Accuracy differences in aboveground woody biomass estimation with terrestrial laser scanning for trees in urban and rural forests and different leaf conditions

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Key Message: TLS data can be converted to reliable woody AGB estimates, but estimation quality is influenced by growing environment, leaf condition, and variation in tree density affecting volume to mass conversion.

Abstract

Both rural and urban forests play an important role in terrestrial carbon cycling. Forest carbon stocks are typically estimated from models predicting the aboveground biomass (AGB) of trees. However, such models are often limited by insufficient data on tree mass, which generally requires felling and weighing parts of trees. In this study, thirty-one trees of deciduous and evergreen species were destructively sampled in rural and urban forest conditions. Prior to felling, terrestrial laser scanning (TLS) data was used to estimate tree biomass based on volume estimates from quantitative structure models, combined with tree basic density estimates from disks sampled from stems and branches after scanning and felling trees, but also in combination with published specific basic density values. Reference woody AGB, main stem, and branch biomass were computed from destructive sampling. Trees were scanned in leaf-off conditions except evergreen and some deciduous trees, to assess effects of a leaf-separation algorithm on TLS-based woody biomass estimates. We found strong agreement between TLS-based and reference woody AGB, main stem, and branch biomass values, using both measured and published basic densities to convert TLS-based volume to biomass, but use of published densities reduced accuracy. Correlation between TLS-based and reference branch biomass was stronger

for urban trees, while correlation with stem mass was stronger for rural trees. TLS-based biomass estimates from leaf-off and leaf-removed point clouds strongly agreed with reference biomass data, showing the utility of the leaf-removal algorithm for enhancing AGB estimation.

Keywords: terrestrial laser scanning, quantitative structure models, aboveground biomass, urban and rural forests, wood density, leaf- wood classification

Introduction

The total aboveground biomass (AGB, kg, oven-dry basis) of trees, an important decision-making element 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 aboveground tree structure (Burt et al. 2021; Kükenbrink et al. 2021). Accurate estimation of forest AGB plays a vital role in understanding a wide range of ecological services in rural and urban forests (e.g., biodiversity, pollination, temperature regulation, water purification and infiltration; Baker et al. 2019; Casalegno et al. 2017; Nowak and Greenfield 2020; Phillips et al. 2019), and is essential for studying terrestrial carbon dynamics at different spatial scales across biomes (Stovall et al. 2017). For example, the finding that Amazonian forests store large amounts of carbon in aboveground live vegetation (approximately 50-60 Pg) is based on estimation of aboveground biomass in Amazonian forests, where approximately 45-50% of live plant biomass is carbon content (Burt et al. 2021). Similarly, urban trees store large amounts of carbon in aboveground biomass that can be comparable to rural forest carbon stocks (McPherson 1998), depending on levels of canopy cover and impervious surfaces (MacFarlane 2009).

However, there remains substantial uncertainty regarding forest carbon offsets due to a dearth of accurate and detailed tree biomass data over multiple spatial and temporal scales (Weiskittel et al. 2015), particularly for urban forests (Tigges and Lakes 2017; Wilkes et al. 2018). Therefore, it is important to continue to develop new data and models for tree AGB across different growing environments.

Urban and rural forest trees can have very different growth and biomass allocation patterns, because lower tree abundance in urban, as compared to rural, areas is associated with reduced competition for light (MacFarlane and Kane 2017; McHale et al. 2009). 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). Trees with fewer neighbors 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 (Bang et al. 2010; Gardiner et al. 2016; Mohamed and Wood 2015; Salim et al. 2015; Telewski et al. 1997). Open-grown, urban trees allocate the largest portion of their AGB to branches (MacFarlane and Kane 2017; Zhou et al. 2015), whereas trees in rural forests and plantations are narrower in crown diameter, and they allocate more mass to stems (Lines et al. 2012; Weiner 2004). 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. Therefore, the significant allometric and structural differences between urban and rural forest trees should be considered when choosing methods to quantify their AGB.

The dry AGB of any tree, regardless its growing environment, can be directly measured by weighing tree components (i.e., branches, stems and leaves), and quantifying the moisture of green biomass 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; Dettmann and MacFarlane 2018; MacFarlane 2010, 2015; Radtke et al. 2017; Ver Planck and MacFarlane 2014, 2015).

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 (Burt et al. 2021; Calders et al. 2015; Disney et al. 2019; Stovall et al. 2018; Weiskittel et al. 2015). Harvesting large numbers of sample trees needed to build allometric equations (Roxburgh et al. 2015; Sileshi et al. 2014) is particularly impractical in cities (Kükenbrink et al. 2021), and equations that have been created for rural forest trees may not be directly applicable to urban trees (Lefsky and McHale 2008; McHale et al. 2009).

Terrestrial laser scanning (TLS) provides a non-destructive approach for quantifying tree architecture and dimensional properties (e.g., woody volume), which can be converted to AGB estimates (Calders et al. 2020; Liang et al. 2018). TLS is an active remote sensing technique where the sensor emits laser pulses and captures the three-dimensional structure of its 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 three-dimensional structure of trees based on TLS data can be achieved by generating Quantitative Structure Models (QSMs; Hackenberg et al., 2015a; Kaasalainen et al. 2014; Raumonen et al. 2013). QSMs fit geometric primitives (i.e., cylinders) to three-dimensional point-clouds (Bournez et al. 2017) in a way that preserves branch and stem topology and provides information about the size, location, hierarchy, and orientation of branching networks. QSMs provide accurate direct estimates of total aboveground volume of trees based on the number and dimension of fitted cylinders, which can be converted to AGB when multiplied by estimates of tree density, typically wood density (i.e., the ratio of dry woody biomass at 0% moisture content to green woody volume) (Burt et al. 2021; Demol et al. 2021). Unlike allometric models, estimating tree AGB from TLS data does not rely on biological assumptions of tree structure (Malhi et al. 2018), but its accuracy depends on (i) generating high-quality point clouds, (ii) assumptions and limitations of the QSM and (iii) representative estimates of the density of different parts of the trees (Disney et al. 2018, 2020; Olagoke et al. 2016).

Point cloud quality and registration accuracy relies on obtaining unobstructed views of all parts of each tree, but is also affected by weather conditions during laser scanning (e.g., branches swaying due to wind) and scanner technical properties. Any point cloud errors are compounded by factors related to QSM quality (e.g., segmentation errors, cylinder fitting problems) (Calders et al. 2015; Disney et al. 2018). Malhi et al. (2018) describe fundamental challenges in accurately estimating tree biomass from QSMs including extraction of high order branches and classification of woody and non-woody parts of scanned trees. Leaves add unwanted noise in point clouds of trees for generating QSMs (Stovall et al. 2017) and inclusion of points from leafy surfaces reduces reconstruction accuracy of woody skeletons (Burt et al. 2021). Therefore, leaf-on point clouds require artificial leaf-removal using leaf-classification algorithms (Moorthy et al. 2020; Vicari et al. 2019; Wang et al. 2019) prior to QSM generation. However, the effect of such classification algorithms on estimates of tree structure remains poorly understood (Arseniou et al. 2021a; Vicari et al. 2019).

Tree wood density varies according to tree mechanical properties (Telewski 2012), hydraulic conductance (Markesteijn et al. 2011) and environmental or evolutionary strategies (Disney et al. 2018). Published values of wood density are nonetheless available for different tree species (Chave et al. 2009; Miles and Smith 2009), because wood density is thought to be phylogenetically preserved (MacFarlane 2020). Despite the potential for high-quality tree component volume estimates from TLS, there can be significant variation in wood density among and within species across different environments (Burt et al. 2021; Demol et al. 2021; MacFarlane 2020), which can lead to bias in AGB estimates. Published averaged values of wood density are available for many species (Chave et al. 2009; Miles and Smith 2009), but few studies have examined their potential for biomass estimation (e.g., Demol et al. 2021; MacFarlane 2015).

In this study, we used TLS-based volume estimates and estimates of within-tree basic density (both wood and bark) to model woody AGB of thirty-one trees, including both needle-leaf evergreen and broad-leaf deciduous species growing in rural forest and urban conditions. The objectives of the study were: (i) to evaluate TLS-based woody AGB and component biomass (main stem and branches) estimates relative to tree mass measurements from destructively sampled trees; (ii) to assess the effect of measured versus published basic density values on the accuracy of total and component woody biomass estimates from TLS-based volumes; (iii) to evaluate use of TLS for total and component woody biomass estimation of trees growing in different environments along a continuum of crowding conditions (i.e., rural forest to open urban); (iv) to assess the effect of artificial leaf-separation from leaf-on point clouds on total and component woody biomass estimates for broad-leaf deciduous and needle-leaf evergreen tree species.

Materials and methods

Tree data

The experimental approach in this study identified healthy trees with undamaged crowns representing different species within two functional groups (broad-leaf deciduous and needle-leaf evergreen), in contrasting growing environments (rural and urban settings), that could be destructively sampled after scanning. Ten rural forest 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*) were sampled at the Harvard Forest, in Petersham, MA, USA. The urban tree dataset included ten trees of three broad-leaf deciduous species (*Acer rubrum, Acer saccharum, Gleditsia triacathos*) and one needle-leaf evergreen species (*Pinus nigra*), sampled on the Michigan State University campus, MI, USA. Trees were selected to cover a large range of sizes (Table 1) and a complete list of all their measured/estimated properties is available in Online Resource 1.

Table 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 Environment	Functional Group	Leaf Condition	DBH (m)	Height (m)	Total Woody AGB (kg)	Main Stem Biomass (kg)	Branch Biomass (kg)
A. rubrum	UF	BD	Off	0.358	7.96	364.099	133.163	230.936
A. saccharum	UF	BD	Off	0.389	12.53	901.250	392.020	509.230
A. saccharum	UF	BD	Off	0.478	13.99	1427.948	497.488	930.459
A. saccharum	UF	BD	Off	0.523	12.66	2081.490	692.070	1389.420
P. nigra	UF	NE	On	0.549	14.57	2008.654	796.001	1212.653
G. triacanthos	UF	BD	On	0.577	15.79	3576.340	996.852	2579.488
G. triacanthos	UF	BD	On	0.467	12.41	1538.288	463.202	1075.087
G. triacanthos	UF	BD	On	0.457	12.68	1663.478	460.320	1203.157
G. triacanthos	UF	BD	On	0.432	14.05	1853.480	526.375	1327.105
G. triacanthos	UF	BD	On	0.429	11.67	1524.280	409.848	1114.432
G. triacanthos	UF	BD	On	0.495	11.80	1769.792	472.779	1297.013
T. canadensis	RF	NE	On	0.401	24.45	708.264	586.594	121.670
P. strobus	RF	NE	On	0.137	15.64	51.457	44.162	7.295
T. canadensis	RF	NE	On	0.231	17.65	181.305	136.519	44.787
P. strobus	RF	NE	On	0.216	20.39	153.642	134.191	19.451
T. canadensis	RF	NE	On	0.180	16.25	120.461	87.697	32.763
T. canadensis	RF	NE	On	0.081	8.63	12.201	9.180	3.021
P. strobus	RF	NE	On	0.427	25.36	752.809	508.206	244.603
P. strobus	RF	NE	On	0.257	20.54	208.891	162.461	46.430
P. strobus	RF	NE	On	0.333	24.60	472.288	370.911	101.377
Q. rubra	RF	BD	Off	0.363	21.60	813.403	596.597	216.806
A. rubrum	RF	BD	Off	0.287	22.74	387.375	301.129	86.246
T. canadensis	RF	NE	On	0.345	24.45	529.965	368.397	161.567
Q. rubra	RF	BD	Off	0.193	21.15	174.977	157.141	17.835
A. rubrum	RF	BD	Off	0.076	11.00	17.721	15.763	1.958
A. rubrum	RF	BD	Off	0.218	23.13	247.392	217.795	29.597
A. rubrum	RF	BD	Off	0.119	13.44	57.312	46.416	10.895
A. rubrum	RF	BD	Off	0.107	16.86	56.248	44.753	11.495
Q. rubra	RF	BD	Off	0.267	23.53	401.772	353.278	48.494
Q. rubra	RF	BD	Off	0.503	24.11	1435.951	1103.754	332.197
Q. rubra	RF	BD	Off	0.323	22.16	648.207	443.782	204.425

Reference tree sampling

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

Standing tree measurements

Total standing tree heights were recorded with a *TruPulse 360* laser range finder and DBH (at 1.37 m from 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 across its semi-major and semi-minor axes. The crowding condition of each tree was categorized as open grown, dominant, co-dominant, intermediate and overtopped, and also using a continuous competition index, which was computed from the DBH of all neighboring trees ≥ 10 cm DBH, within a 7.3 m radius and their distance to the focal tree (see MacFarlane and Kane 2017).

Destructive measurements for green weights

After felling, the main stem of each tree was determined by following the largest and straightest stems from the cut bottom to the top. All other stems connected to the main stem were defined as branches. After separating branches, the main stem was cut at 1.37 m, 2.44 m, and at subsequent 1.22 m intervals. All weights were measured with at least three significant figures. The green (fresh) weight of all main stem sections was measured with an Intercomp Crane Scale which is accurate to 0.23 kg. Disks of thickness approximately 5 cm were extracted at 0.15 meter (stump height), 1.37 meters (breast height), and every subsequent 1.22 m section. Depending on the size of a disk its green weight (including bark) was measured in the field using an Ohaus scale which is accurate to 0.01 g or an Adam scale which is accurate to 5 g, and it was used to estimate disk basic density (see below, *Measurements and computations in the laboratory*). Two perpendicular disk diameters inside- and outside- bark were recorded, as well as four measurements of disk thickness from diameter endpoints (all measures to the nearest 0.1 cm).

Branch measurements followed different protocols for trees of broad-leaf and needle-leaf species. Starting at the base of a broad-leaf specimen and working upward, first-order branches (branches attached directly to the main stem) were systematically removed. Each branch was measured for basal diameter (bd) and classified as either a "small" branch (bd < 2.5 cm) or branch (bd ≥ 2.5 cm). For every branch with bd ≥ 2.5 cm, basal diameter, linear length, status (live or dead), and its position on the main stem (the height of the branch "center" attached to the main stem) was recorded. Branches were further separated and weighed using the crane scale, including second and higher order portions of a branch with leaves. After weighing the total green weight of each branch, leaves and attached twigs were clipped from the branch, weighed separately, and subtracted from the total green weight. One disk was removed from the mid-section of each branch, weighed green and measured (as above) to compute disk green volume. 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, first-order branches are generally smaller and more numerous than those of broad-leaf species. So, for these species, the trunks were divided into 1.22 m sections, starting from the base, and all branches were removed from each section and weighed in the field. Live and dead branches were weighed separately in each section, and three branches from a representative whorl were 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, then 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 below, *Measurements and computations in the laboratory*).

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 "green" as soon as possible and the green-biomass of wood and bark components were weighed separately. Finally, bark and wood components of all disks were oven-dried at 105 °C for 48 hours, then weighed and recorded. The following computations include both the wood and bark components of a disk.

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

$$MC_{disk} = \frac{(GW_{disk} - DW_{disk})}{GW_{disk}}, \qquad \text{(eq. 1)}$$

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

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

$$DW_{section} = (1 - MC_{disk}) * GW_{section}, \quad \text{(eq. 2)}$$

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.

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

The basic density of each sampled disk (BD_{disk} in g/cm^3) included both bark and wood tissues and it was computed from the following equation:

$$BD_{disk} = \frac{DW_{disk}}{GV_{disk}}, \quad \text{(eq. 3)}$$

where GV_{disk} is the green-volume of the disk (in cm^3) computed from the laboratory-measured dimensions of the disk whose shape was assumed cylindrical. Basic density values of disks were extrapolated to corresponding sections of the main stem or branch from which they were sampled.

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

Finally, the competition that each urban and rural forest tree faced was quantified, because we hypothesized that uncertainty of TLS-based biomass estimates should increase with competition strength due to occlusion of tree parts in point clouds from neighboring trees. The competition index was computed as follows:

$$\mathrm{CI} = \sum_{i=1}^{n} \sum_{j=1}^{s} \frac{\frac{DBH_j}{DBH_i}}{Dist_{ij}}, \quad \text{(eq. 4)}$$

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).

Terrestrial laser scanning of trees and point cloud processing

All urban trees were scanned with a FARO Focus^{3D} X 330 terrestrial laser scanner (FARO Technologies Inc., Lake Mary, FL, USA). The *G. triacanthos* trees were scanned during the leaf-on period in July, 2019. The remaining urban trees of the other species were laser-scanned during the leaf-off period in November, 2017. An example of a leaf-off and leaf-on point cloud of an urban tree is available in Online Resource 2. 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 in calm wind conditions from a minimum of four different directions at different distances 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 to densify branch laser returns. Spatial registration of scans was enhanced by six reference target-spheres placed around each tree, following 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 co-register and filter all scans. The same software was used to manually isolate the point cloud from its background. 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[1]: the 50 m x 50 m Main plot (16 trees; 48 scans: 36 scans on 10 m centers in the 50 m x 50 m area and 12 additional scans in the buffer area and at 25 m diagonally from the corners) and the 20 m x 20 m North plot (4 trees; 9 scans: 1 scan at center, 4 scans at corners, and 4 scans at midpoints of sides of the square plot). Retroreflective targets were used to guide the co-registration of individual scans in RiSCAN PRO. Trees were extracted with *treeseg* (Burt et al. 2018), followed by visual inspections for 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*). *TLSeparation* employs unsupervised classification of geometric features and "shortest-path" analysis to enhance detection of high-frequency paths through the branching network (Vicari et al. 2019). Woody structure was thus separated and isolated from foliage in a woody structure point cloud.

[1] More information on this campaign can be found here: http://tlsrcn.bu.edu/index.php/harvard-forest-calibration-activity/

QSMs were generated from the leaf-off and leaf-removed point clouds of the study trees (Fig. 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) point cloud segmentation into stem and branches based on cover sets, and (ii) segment volume and surface area reconstruction 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, 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 to estimate variation of 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).

The total woody volume (including bark tissues) was computed from optimal QSMs of leaf-off and leaf-removed point clouds of study trees as the sum of all cylinders fitted to each point cloud (see close-up in Fig. 1-c). Total woody volumes were further separated into main stem and branch components and converted to biomass by multiplying volumes by corresponding basic density values computed from disks removed during destructive sampling (see *Measurements and computations in the laboratory*). Published values of species bark and wood density (Miles and Smith 2009) were applied to TLS-based volumes as an alternative biomass estimation process. Total woody AGB of a tree was computed by adding together the component biomass values of the tree.

Fig. 1 Digital representations of an urban tree (first row) and a rural forest tree (second row) of the same species (*A. rubrum*) showing (a, d) leaf-off point clouds, (b, e) generated QSMs, and (c, f) close-ups of the QSMs illustrating cylinders fitted to the point cloud of the trees. QSM colors denote different branching orders (i.e., blue is main stem, green is 1st order, red is 2nd order, etc.)

Comparison between TLS-based biomass estimates and reference biomass measurements

Agreement between TLS-based tree woody AGB and tree component biomass estimates with reference biomass values was quantified with a concordance correlation coefficient (CCC; Lin 1989), which ranges between -1 (complete discordance) and 1 (complete concordance) (Calders et al. 2015; Gonzalez de Tanago et al. 2018). Pearson's correlation coefficient (r) was used to quantify the relationship between absolute errors of TLS-based biomass estimates and reference biomass values, and to quantify the relationship between relative errors in TLS-based biomass estimates and the competition index. Statistical significance of all relationships was assessed at $\alpha = 0.05$ and all analyses were performed within the *R* 3.6.1 environment (R Core Team 2015).

Different error metrics were computed to assess the quality of TLS-based biomass estimates (Burt et al. 2021; Calders et al. 2015; Fan et al. 2020):

- the error for each tree: $\varepsilon = Biomass_{TLS} - Biomass_{Ref}$ (eq. 5)

- the relative error for each tree: $RE = \frac{|\varepsilon|}{Biomass_{Ref}}$ (eq. 6)
- the mean relative error across all trees (%): $MRE\% = \frac{1}{n}\sum_{i=1}^{n} RE_i * 100\%$ (eq. 7)
- the root mean square error that refers to the overall accuracy across all trees:

$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n} {\varepsilon_i}^2}$ (eq. 8)

- relative $RMSE\% = \frac{RMSE}{Biomass_{Ref.mean}} * 100\%$ (eq. 9)

In the above equations (eqs. 5-9), $Biomass_{TLS}$ is the TLS-based woody AGB or component biomass of the main stem and branches, $Biomass_{Ref}$ is the AGB or component biomass from reference measurements, $Biomass_{Ref.mean}$ is its mean value across trees, *n* represents the total number of trees and the index *i* refers to individual trees.

Accuracy of TLS-based woody AGB and component biomass estimates was evaluated for urban versus rural forest trees, and for leaf-off versus leaf-removed point clouds. Since the trees were in different conditions, we fitted the following linear mixed-effects model to better understand how TLS-based woody AGB estimates of study trees were affected by tree condition:

$$AGB_{TLS} = b_0^{(L+H)} + {b_1}^{(L+H)} * AGB_{Ref} + \varepsilon, \quad \text{(eq. 10)}$$

where AGB_{TLS} is total aboveground biomass (kg) of study trees from TLS data, AGB_{Ref} is total aboveground biomass (kg) based on reference data, b_0 is the intercept, and b_1 is the slope of the relationship. *L* and *H* are nested random effects representing the leaf condition of the point clouds (L is a factor with two levels: leaf-off versus leaf-removed) as well as the growing environment (H is a factor with two levels: urban versus rural forest), respectively. The additive error term (ε) is normally distributed. Without nested random effects L and H, Eq. 10 becomes a simple, linear, fixed-effects model:

$$AGB_{TLS} = b_0 + b_1 * AGB_{Ref} + \varepsilon, \quad \text{(eq. 11)}$$

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. The coefficient of variation (CV) of woody mass was used to characterize uncertainty in estimating total woody AGB and components biomass associated with consecutive QSM reconstructions of the same point cloud of a tree (QSM reconstructions only contribute the volume component of AGB estimation).

Results

Uncertainty in estimated woody biomass from multiple QSM reconstructions

Coefficients of variation indicated that uncertainty due to consecutive QSM reconstructions of the same point cloud (30 QSM reconstructions per tree) averaged 4.3%, 3.1% and 6.3% of estimated total woody AGB, main stem biomass, and branch biomass, respectively across all study trees. CV distributions of woody AGB and main stem biomass were positively skewed, but more uniform for branch biomass (Fig. 2).

Fig. 2 Histogram of the coefficient of variation of (a) total woody AGB, (b) main stem biomass, and (c) branch biomass of study trees, based on 30 QSM reconstructions from the same point cloud of every tree.

AGB and components biomass across all study trees

Biomass estimates from TLS were strongly correlated with those from destructive reference data using both reference and published basic density values for total woody AGB, main stem, and branch biomass (Fig. 3). However, TLS-based biomass values of larger trees were mostly underestimated using published basic densities, and for some larger trees, there was also a significant underestimation with the reference basic density values applied (Fig. 3).

Fig. 3 Regression of TLS-based biomass versus reference biomass (kg) among 31 study trees for (a) Total woody AGB, (b) Main stem biomass, and (c) Branch biomass. Different colors represent different sources for basic density values, whereas rural forest and urban trees are represented with different symbols. Shading indicates 95% confidence interval around each regression line, and the 1:1 dashed line is shown in black

The exponential relationship of total woody AGB and diameter at breast height (DBH) was similar among reference and TLS-based biomass data with reference and published basic density values (note the substantial confidence interval overlap in Fig. 4). However, underestimation bias of total woody AGB was greatest for large DBH trees when published basic density values were used (Fig. 4).

Fig. 4 Relationship between the total woody AGB of 31 study trees and their diameter at breast height (DBH) based on reference biomass, TLS-based biomass estimates using reference and published basic density values. Shading indicates 95% confidence intervals around the fitted lines. Different colors represent different sources for biomass values, whereas rural forest and urban trees are represented with different symbols

Table 2. Statistical metrics to assess the performance of TLS-based biomass estimates across all study trees

Metric	Total woody AGB	Main stem biomass	Branch biomass	Total woody AGB	Main stem biomass	Branch biomass
	With reference basic density values			With published basic density values		
Mean Relative Error (%)	24.5	13.8	124.1	26.3	14.1	107.7
RMSE (kg)	147.743	114.973	167.434	244.846	133.144	194.127
Relative 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

To examine if overall error in TLS-based biomass estimates was independent of tree size we examined the relationship between absolute errors of TLS-based biomass estimates and reference biomass values using reference and published basic densities (Burt et al. 2021). Absolute errors of TLS-based total woody AGB and branch biomass using reference basic densities were not significantly correlated with the respective reference biomass values ($p > 0.05$), whereas absolute errors of TLS-based main stem biomass increased with the reference main stem biomass values (Pearson's $r = 0.54$, $p = 0.0019$). Absolute errors of TLS-based total woody AGB, main stem, and branch biomass using published basic densities increased with reference biomass values (Pearson's $r = 0.75$, $p < 0.001$; $r = 0.62$, $p < 0.001$; $r = 0.61$, $p < 0.001$ respectively).

Growing environment and leaf-condition factors affecting the accuracy of TLS-based biomass estimates

The fixed-effects model of TLS-based woody AGB as a linear function of reference AGB values (eq. 11) showed strong explanation power (adj. $R^2 = 0.927$), and the mixed-effects model (eq. 10), including the nested effects of L and H, had stronger explanatory power (adj. $R^2 = 0.986$). The effect L (leaf conditions: leaf-off versus leaf-removed point clouds) explained 45.9% of the difference between the fixed-effects and mixed-effects models, whereas the effect H (growing environment: urban versus rural forest conditions) explained 42.4%. Overall, the effect of L and H together explained only 5.9% of the total variation in AGB, showing that most of the variation between TLS-based and reference AGB was not due to the growing environment or the leaf-removal algorithm.

AGB and components biomass for urban and rural forest trees

Strong positive correlations were found between biomass estimates from TLS data and reference data for total woody AGB, main stem, branch biomass, and trunk biomass (the section of main stem up to the crown base height; as defined in MacFarlane 2015) of rural forest trees and urban trees. Error analysis showed that TLS-based woody AGB of rural forest trees was less accurate compared to urban trees (see relative RMSE (%) in Table 3, and Fig. 5). TLS-based stem biomass estimates of urban trees were less accurate compared to rural forest trees, and the opposite pattern was observed for TLS-based branch biomass estimates. However, in both urban and rural growing environments the mass of the trunk was predicted with a high level of accuracy (Fig. 5-d).

Fig. 5 Relationship between TLS-based biomass and reference biomass (kg) of study trees for their (a) Total woody AGB, (b) Main stem biomass, (c) Branch biomass, and (d) Trunk biomass (the section of main stem up to the crown base height; MacFarlane 2015). Colors distinguish urban and rural forest trees, and symbols distinguish leaf-off and leaf-removed point clouds. Shading indicates a 95% confidence interval around regression lines, and the 1:1 dashed line is drawn in black

Table 3. Statistical performance metrics of TLS-based biomass estimates for rural forest and urban trees, and trees with leaf-off or leaf-removed point clouds

Metric	Total woody AGB	Main stem biomass	Branch biomass	Total woody AGB	Main stem biomass	Branch biomass
	Rural forest trees			Urban trees		
Mean Relative Error (%)	36.2	8.7	184.7	3.2	23	14.1
RMSE (kg)	109.02	43.741	99.147	199.764	183.777	247.250
Relative 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 with leaf-off point clouds			Trees with leaf-removed point clouds		
Mean						

Relative Error (%)	14.9	14.4	93.1	32.4	13.2	149.7
RMSE (kg)	47.26	111.693	108.349	194.846	117.605	203.601
Relative 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

The competition strength experienced by study trees had a small, positive effect on the relative error (RE) of TLS-based branch biomass estimates. Urban trees had generally lower RE and were open-grown and faced very little competition from other trees. Whereas most rural forest trees of dominant, co-dominant, intermediate and overtopped canopy classes showed increasingly greater RE (Table 4, Fig. 6), and an ANOVA statistical test showed significant differences among the mean competition index values of the different tree canopy classes (p = 0.001, Table 4). RE in TLS-based branch woody biomass of the study trees was positively related to the competition index (Pearson's r = 0.38, p = 0.033; Fig. 6) indicating occlusion effects in point clouds of tree crowns due to increasing crowding. However, the competition index was not related to relative errors in either TLS-based woody AGB or main stem biomass.

Fig. 6 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. Shading indicates 95% confidence interval around the fitted line

Table 4 Competition index (CI) values per canopy class of the study trees

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]

AGB and components biomass of leaf-off and leaf-removed tree point clouds

Strong positive correlations were found between biomass estimates from TLS and reference data for total woody AGB, main stem biomass, and branch biomass of trees with both leaf-off and leaf-removed point clouds. The fitted regression lines (Fig. 7) did not show much contrast for biomass estimates from leaf-off versus leaf-removed point clouds, but the error analysis showed that the total woody AGB estimates from leaf-off point clouds were more accurate (see relative RMSE (%) in Table 3).

Fig. 7 Relationship between TLS-based biomass and the reference biomass (kg) of study trees for their (a) Total woody AGB, (b) Main stem, and (c) Branch biomass. Trees with leaf-off and leaf-removed point clouds are plotted with different colors, and urban and rural forest trees are plotted with different symbols. Shading indicates a 95% confidence interval around regression lines, and the 1:1 dashed line is drawn in black

Discussion

Terrestrial laser scanning (TLS) data have been systematically used in forest ecology since the early 2000s (Calders et al. 2020; Hackenberg et al. 2015b; Hopkinson et al. 2004). To the best of our knowledge, this is one of few studies that evaluated and compared total TLS-based woody AGB and component biomass accuracy for trees growing in fundamentally different environments and in different seasonal leaf conditions. Previous studies have mostly focused on total AGB and woody volume of trees growing in either rural forest or urban conditions (Burt et al. 2021; Calders et al. 2015; Holopainen et al. 2011; Kankare et al. 2013; Moskal and Zheng 2011; Olschofsky et al. 2016; Polo et al. 2009; Rahman et al. 2017; Stovall et al. 2017; Tanhuanpää et al. 2017; Vonderach et al. 2012), while other studies focused on crown architecture (Jung et al. 2011; Metz et al. 2013; Moorthy et al. 2010), stem profile (Maas et al. 2008), or woody surface area (Arseniou et al. 2021b). More comparative studies are needed to understand how to achieve the best results under a variety of field conditions.

Overall accuracy of TLS-based biomass estimates

The overall accuracy of AGB across all study trees using reference basic density values (see Relative *RMSE (%)*, Table 2), was comparable to overall accuracies reported by Calders et al. (2015) and Olagoke et al. (2016) (CV(RMSE) = 16.1%; %RMSE = 13.5%). AGB estimation from QSMs can be within 10% of measured biomass from destructive sampling (Wilkes et al. 2018). Error analysis across all study trees showed that overall accuracy of the TLS-based main stem biomass estimates was higher compared to the accuracy of branch biomass estimates (see error metrics in Table 2). This result was expected due to challenges associated with branch reconstruction in QSMs (Disney et al. 2018). Smaller branches are often overestimated with TLS data (Disney 2019; Momo Takoudjou et al. 2018), although branch-size underestimation of 8% from QSMs has been described for branches with base diameters between 20 cm and 60 cm, and 6% underestimation for branches with greater than 60 cm base-diameters (Lau et al. 2018; Lau et al. 2019a).

Influence of measured versus published values of basic tree density

Previous studies have shown that AGB estimates from allometric models based on locally collected TLS data can be more accurate than biomass estimates from general, regional, allometric models (Holopainen et al. 2011; Kankare et al. 2013; Kükenbrink et al. 2021; Lau et al. 2019b; Stovall et al. 2018; Wilkes et al. 2018; Zheng et al. 2019). However, local TLS-based allometric models require estimates of basic density to generate tree AGB estimates from TLS volume data. The similar allometric relationship that was found in this study between TLS-based total woody AGB and DBH, with either reference or published basic density values (their confidence intervals significantly overlapped), and the strong agreement between TLS-based and reference values of total woody AGB, main stem, and branch biomass, using either reference or published basic density values, underscores the precision of the TLS-based AGB estimates across all study trees. However, TLS-based biomass estimates from published basic density values were less accurate compared to those using reference basic densities (see Relative RMSE (%), Table 2), corroborating previous studies using direct wood density measurements (Burt et al. 2021; Demol et al. 2021).

Previous studies have found that errors in TLS-based AGB and branch biomass, using reference basic density values from destructive measurements, were generally independent of tree size (Burt et al. 2021; Calders et al. 2015). However, when we used published basic density values instead of measured reference values, the errors in AGB estimation were larger for bigger trees, similar to results reported by Gonzalez de Tanago et al. (2018) and Burt et al. (2021). MacFarlane (2020) showed that branch wood density was relatively higher than stem wood density for larger trees, experiencing less competition, and Takoudjou et al. (2020) reported 10% bias in TLS-based woody AGB estimates, with published wood density values, due to vertical, within-tree, variation in wood density. Overall, this suggests that the use of published density values, which are almost always taken from samples collected low on the trunk (i.e., breast height, 1.3 m), could contribute to bias in TLS-based AGB and branch biomass for larger open-grown urban or canopy-dominant, forest-grown trees.

Moving forward, reliable TLS-based biomass estimates of individual trees may be possible without reference basic density values from destructive sampling. This will be especially important for studying tree AGB in urban areas and protected forests, where tree destructive sampling may not be feasible (Calders et al. 2020; Kükenbrink et al. 2021; Lefsky and McHale 2008). Some studies have developed corrective models from literature values of wood specific gravity and tree size and structural metrics to estimate tree-level, volume-averaged wood specific gravity (Sagang et al. 2018; Takoudjou et al. 2020) and to calibrate species-averaged basic density values for trees in various regions. Promising advances in x-ray tomography (Van den Bulcke et al. 2019) are also expected to significantly contribute to increased accuracy in non-destructive estimation of basic density values.

Influence of QSM stochasticity

According to Disney et al. (2018), tree volume estimation from QSMs involves some inherent stochasticity, due to non-deterministic procedures for fitting geometric primitives (e.g., cylinders) to tree point clouds. Here, only a relatively small portion of total uncertainty in mean woody AGB was associated with multiple QSM reconstructions, indicating that *TreeQSM* algorithm was robust. Coefficient of variation of the branch biomass was larger than the coefficient of variation of the woody AGB or main stem biomass, indicating that branch reconstruction involves greater uncertainty than main stems; most likely a function of branch size (Disney et al. 2018) or the topological complexity of the tree.

Influence of urban versus rural environments on TLS-based biomass accuracy

In general, we found strong agreement between TLS-based biomass estimates and reference biomass data for both rural and urban forest trees, though the urban tree results were based on a smaller sample size and thus less generalizable. Calders et al. (2015) and Gonzalez de Tanago et al. (2018) also found strong correlations between total woody AGB from TLS and reference data (concordance correlation coefficients were 0.98 and 0.95, respectively) in rural forests. Momo Takoudjou et al. (2018) compared total woody volume, as well as component volumes of stumps, stems, and crowns, of rural forest trees, between TLS and reference data and found TLS-based volume estimates were highly accurate (R^2 values greater than 0.98). Fewer studies have focused on TLS-based biomass estimation for urban trees, but a recent study by Kükenbrink et al. (2021) reported R^2 value of 0.95 for TLS-based woody AGB of urban trees compared to reference AGB data.

Despite strong correlations between TLS-based and reference biomass values, error analysis revealed that TLS-based woody AGB of the rural forest trees we studied was less accurate and had a greater relative RMSE (%) compared to the urban trees. The rural forest tree errors we found were comparable to error values for the TLS-based AGB of tropical forest trees

(CV(RMSE) = 28%, reported by Gonzalez de Tanago et al. (2018). Momo Takoudjou et al. (2018) found that the % mean relative error of TLS-based woody AGB of rural forest trees was 23%, comparable to the mean relative error of the TLS-based woody AGB of the rural trees in this study. Calders et al. (2015) reported CV(RMSE)% equal to 16.1% for TLS-based woody AGB for rural forest trees, which is more comparable to the relative RMSE (%) of AGB of the urban trees in this study. According to Kükenbrink et al. (2021), the RMSE of 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 relative RMSE (%) of AGB, which accounts for differences in tree mass, 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 stronger correlation between the TLS-based branch biomass and reference biomass for urban trees may be related to the general lack of branch occlusion from neighboring trees, compared to rural forest conditions, where the laser scanner can be obstructed by other vegetation (Wilkes et al. 2017). This idea is supported by the increasing relative error in TLS-based branch biomass with competition strength faced from tree neighbors. However, the two groups of trees were also scanned using different scanning patterns and with different laser scanning systems, both of which can affect the quality of TLS data (Wilkes et al. 2017). It is worth noting that the TLS-based branch biomass estimates of urban trees were better, even though the Harvard Forest trees were scanned with a RIEGL VZ-400 laser scanner, which typically captures higher quality point clouds of trees (with less noise, due to its greater maximum range and better resolution of small branches) than the FARO Focus^{3D} X 330 terrestrial laser scanner (Calders et al. 2020) used to scan the urban trees.

Our study showed that urban trees allocated more biomass to branches compared to rural forest trees (see Online Resource 2). This greater allocation to branches has been shown to enhance mechanical stability against strong wind loads in the absence of or reduced competition for light from neighbors (MacFarlane and Kane 2017). The fact that the TLS-based stem biomass estimates of urban trees were less accurate compared to main stem biomass estimates of rural forest trees, could be explained by the fact that urban trees tend to have wider crowns and less discrete main stems compared to rural forest 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, so our result is not unique. One explanation is that detection of main stems in the QSMs may not have aligned well with main stems based on destructive measurements, and no special treatment was implemented to ensure that tree main stem from reference measurements perfectly matches with tree main stem in a QSM; we simply allowed the QSM to choose the main stem. Therefore, this interpretation is further supported by the strong agreement between TLS-based biomass and reference biomass values for the trunk of the urban trees, which is the section of the main stem up to the crown base height (MacFarlane 2015).

Influence of the leaf-removal algorithm on TLS-based biomass accuracy

There was a strong agreement between both leaf-off and leaf-removed TLS-based biomass estimates and reference biomass data. Momo Takoudjou et al. (2018) also reported a strong agreement between TLS-based woody AGB and reference biomass data (R^2 = 0.97), when performing a manual (rather than automated) leaf-removal from the leaf-on point clouds in their study. 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. Our study showed that overall accuracy of TLS-based biomass of main stem from leaf-off point clouds was similar to overall accuracy of main stem biomass from leaf-removed point clouds, which was expected because the leaf-separation algorithm should not affect the main stem. It was surprising that the accuracy of TLS-based branch biomass estimates after the artificial leaf-removal was comparable to the branch biomass estimates from leaf-off point clouds (see relative RMSE (%), Table 3), because we expected some confusion between leaf and branch material (Demol et al. 2022).

The tree with the largest underestimation in TLS-based AGB and branch biomass was an urban *G. triacanthos* tree, whose leaves were artificially removed (see Figs. 7-a and 7-c). *G. triacanthos* trees have compound leaves with modular architecture (i.e., the leaf blade consists of several leaflets stemming from the leaf rachis; Champagne and Sinha 2004; Klingenberg et al. 2012). The leaf type of a tree species can affect the quality of artificial leaf-removal (Moorthy et al. 2020). 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 *G. triacanthos* trees may confuse the leaf-separation algorithms. However, the TLS-based biomass estimates of the remaining *G. triacanthos* trees, which had lower AGB and branch biomass, were not significantly underestimated after the artificial leaf-removal. This could imply that the effect of leaf type may also depend on branching complexity. Arseniou et al. (2021a) found that artificial leaf-removal using the *TLSeparation* algorithm introduced an underestimation of the structural complexity of urban trees of *G. triacanthos* species which increased with maximum branch order, and larger trees tend to have higher branch orders (Seidel et al. 2019). According to Demol et al. (2022), leaf-removal algorithms may also remove small branches (less than 5 cm in diameter) whose TLS-based volume can be otherwise overestimated in a QSM depending on point cloud quality and scanner characteristics. In general, despite the existence of different algorithms to separate leaves from leaf-on point clouds of trees (Moorthy et al. 2020; Stovall et al. 2017; Vicari et al. 2019; Wang et al. 2019), more work is likely needed to further improve leaf versus wood classification systems.

Conclusions

The results of this study have important implications for estimating biomass and carbon stocks of forests, especially urban forests, which currently have limited data and models for tree biomass estimation. TLS data can provide reliable estimates of the aboveground biomass of trees and could provide comparable data for calibrating tree biomass equations, without the need for destructive sampling. This study suggests that both measured and published basic densities can be used to successfully convert TLS-based volume to biomass, but the use of published densities can reduce accuracy. This study also shows how 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) affects the accuracy of TLS-based tree biomass estimation. Occlusion from surrounding trees is an important contributor to biomass estimation uncertainty, particularly for branches. However, future studies should include more trees of more species growing in different urban and rural forest locations to better understand how species functional traits and fundamentally different growing environments influence the accuracy of TLS-based biomass estimates.

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Statements and Declarations

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Competing Interests

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

Author contributions

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

Data Availability

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