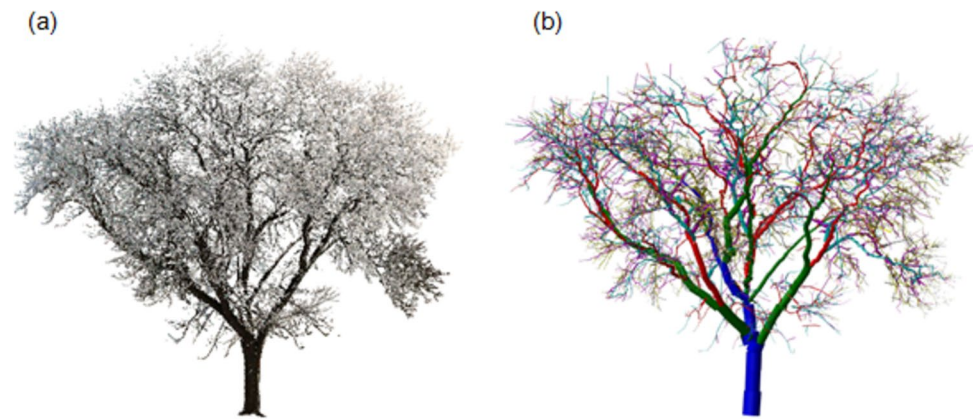


Fig. 2 Digital representation of an urban *G. triacanthos* tree showing **a** Leaf-off point cloud, **b** Generated QSM. QSM colors denote different branching orders (i.e., blue is main stem, green is 1st order, red is 2nd order)



2013). Here, 190 QSM reconstructions were generated for each tree prior to selecting the optimal QSM. Based on optimal QSMs of leaf-off point clouds of the study trees, their total woody volume and woody surface area (WSA, including bark tissues) was computed as the sum of all volumes and surface areas of the cylinders that were fitted to the point cloud of a tree. The total woody volume and WSA of a tree was also separated into main stem and branch components.

Modeling the proportion of heartwood area of stem and branch disks from harvested trees

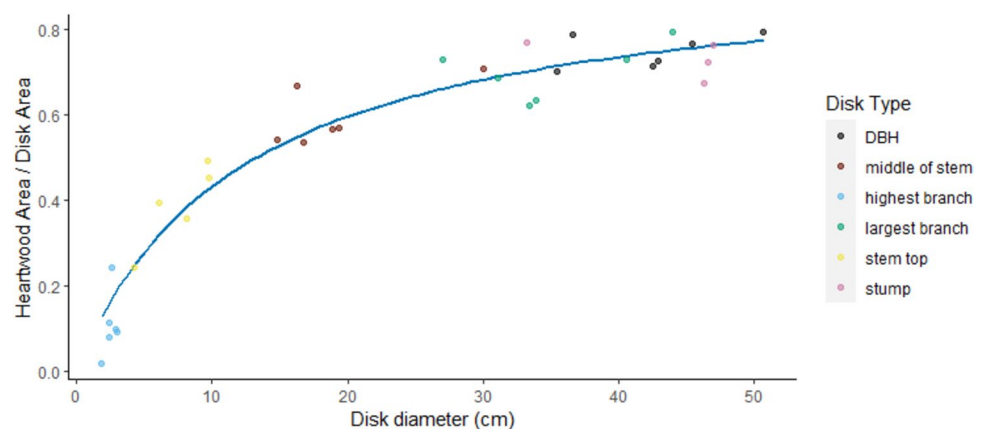
The data showed that heartwood proportion in main stem disks monotonically decreases with disk relative height above ground, and it approaches zero at stem top; this pattern has also been previously reported for other trees (Knapic et al. 2006; Cardoso and Pereira 2017). So, the surface area of heartwood as a proportion of total surface area of a stem disk was modeled following an inverse S-shaped function with the relative height of the stem disk as predictor:

$$\frac{HW}{TA} = \frac{1 - c}{1 + e^{a\left(\frac{2sHTrel}{D}\right) - 1}} + c + \varepsilon \quad (1)$$

where HW and TA are the heartwood and total surface area (m^2) of the stem disk, respectively, and $HTrel$ is the relative height of the stem disk. Parameters a and D determine the rate of decrease of HW proportion and were estimated (Wang et al. 2019). Parameter c was set to zero, because it is the asymptotic minimum HW proportion (i.e., 100% sapwood) and it cannot be negative for biological reasons. Error term (ε) has a multiplicative structure.

The data collection procedure called for only two sample branch disks per tree, so the possibility of using stem disks for branch modeling was explored to increase sample sizes. It was determined that the proportion of heartwood surface area of disks depended principally on the diameter of a disk and not on disk type (i.e., branch or stem disk) (Fig. 3). So, the proportion of heartwood surface area of a branch disk was modeled following the Michaelis–Menten function (MacFarlane and Kobe 2006) with the diameter of the disk as predictor (Eq. 2). The Michaelis–Menten function was selected because the proportion of heartwood

Fig. 3 Relationship between proportion of heartwood surface area and disk diameter across all stem and branch disks from six harvested *G. triacanthos* trees



content is expected to increase with disk diameter following a rectangular hyperbola until it reaches an asymptote (Sellin 1994; Knapic et al. 2006; Cardoso and Pereira 2017).

$$\frac{HW}{TA} = \frac{b * Disk.diam}{k + Disk.diam} + \epsilon \tag{2}$$

where *HW* and *TA* are the heartwood and total surface area (m²) of the disk respectively, and *Disk.diam* is the diameter of the disk (cm). Parameter *b* is the asymptotic maximum HW proportion, and *k* is the slope of the initial increase of HW proportion. Error term (ϵ) has a multiplicative structure.

The explanatory power of fitted models was quantified with the coefficient of determination (adjusted R²). Agreement between modeled and actual values of the proportion of heartwood surface area of main stem and branches was quantified with a concordance correlation coefficient (CCC; Lin 1989), which ranges between -1 (complete discordance) and 1 (complete concordance) (Calders et al. 2015). Pearson’s correlation coefficient (*r*) was also used to quantify statistical correlations. Relative *RMSE*(%) was used to quantify estimation accuracy of heartwood surface area proportion for main stem and branches separately (Burt et al. 2021).

$$\text{Relative } RMSE\% = \frac{RMSE}{HW.proportion_{Ref.mean}} * 100\% \tag{3}$$

where *RMSE* is the root mean square error of heartwood area proportion for stem and branches separately across harvested trees, and *HW.proportion_{Ref.mean}* is the corresponding mean reference heartwood area proportion across harvested trees.

Statistical significance of all relationships was assessed at $\alpha=0.05$ and all analyses were performed within R 3.6.1 environment (R Core Team 2015).

Estimation of sapwood and heartwood volume of non-harvested trees

Vertical accumulation (from tree base to treetop) of heartwood and sapwood volume of the main stem of non-harvested study trees was computed by multiplying the proportion of heartwood content estimated from Eq. 1 with the main stem volume at one-meter height intervals, derived from a QSM. *TreeQSM* also computes branch diameters in

every one-meter height class from tree base to top. Therefore, heartwood volume of branches within each height class was estimated by multiplying the heartwood content estimated from Eq. 2 with the volume of every branch within each height class. Heartwood volume of all branches in every one-centimeter branch diameter class was also computed by multiplying the heartwood content estimated from Eq. 2 with each branch’s volume, within each branch diameter class estimated from the tree’s QSM. In all analyses, sapwood volume was calculated by subtraction of heartwood volume from total woody volume. Finally, it is important to note that QSM-based volumes include bark tissues, which were removed based on published averaged values of bark volume proportion for *G. triacanthos* species (Miles and Smith 2009). So, the models were only applied to the estimated total woody volume.

Results

Heartwood area proportion models of stem and branches of harvested trees

The relative height of a stem disk and the disk diameter explained most of the variation of the proportion of heartwood content of the main stem and branches (see Adjusted R² in Table 1). Strong agreement was also found between modeled and actual values of the proportion of heartwood surface area of the main stem and branches (see CCC in Table 1), suggesting the inverse S-shaped function and the Michaelis–Menten function were good model choices.

The relative RMSE (%) of the two models showed nearly identical estimation accuracy for main stem and branches (see relative RMSE (%) in Table 1), and the model residuals plotted against the actual values of heartwood surface area proportion showed no clear pattern (unbiased estimation) for both main stem and branches (see Fig. 4).

Stem vertical profile of cumulative and absolute sapwood and heartwood volume of non-harvested trees

Across all trees, most of the vertically-cumulative volume in the stem was heartwood compared to sapwood (Fig. 5).

Table 1 Model statistics of heartwood surface area proportion (HW/TA) of the main stem and branches modeled as a function of stem disk relative height (HTrel) and disk diameter (Disk.diam) respectively

Tree component	Model	Adjusted R ²	CCC	Relative RMSE (%)
Main stem	HW/TA ~ HTrel + ϵ	0.835	0.91	10.18
Main stem + Branches	HW/TA ~ Disk.diam + ϵ	0.944	0.97	10.66

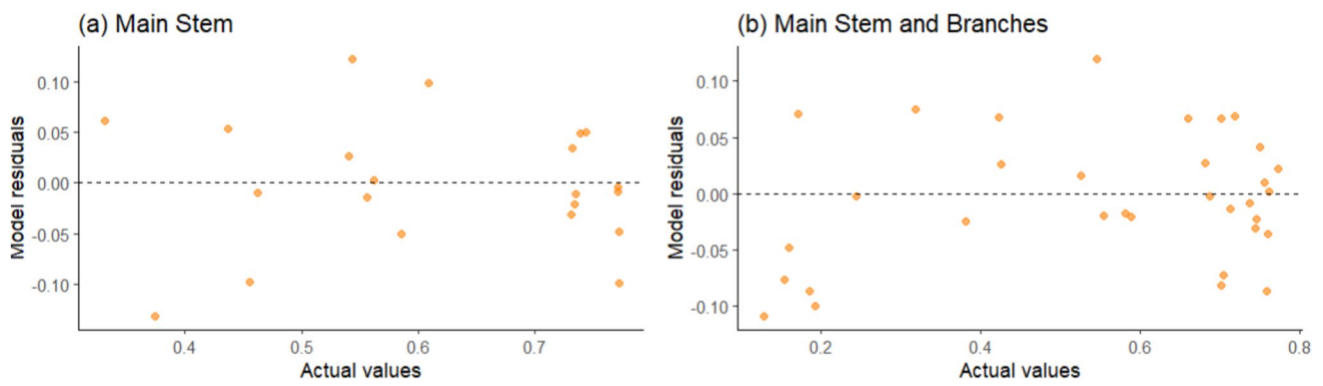


Fig. 4 Model residuals plotted against the actual values of heartwood surface area proportion for main stem and branches. Note that stem and branch disks were used for branch modeling

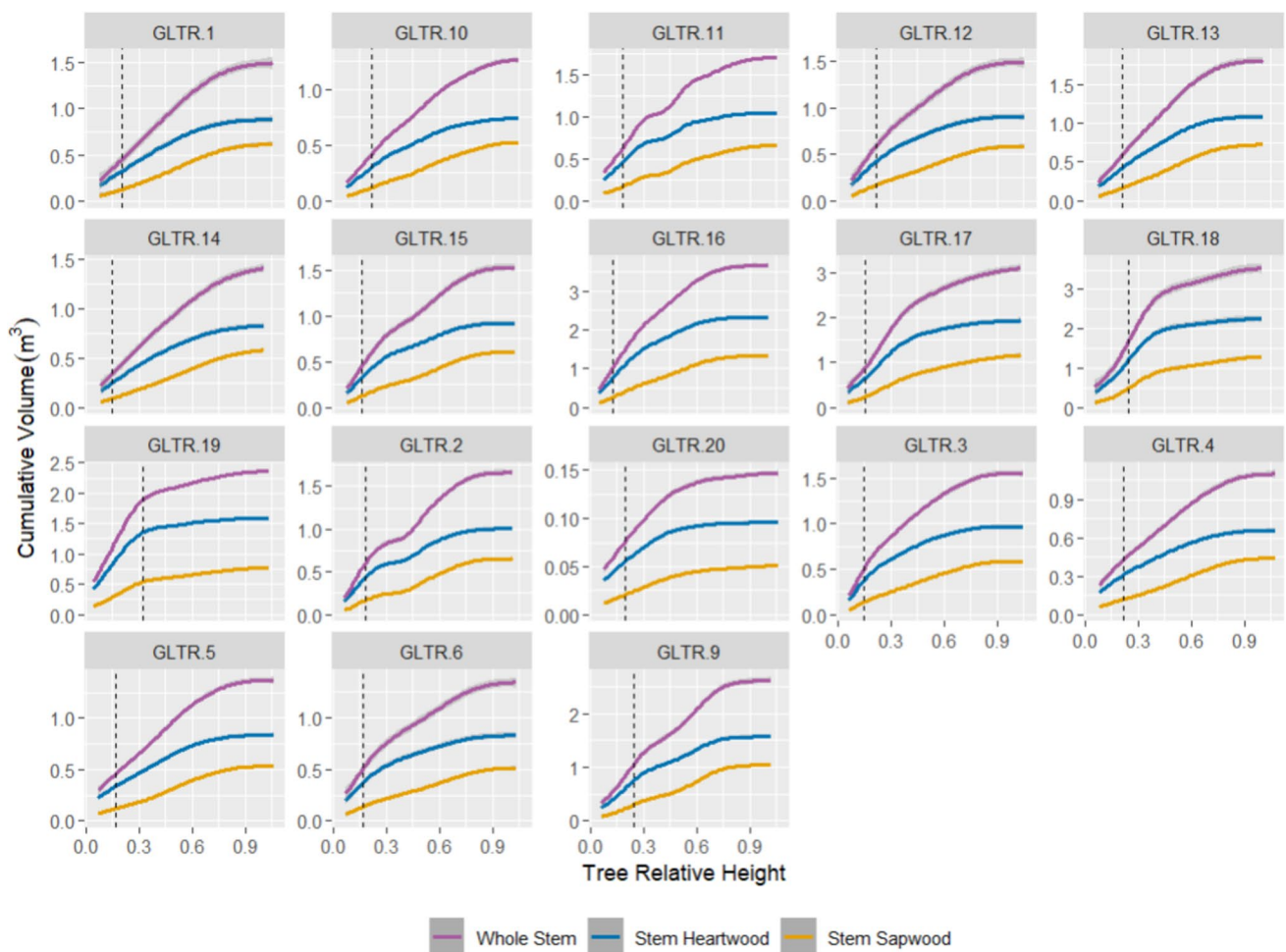


Fig. 5 Cumulative whole-stem volume (purple curve), cumulative stem heartwood volume (blue curve), and cumulative stem sapwood volume (yellow curve) as a function of stem relative height. The vertical dashed line indicates the relative height to the crown base

The absolute heartwood volume decreased monotonically with tree relative height approaching zero at the stem top (Fig. 6; across trees: min = $3.19 \times 10^{-6} \text{ m}^3$; max = 6.19×10^{-1}

m^3), whereas the absolute sapwood volume reduced sharply from stem base up to near the crown base (except GLTR.19) and then remained relatively constant within crown (Fig. 6;

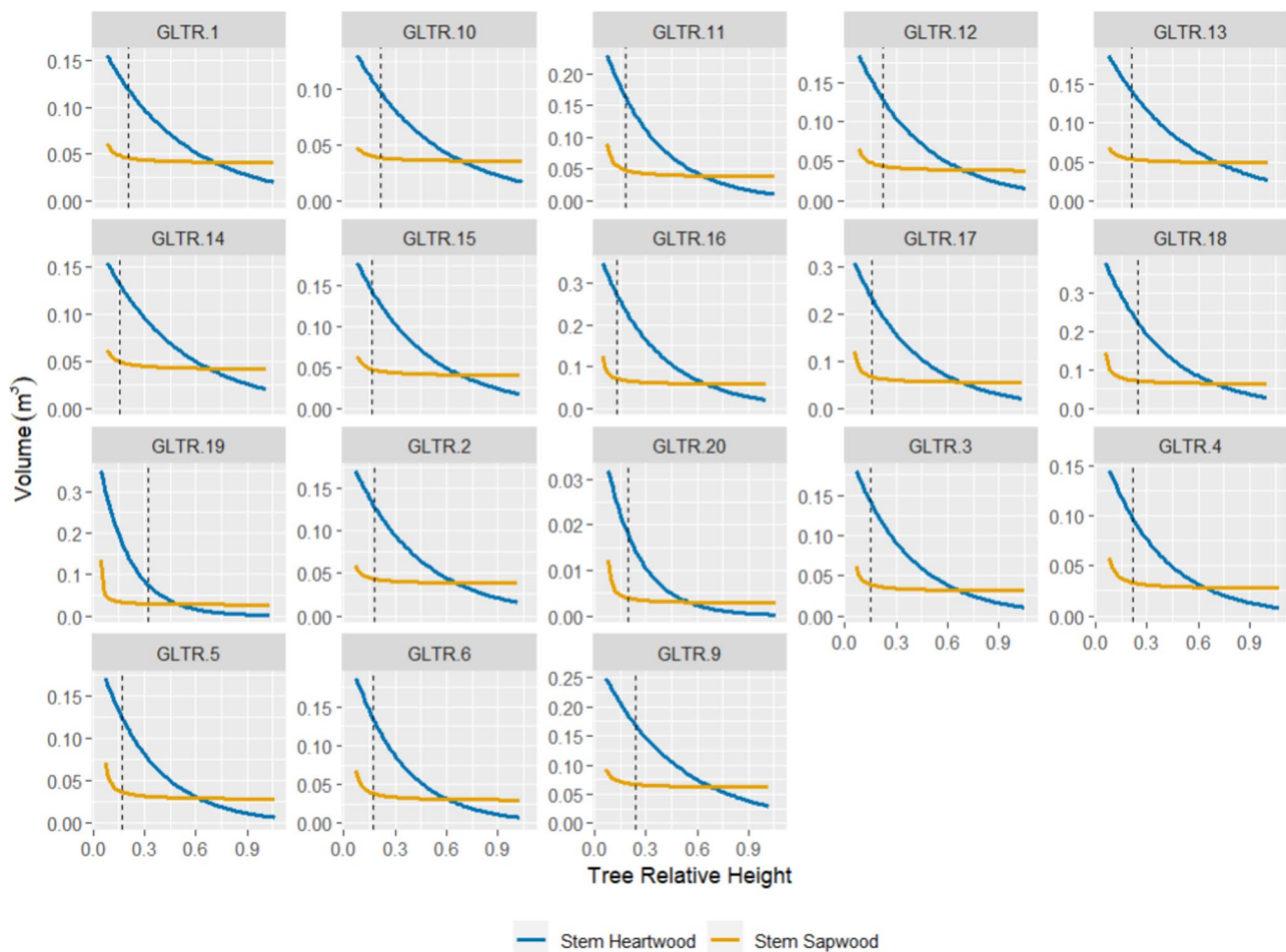


Fig. 6 Stem vertical profile of absolute heartwood (blue curve) and sapwood (yellow curve) volumes. The vertical dashed line indicates the relative height to the crown base

across trees: $\min = 7.88 \times 10^{-6} \text{ m}^3$; $\max = 3.28 \times 10^{-1} \text{ m}^3$). This revealed a point higher up in the tree (about 60–70% of the total height), in each tree's height profile, where stem heartwood volume was less than stem sapwood volume. Shape differences of curves in Figs. 5 and 6 reflect the method's ability to capture tree to tree variation in the cumulative and absolute vertical stem volume of sapwood and heartwood, but also revealed a relatively consistent pattern, despite size variation among the trees; e.g., GLTR.20 was the smallest study tree (DBH = 18.4 cm).

Sapwood and heartwood volume of branches per branch diameter and tree relative height

Total heartwood and sapwood volume, averaged across trees by branch basal diameter class ($\min = 2 \text{ cm}$, $\max = 39 \text{ cm}$), indicated a positive skewness (Fig. 7). Study trees allocated most of their total branch volume into small and medium-sized branches, which are more

abundant and mainly consist of sapwood. Whereas larger branches (approximately $> 19 \text{ cm}$) mainly consisted of heartwood. Some very large branches (basal diameter greater than 35 cm) were observed in the largest trees; these were large forks above the trunk, which is typical for open-grown, urban trees (see Fig. 2). Both the destructive sampling method and the *TreeQSM* algorithm defined them as branches, so this reflects a real pattern, not one produced through model – destructive sampling inconsistency.

Branch cumulative volume, as a function of tree relative height, showed an accumulation of mostly sapwood compared to heartwood (Fig. 8). The shape differences of curves in Fig. 8 show how the new method captures tree-level variation across trees of different sizes and branching architecture, but the general pattern was similar among trees; a steep rise in sapwood volume moving from crown base to treetop, and a slower accumulation of heartwood volume from the growth of larger branches closer to the base of the crown.

Fig. 7 Distribution of total branch heartwood and sapwood volume per branch-base diameter class of 1 cm size (min = 2 cm, max = 39 cm) averaged across trees

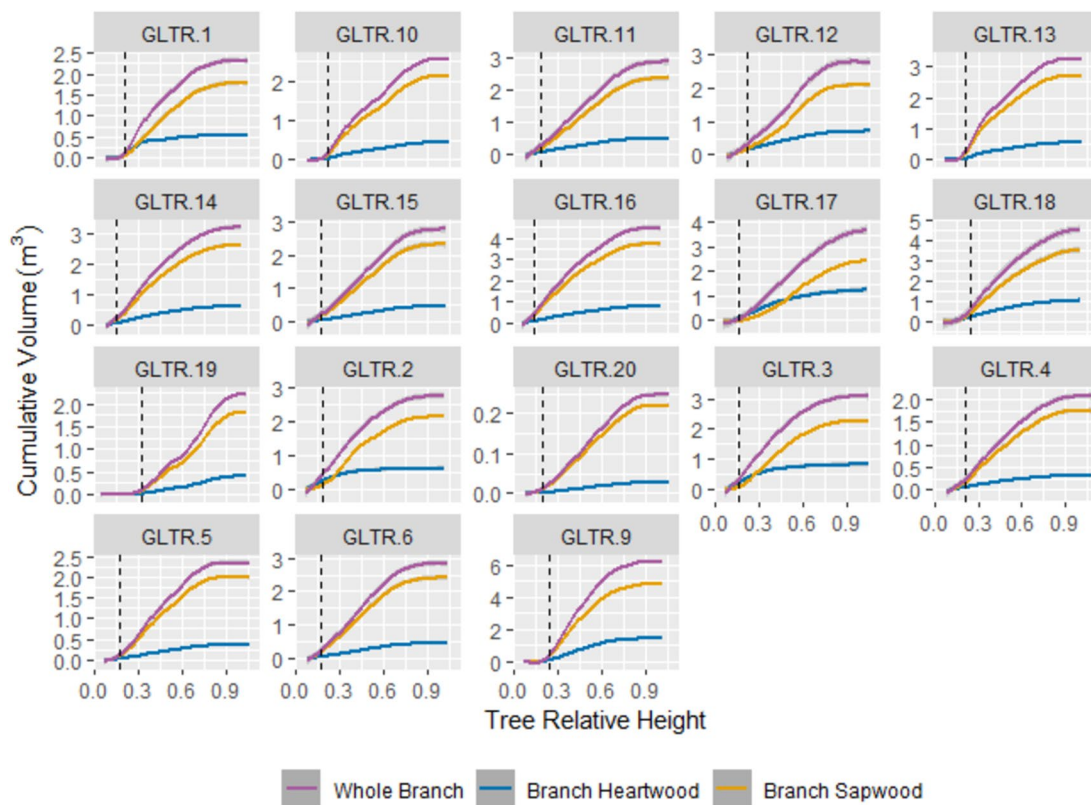
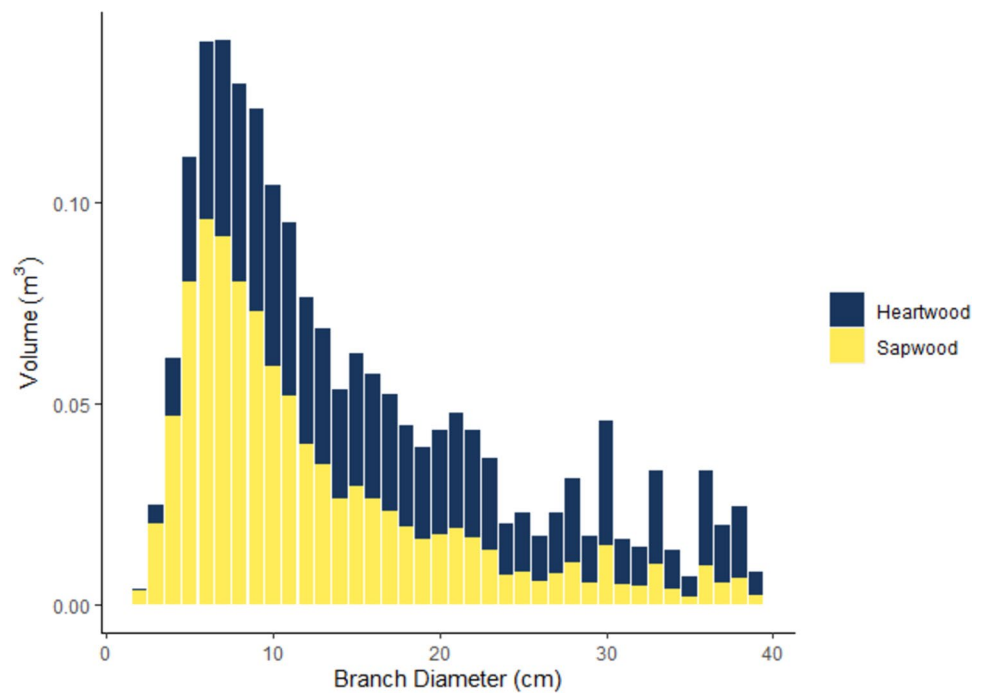


Fig. 8 Cumulative branch volume (purple curve), cumulative branch heartwood volume (blue curve), and cumulative branch sapwood volume (yellow curve) as a function of tree relative height. The vertical dashed line indicates the relative height to the crown base

Total vertical accumulation of sapwood and heartwood volume

Branches comprised the greatest portion of woody volume of the studied trees (except GTR.19); the branch to main stem woody volume ratio ranged between 0.94 and 2.36, with a mean value of 1.72. Whole-tree accumulation of sapwood and heartwood volume, as a function of tree relative height, showed most trees accumulating greater heartwood than sapwood up to a point near or after the relative height to the crown base (see vertical dashed lines in Fig. 9). Beyond this point, sapwood cumulative volume was greater indicating greater vertical accumulation of sapwood volume of branches compared to vertical accumulation of sapwood volume of main stem (see Figs. 8 and 9). This also reflected the fact that some of the heartwood formation was from the continuation of the main stem into the crown.

Functional relationship of sapwood volume and woody surface area

The WSA of study trees was positively correlated with their sapwood volume (see Fig. 10) at the whole-tree level ($r = 0.93$, $p < 0.001$), for branches ($r = 0.92$, $p < 0.001$),

and the main stem ($r = 0.80$, $p < 0.001$). The WSA of the branches greatly exceeded that of the main stem and the slope of the relationship was much shallower.

Discussion

Advances in whole tree estimation of sapwood and heartwood volume of trees

In this study, we used active remote sensing (TLS) combined with heartwood and sapwood proportion data from disks sampled from stems and branches, to develop a novel method for modeling the total sapwood and heartwood volume of trees. Quantifying sapwood and heartwood volume of trees is always challenging, because proportions vary within different parts of trees and are not visible externally, and previous studies rarely include branches (Kyker-Snowman and Wilson 1988). TLS provided measurements of the size, shape, and location of every branch, in addition to the dimensions of the main stem, which wasn't possible to measure on a standing tree prior to the advent of TLS technology. However, while TLS provides accurate representations of the three-dimensional tree architecture (Malhi

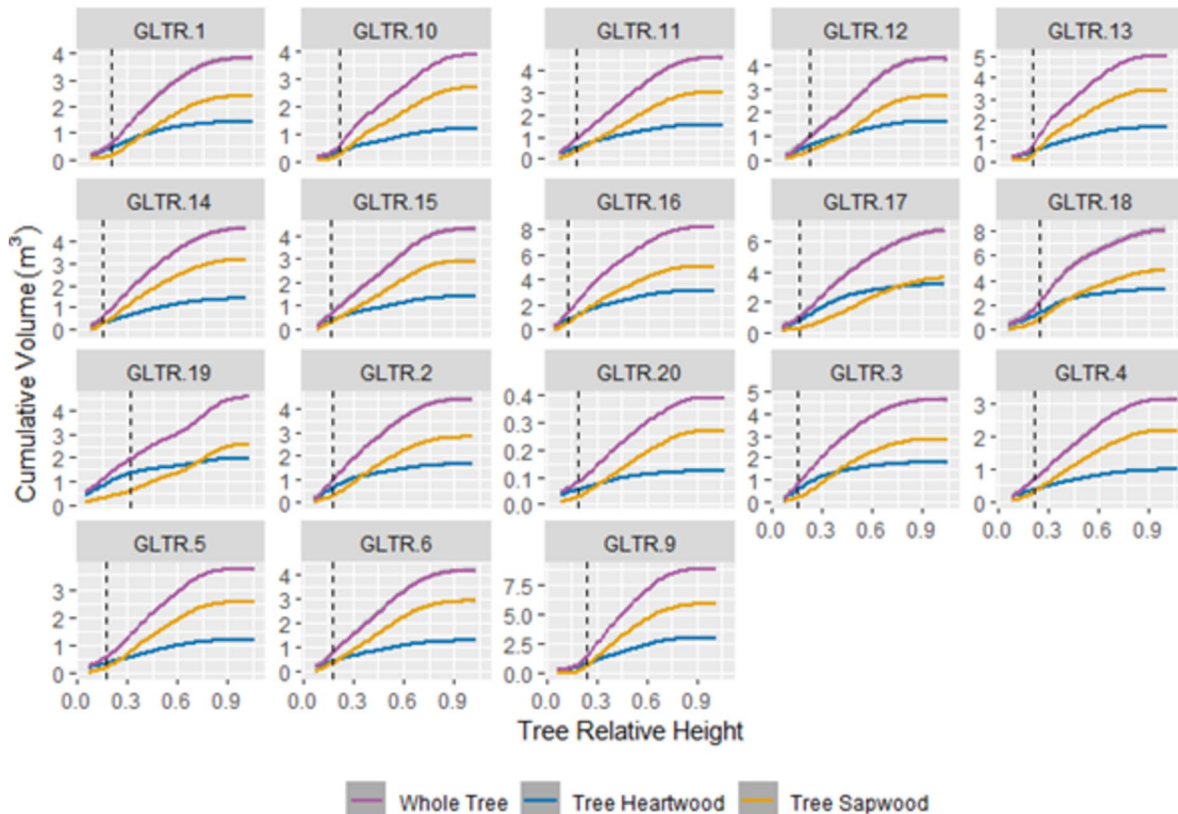
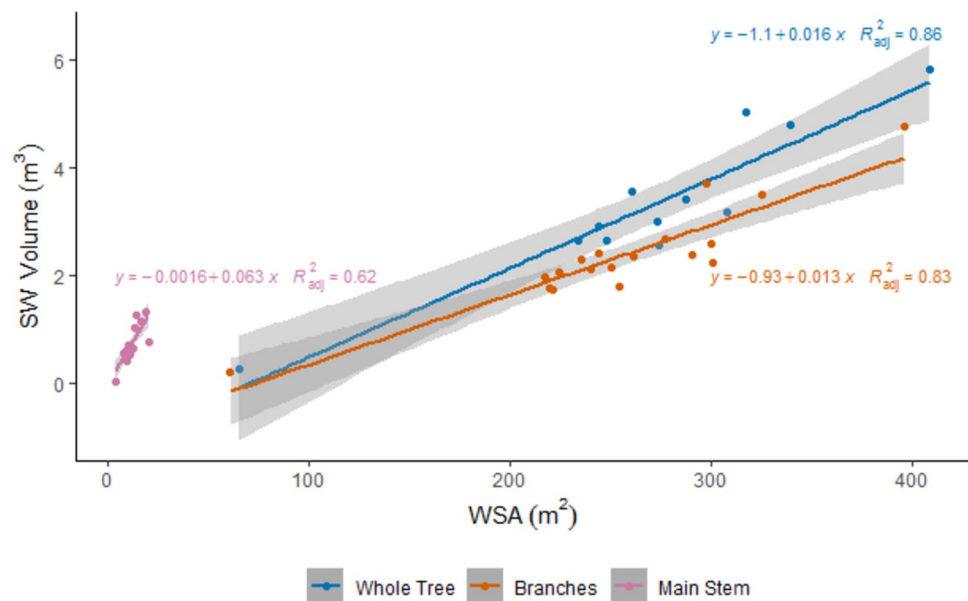


Fig. 9 Cumulative whole tree volume (purple curve), cumulative tree heartwood volume (blue curve), and cumulative tree sapwood volume (yellow curve) as a function of tree relative height. The vertical dashed line indicates the relative height to the crown base

Fig. 10 Relationship of sapwood volume (SW in m³) and woody surface area (WSA in m²) for whole tree (blue line), branches (brown line), and main stem (purple line) across study trees. The 95% confidence interval has been plotted around the regression lines. Note: The "outlier" data-point in Fig. 10 (smallest tree GLTR.20, blue and brown points, bottom-left) did not drive the observed relationships, because patterns did not change after removing this data-point



et al. 2018; Disney et al. 2018), some studies have shown that QSM-based volume of small branches (base-diameter less than 5 cm) can be overestimated (Demol et al. 2022) and large branch volume can be underestimated (Lau et al. 2019, e.g., showed 8% underestimation in QSM-based diameters of branches between 20 and 60 cm). Consequently, WSA might also be biased for some smaller parts of the tree. So, more research is needed to better understand the effect of branch size on the accuracy of QSM-based volume and surface area estimates (Morales and MacFarlane 2024). If the size of branches is overestimated by TLS, then the proportion of sapwood would be underestimated, based on our findings. The sapwood and heartwood volume estimates in this study also depend on the inherent stochasticity of QSM-based volumes estimation due to non-deterministic fitting of cylinders to point clouds (Disney et al. 2018). Arseniou et al. (2023) found that only a small percentage of the total uncertainty in aboveground biomass estimation originated from the inherent QSM stochasticity (i.e. 4.3%), which implies that *TreeQSM* algorithm is relatively robust.

The models for predicting heartwood proportion of destructively sampled main stem and branch sections were highly accurate (see Table 1 and Fig. 4), suggesting that heartwood formation is generally a function of diameter. Previous studies have also shown that heartwood content of woody disks depends on their size (Kyker-Snowman and Wislon 1988; Knapic et al. 2006). That makes the TLS-based approach shown here, which employs a three-dimensional model of the tree with estimated diameters of all stems and branches, a potentially powerful method. Nonetheless, the method still requires a minimal amount of destructive sampling (wood disks or cores) for calibration, which could be particularly challenging for trees in urban

areas. Increment borer samples radially collected from pith to bark (Wiemann and Williamson 2012), combined with branch disks of urban trees that are typically pruned could alleviate this challenge. However, more research is needed to determine the appropriate number and distribution of increment borer samples within a tree to collect accurate data of heartwood and sapwood volume due to vertical and radial variation of wood properties within a tree (Williamson and Wiemann 2010).

This new method could be applied to any tree, but some of the patterns observed in allocation may be an adaptation of the study trees to an open-grown, urban environment (MacFarlane and Kane 2017). Trees tend to invest more resources in expanding their crowns and they build complex branching structures, compared to the main stem, in the absence of light competition or if crowding conditions are reduced (Weiner 2004). Open-grown, urban trees typically have a squat form (i.e., wide crown with a short and sharply tapered trunk), which provides them mechanical stability against wind loads (Long et al. 1981; MacFarlane and Kane 2017). By contrast, the crown structure of trees growing in forest stands is significantly affected by competition for light and their inherent tolerance to shade. However, crown structure of open-grown trees is also affected by their response to self-shading of leaves and branches and light attenuation within crown (Mäkelä 1997; Duursma et al. 2010). According to Niinemets and Valladares (2006) *G. triacanthos* is a species with low shade tolerance (shade tolerance index for *G. triacanthos* = 1.61; numerical scale from 1 = very intolerant to 5 = very tolerant). Previous studies have showed that species with high shade tolerance distribute their foliage more evenly within their crown volume (Arseniou and MacFarlane 2021; Arseniou et al. 2021a), whereas species

with low shade tolerance distribute their leaves mainly in the crown top to increase crown porosity and reduce local self-shading (Sack et al. 2006). Therefore, self-shading of the study trees, combined with their inherently low shade tolerance, may explain the distinct branch cumulative volume profile, which largely consists of sapwood particularly in the upper crown parts. However, the vertical accumulation of stem sapwood and heartwood volume in these urban trees was consistent with previous studies of forest-grown trees (Knapic et al. 2006), which supports the idea of a general pattern across growing environments.

Urban forests provide multiple ecological services (e.g., shade, air pollutants uptake, etc. (McPherson 1998; Nowak and Crane 2002)) and can potentially provide new sources of wood products and bio-based fuels for energy generation (MacFarlane 2009), yet there is limited understanding of the aboveground biomass, carbon offset and wood products potential, due to inadequate data and models that quantify urban tree structure (Tigges and Lakes 2017). So this study addresses both the general problem of quantifying whole aboveground tree heartwood and sapwood volume accumulation, while exploring new, urban-tree specific allometric scaling relationships using TLS that can inform urban forest management strategies for enhancing urban wood utilization.

Whole-tree sapwood and heartwood volume in the context of tree physiology

The precise characterizations of the metabolically active (sapwood) and non-active (heartwood) components of tree woody volume produced in this study, can provide new insights into the growth and carbon balance of trees. It has long been understood that respiration, photosynthesis, and hydraulic balance are fundamental physiological processes that relate to surface area and volume of trees (Whittaker and Woodwell 1967). In general, tree-level variation of heartwood and sapwood accumulation is due to potential differences in factors like tree age, size, foliage mass and site characteristics (as suggested by Wilkins 1991). Here, the main difference between the trees was their size, but the methods developed here could be applied to study trees across a range of determinants, to help understand similarities and differences in physiology.

The largest amount of absolute sapwood volume was near the base of most of the study trees, reducing up the stem up to the crown base, beyond which it remained constant. Previous studies (of rural forest trees) found that stem sapwood volumes are large near the tree base to maintain water flow, because wood conduits of some species become longer and wider with increasing diameter and age near stem base which increases risk of embolism due to drought (Domec et al. 2012; Cruickshank et al. 2015). Other studies suggest that large amount of sapwood volume near tree base of

some species is due to thick cell walls optimizing hydraulic conductivity and safety near stem base (Climent et al. 2003). A constant sapwood volume above crown base can be interpreted based on pipe model theory (Shinozaki et al. 1964), because stem heartwood formation regulates sapwood content to a specific proportion based on the hydraulic needs of the crown (Yang et al. 1985; Yang and Murchison 1992; Knapic and Pereira 2005; Knapic et al. 2006; Cardoso and Pereira 2017). As trees grow, total sapwood volume increases to cover the hydraulic demands of leaves, which implies increased maintenance respiration (Ryan et al. 1995). At a certain size, trees may cease their sapwood volume growth to prevent excessive respiration costs and to maintain a positive carbon balance (Sellin 1994). However, there might be a mechanism other than maintaining hydraulic and carbon balance in leaves that explains the observed pattern. The existence of younger branches in the upper crown, which mostly consist of sapwood due to the negative relationship between sapwood proportion and branch size/age (Kyker-Snowman and Wilson 1988; Sellin 1994; Yang and Murchison 1992) may also explain the pronounced difference between branch sapwood and heartwood vertical volume accumulation.

The observed decrease of absolute heartwood volume from the base of the study trees upwards is also a well-documented pattern in literature (Hillis 1987; Wilkes 1991; Wilkins 1991; Mäkelä 2002; Pinto et al. 2004; Knapic and Pereira 2005; Cardoso and Pereira 2017). One explanation is that heartwood content increases with stem age as heartwood formation progresses outward on a set fraction of a growing ring per year (Hazenbergh and Yang 1991; Wilkes 1991). In other studies, the allocation of large portion of heartwood volume near tree base has been attributed to greater proportion of latewood, which has lower hydraulic conductivity and enhances stem mechanical stability (Domec and Gartner 2002; Cruickshank et al. 2015).

This study showed that for most trees there was an inflection point of whole-tree sapwood volume accumulation at a height near the crown base, which is consistent with previous studies of forest-grown trees; sapwood volume at crown base strongly correlates with leaf biomass (Long et al. 1981; Ogawa 2022). The stem heartwood volume of the study trees was significantly greater than their stem sapwood volume near crown base, which is expected for open-grown trees with large crowns and little crown rise, because crown rise affects stem heartwood formation (Mäkelä and Valentine 2006). Tree GLTR.19 had a relatively smaller heartwood and sapwood volume difference at the crown base, but this tree had an elongated stem and relatively narrow crown. The crown is composed of branches, so more detailed understanding may arise from examination of sapwood and heartwood formation in branches within the crown. Further, pipe

model theory directly connects stem heartwood formation to branch senescence (Shinozaki et al. 1964; Mäkelä and Valentine 2006).

Branch characteristics are affected by branch size and position in crown (Weiskittel and McGuire 2006). Small and medium-sized branches in QSMs accumulated most of total branch sapwood averaged across trees, whereas large branches accumulated more heartwood. Due to the fractal-like architecture of trees, the vascular structure of branches is a confluence of metabolically active (sapwood) and non-active (heartwood) self-similar tubes (Lehnebach et al. 2018). As branches grow in size and become older, they accumulate more heartwood in the center of their base while sapwood eventually stops growing causing branch senescence (Kyker-Snowman and Wilson 1988; Enquist 2002). Branch sapwood was highest higher in the crown, where the branches were also smaller, so size and position are to some extent confounded. One limitation in this study was that dead branches couldn't be effectively separated out from live ones in TLS data. Though dead branches were a relatively small proportion of the total volume, these were essentially modeled as live ones.

New advances in TLS also allow for precise quantification of total WSA of trees including main stem and branches (Arseniou et al. 2021b). Here, we combined them with novel sapwood volume estimates of the main stem and branches. Growth and maintenance respiration are the two main components of tree respiration (Sprugel 1990). Growth respiration of woody tissues occurs in the cambial sheath and the living annual growing rings around heartwood (Kinerson 1975) and it relates to WSA (Bosc et al. 2003; Kim et al. 2007), while maintenance respiration relates to sapwood volume of trees (Sprugel 1990; Ryan et al. 1995; Lavigne and Ryan 1997). The observed increase of sapwood volume with WSA across study trees implies that as growth respiration rate of a tree increases, its maintenance respiration should similarly increase to maintain sustainable growth. Additionally, the living woody volume to surface ratio of main stem of sampled trees increased at a higher rate compared to their branches (see regression slopes in Fig. 10) indicating greater maintenance energy cost for stems compared to greater growth energy cost of branches that carry leaf photosynthetic tissues. Ultimately, more detailed studies of tree physiology are needed, and the types of data and models demonstrated here could be used to develop new process models of forest growth (Mäkelä 1997), to better understand factors affecting tree hydraulic balance based on physiological relationships between sapwood area and the photosynthetically active and non-active surface area of trees (Domec et al. 2012).

Conclusions

This study explored a novel methodology for quantifying the total aboveground sapwood and heartwood volume of trees using a combination of TLS data and models calibrated with destructive sampling data. Previous methods are mostly limited due to exclusion of branches and a priori assumptions of stem form and growth. However, here we directly measured the actual tree form, and we quantified sapwood and heartwood content in both stems and branches. Therefore, a major novelty of the proposed method is the explicit inclusion of branch volumetric estimates from QSMs, which requires more research to understand the effect of QSM-based branch volume variation on whole-tree sapwood and heartwood volume quantification. Although this study included data from a single species in urban settings, the proposed method could be applied to any tree if new data is collected to calibrate for different species and different growing environments.

Finally, accurate measurements of heartwood and sapwood volumes are fundamental to understanding the structure and function of woody plant species, and testing major theories of plant biology, including the 'pipe model' theory and 'WBE' metabolic scaling theory. Future studies should focus on developing new process models of tree growth and production efficiency combining whole-tree sapwood and heartwood volume estimates based on the proposed method with TLS-based leaf surface area estimates within the framework of the above-mentioned theories.

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Author contributions GA and DM conceived the ideas and designed the methodology for the study; GA, DM and PR collected and analyzed the data; GA and DM led the manuscript writing. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data generated and analyzed during the study are available upon reasonable request from the corresponding author GA.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose, which could influence the study.

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References

- Arseniou G, MacFarlane DW (2021) Fractal dimension of tree crowns explains species functional-trait responses to urban environments at different scales. *Ecol Appl* 31(4):e02297. <https://doi.org/10.1002/EAP.2297>
- Arseniou G, MacFarlane DW, Seidel D (2021a) Measuring the contribution of leaves to the structural complexity of urban tree crowns with terrestrial laser scanning. *Remote Sensing* 13:2773. <https://doi.org/10.3390/rs13142773>
- Arseniou G, MacFarlane DW, Seidel D (2021b) Woody surface area measurements with terrestrial laser scanning relate to the anatomical and structural complexity of urban trees. *Remote Sensing* 13:3153. <https://doi.org/10.3390/rs13163153>
- Arseniou G, MacFarlane DW, Calders K, Baker M (2023) Accuracy differences in above-ground woody biomass estimation with terrestrial laser scanning for trees in urban and rural forests in different leaf conditions. *Trees: Structure Function*. <https://doi.org/10.1007/s00468-022-02382-1>
- Bosc A, Grandcourt A, Loustau D (2003) Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree. *Tree Physiol* 23:227–236
- Burt A, Boni Vicari M, da Costa ACL, Coughlin I, Meir P, Rowland L, Disney M (2021) New insights into large tropical tree mass and structure from direct harvest and terrestrial lidar. *Royal Soc Open Sci* 8:201458. <https://doi.org/10.1098/rsos.201458>
- Calders K, Newnham G, Burt A, Murphy S, Raunonen P, Herold M, Culvenor D, Avitabile V, Disney MI, Armston J, Kaasalainen M (2015) Nondestructive estimates of above-ground biomass using terrestrial laser scanning. *Methods Ecol Evol* 6:198–208
- Cardoso S, Pereira H (2017) Characterization of Douglas-fir grown in Portugal: heartwood, sapwood, bark, ring width and taper. *Eur J Forest Res* 136:597–607
- Celedon JM, Bohlmann J (2017) An extended model of heartwood secondary metabolism informed by functional genomics. *Tree Physiol* 38:311–319. <https://doi.org/10.1093/treephys/tpx070>
- Climent J, Chamber MR, Gil L, Pardos JA (2003) Vertical heartwood variation patterns and prediction of heartwood volume in *Pinus canariensis* Sm. *For Ecol Manage* 174(2003):203–211
- Cruickshank MG, Cameron IR, Groot A, Stewart JD, Goudie JW (2015) Models of the vertical distribution of Sapwood Area for Lodgepole Pine and Western Hemlock in Western Canada. *Forest Science* 61(6):973–987. <https://doi.org/10.5849/forsci.14-206>
- Dean TJ, Long JN (1986) Variation in sapwood area -leaf area relations within two stands of Lodgepole Pine. *Forest Sci* 32(3):749–758
- Debell JD, Lachenbruch B (2009) Heartwood/sapwood variation of western redcedar as influenced by cultural treatments and position in tree. *For Ecol Manage* 258:2026–2032
- Demol M, Wilkes P, Raunonen P, Krishna Moorthy SM, Calders K, Gielen B, Verbeeck H (2022) Volumetric overestimation of small branches in 3D reconstructions of *Fraxinus excelsior*. *Silva Fennica* 56:1. <https://doi.org/10.14214/sf.10550>
- Disney MI, Boni Vicari M, Burt A, Calders K, Lewis SL, Raunonen P, Wilkes P (2018) Weighing trees with lasers: advances, challenges and opportunities. *Interface Focus* 8:20170048. <https://doi.org/10.1098/rsfs.2017.0048>
- Domec JC, Gartner B (2002) Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: Inferring the design criteria for Douglas-fir wood structure. *Tree Physiol* 22:91–104
- Domec JC, Lachenbruch B, Pruyn ML, Spicer R (2012) Effects of age-related increases in sapwood area, leaf area, and xylem conductivity on height-related hydraulic costs in two contrasting coniferous species. *Ann for Sci* 69:17–27
- Duursma RA, Mäkelä A, Reid DE, Jokela EJ, Porté AJ, Roberts SD (2010) Self-shading affects allometric scaling in trees. *Funct Ecol* 24(4):723–730
- Enquist BJ (2002) Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiol* 22(15–16):1045–1064
- Hazenberg G, Yang KC (1991) The relationship of tree age with sapwood and heartwood width in black spruce, *Picea mariana* (Mill.) B.S.P. *Holzforchung* 45(5):317
- Hillis WE (1987) Heartwood and tree exudates. Springer, Berlin
- Kampe A, Magel E (2013) New insights into heartwood and heartwood formation. In: Fromm J (ed) Cellular aspects of wood formation. Springer, Berlin, pp 71–95
- Kim MH, Nakane K, Lee JT, Bang HS, Na YE (2007) Stem/branch maintenance respiration of Japanese red pine stand. *For Ecol Manage* 243(2–3):283–290
- Kinerson RS (1975) Relationships between plant surface area and respiration in Loblolly pine. *J Appl Ecol* 12(3):965–971
- Knapic S, Pereira H (2005) Within-tree variation of heartwood and ring width in maritime pine (*Pinus pinaster* Ait.). *For Ecol Manage* 210:81–89
- Knapic S, Tavares F, Pereira H (2006) Heartwood and sapwood variation in *Acacia melanoxylon* R. Br *Trees Portugal Forestry* 79(4):2006. <https://doi.org/10.1093/forestry/cpl010>
- Kyker-Snowman TD, Wilson BF (1988) Total wood, sapwood, and heartwood in branch bases of three conifers. *Can J for Res* 18:1332–1336
- Lau A, Martius C, Bartholomeus H, Shenkin A, Jackson T, Malhi Y, Herold M, Bentley LP (2019) Estimating architecture-based metabolic scaling exponents of tropical trees using terrestrial LiDAR and 3D modelling. *For Ecol Manage* 439(2019):132–145
- Lavigne MB, Ryan MG (1997) Growth and maintenance respiration rates of aspen, black spruce, and jack pine, stems at northern and southern BOREAS sites. *Tree Physiol* 17:543–551
- Lehnebach R, Beyer R, Letort V, Heuret P (2018) The pipe model theory half a century on: a review. *Ann Bot* 121(5):773–795
- Lin L (1989) A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 45:255–268
- Long JN, Smith FW, Scott DRM (1981) The role of Douglas-fir stem sapwood and heartwood in the mechanical and physiological support of crowns and development of stem form. *Can J for Res* 11:459–464
- MacFarlane DW (2009) Potential availability of urban wood biomass in Michigan: Implications for energy production, carbon

- sequestration and sustainable forest management in the USA. *Biomass Bioenergy* 33(2009):628–634
- MacFarlane DW, Kane B (2017) Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistance. *Funct Ecol* 31:1624–1636
- MacFarlane DW, Kobe RK (2006) Selecting models for capturing tree-size effects on growth-resource relationships. *Can J for Res* 36:1695–1704
- MacFarlane DW, Kuyah S, Mulia R, Dietz J, Muthuri C, Noordwijk MV (2014) Evaluating a non-destructive method for calibrating tree biomass equations derived from tree branching architecture. *Trees* 28:807–817. <https://doi.org/10.1007/s00468-014-0993-2>
- Maguire DA, Batista JLF (1996) Sapwood taper models and implied sapwood volume and foliage profiles for coastal Douglas-fir. *Can J for Res* 26:849–863
- Mäkelä A (1997) A carbon balance model of growth and self-pruning in trees based on structural relationships. *Forest Science* 43(1):1997
- Mäkelä A (2002) Derivation of stem taper from the pipe model theory in a carbon balance framework. *Tree Physiol* 22(891–905):2002
- Mäkelä A, Valentine HT (2006) Crown ratio influences allometric scaling in trees. *Ecology* 87(12):2967–2972
- Malhi Y, Jackson T, Patrick Bentley L, Lau A, Shenkin A, Herold M, Calders K, Bartholomeus H, Disney MI (2018) New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning. *Interface Focus* 8:20170052
- Mandelbrot BB (1983) *The fractal geometry of nature*. W. H. Freeman, New York
- McPherson EG (1998) Atmospheric carbon dioxide reduction by Sacramento's urban forest. *J Arboric* 24(4):215–223
- Miles PD, Smith WB (2009) Specific gravity and other properties of wood and bark for 156 tree species found in North America. *Res. Note NRS-38*. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 35 p.
- Morales A, MacFarlane DW (2024). Reducing tree volume overestimation in quantitative structure models using modeled branch topology and direct twig measurements. *Forestry: An International Journal of Forest Research*, p. cpae046.
- Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol Monogr* 76(4):521–547
- Noordwijk VM, Mulia R (2002) Functional branch analysis as tool for fractal scaling above and belowground trees for their additive and non-additive properties. *Ecol Model* 149(2002):41–51
- Nowak DJ, Crane DE (2002) Carbon storage and sequestration by urban trees in the USA. *Environ Pollut* 116(2002):381–389
- Ogawa K (2022) Allometric scaling of leaf mass based on the pipe model theory for woody plant species. *Eur J Forest Res* 141(481–487):2022
- Ojansuu R, Maltamo M (1995) Sapwood and heartwood taper in Scots pine stems. *Can J for Res* 25:1928–1943
- Pinto I, Pereira H, Usenius A (2004) Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems. *Trees* 18:284–294. <https://doi.org/10.1007/s00468-003-0305-8>
- R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Raumonen P, Kaasalainen M, Åkerblom M, Kaasalainen S, Kaartinen H, Vastaranta M, Holopainen M, Disney MI, Lewis PE (2013) Fast automatic precision tree models from terrestrial laser scanner data. *Remote Sensing* 5:491–520
- Raumonen P, Åkerblom M (2022) InverseTampere/TreeQSM: Version 2.4.1 (2.4.1). Zenodo. <https://doi.org/10.5281/zenodo.6539580>.
- Ryan MG, Gower ST, Hubbard RM, Waring RH, Gholz HL, Cropper WP, Running SW (1995) Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia* 101:133–140
- Sack L, Melcher PJ, Liu WH, Middleton E, Pardee T (2006) How strong is intracanalopy leaf plasticity in temperate deciduous trees? *Am J Bot* 93(6):829–839
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to imageJ: 25 years of image analysis. *Nat Methods* 9(7):671–675. <https://doi.org/10.1038/nmeth.2089>
- Sellin A (1994) Sapwood-heartwood proportion related to tree diameter, age, and growth rate in *Picea abies*. *Can J for Res* 24:1022–1028
- Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form—the pipe model theory I & II. *Japanese J Ecol* 14(97–105):133–139
- Sprugel DG (1990) Components of woody-tissue respiration in young *Abies amabilis* (Dougl.) Forbes trees. *Trees* 4(2):88–98
- Taylor AM, Gartner BL, Morrell JJ (2002) Heartwood formation and natural durability—a review. *Wood Fiber Sci* 34:587–611
- Tigges J (2017) Lakes T (2017) High resolution remote sensing for reducing uncertainties in urban forest carbon offset life cycle assessments. *Carbon Balance Manage* 12:17. <https://doi.org/10.1186/s13021-017-0085-1>
- Wang W, Jiao L, Dong T, Xu Z, Xu G (2019) Simulating urban dynamics by coupling top-down and bottom-up strategies. *Int J Geogr Inf Sci* 33(11):2259–2283. <https://doi.org/10.1080/13658816.2019.1647540>
- Weiner J (2004) Allocation, plasticity and allometry in plants. *Perspectives Plant Ecol Evol Syst* 6(4):207–215
- Weiskittel AR, Maguire DA (2006) Branch surface area and its vertical distribution in coastal Douglas-fir. *Trees* 20(6):657–667
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *SCIENCE*, vol. 276, (1997). <http://www.sciencemag.org>.
- Whittaker RH (1967) Woodwell GM (1967) Surface area relations of woody plants and forest communities. *Am J Bot* 54(8):931–939
- Wiemann MC, Williamson GB (2012) Testing a novel method to approximate wood specific gravity of trees. *Forest Sci* 58(6):577
- Wilkes J (1991) Heartwood development and its relationship to growth in *Pinus radiata*. *Wood Sci Technol* 25:85–90
- Wilkes P, Lau A, Disney M, Calders K, Burt A, Tanago JG, Bartholomeus H, Brede B, Herold M (2017) Data acquisition considerations for Terrestrial Laser Scanning of forest plots. *Remote Sens Environ* 196:140–153
- Wilkins AP (1991) Sapwood, heartwood, and bark thickness of silviculturally treated *Eucalyptus grandis*. *Wood Sci Technol* 25(6):415–423
- Williamson GB, Wiemann MC (2010) Measuring wood specific gravity. *Correctly*. *Am J Botany* 97(3):519–524
- Yang KC, Murchison HG (1992) Sapwood thickness in *Pinus contorta* var. *latifolia*. *Can J for Res* 22:2004–2006
- Yang KC, Hazenberg G, Bradfield GE, Maze JR (1985) Vertical variation of sapwood thickness in *Pinus banksiana* Lamb. and *Larix laricina* (Du Roi) K. Koch. *Canadian J Forest Res* 15(5):822

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