

RESEARCH ARTICLE

Conductive sapwood area prediction from stem and canopy areas—allometric equations of Kalahari trees, Botswana

Maciek W. Lubczynski¹  | Diana C. Chavarro-Rincon^{2*} | David G. Rossiter^{3,4*}

¹ Faculty of Geo-Information Science and Earth Observations, University of Twente, Enschede, The Netherlands

² Ambient Sensing, Enschede, The Netherlands

³ Section of Soil and Crop Sciences, Cornell University, Ithaca, NY, USA

⁴ ISRIC-World Soil Information, Wageningen, The Netherlands

Correspondence

Maciek W. Lubczynski, Faculty of Geo-Information Science and Earth Observations, University of Twente, P.O. Box 217, 7500 AE Enschede, the Netherlands.
Email: m.w.lubczynski@utwente.nl

Funding information

Netherlands Organization for Scientific Research through a WOTRO grant

Abstract

Conductive sapwood (xylem) area (A_x) of all trees in a given forested area is the main factor contributing to spatial tree transpiration. One hundred ninety-five trees of 9 species in the Kalahari region of Botswana were felled, stained, cut into discs, and measured to develop allometric equations predicting A_x from estimates of stem (A_s) and canopy (A_c) areas. Stem discs were also subjected to laboratory-based computed tomography, which well detected wood density contrasts but was not diagnostic with regard to delineation of A_x . The staining experiment, along with the help of visual and computed tomography analysis, allowed the definition of 4, tree-species categories of A_x , C1–C4. In C1 (*Acacia erioloba*, *Terminalia sericea*, and *Burke Africana*), the staining and visual delineation of A_x matched the natural color difference between sapwood and heartwood; in C2 (*Dichrostachys cinerea* and *Ochna pulchra*), sapwood was divided into external conductive and internal nonconductive annuli; in C3 (*Acacia fleckii* and *Acacia luederitzii*), sapwood had sharp staining boundary between external highly conductive and internal low-conductive annuli; and in C4 (*Lonchocarpus nelsii* and *Boscia albitrunca*), stems had no heartwood. Per-species 0-intercept linear regression models, $A_x = \text{slope} \cdot A_s$ (slope = $0.392 \div 0.794$; $R^2 = 96.7 \div 99.8\%$) and $A_x = \text{slope} \cdot A_c$ (slope = $1.477 \div 17.044$; $R^2 = 82.1 \div 92.2\%$) yielded excellent to good predictive allometric equations. The first equation is suitable for A_x scaling of small-size Kalahari areas, where the A_s of all trees can be estimated on the ground, whereas the second, as contribution to automated tree transpiration mapping of large-size Kalahari areas, where the A_c of trees can be derived through remote sensing interpretation of high-resolution images.

KEYWORDS

allometric equations, conductive sapwood area, CT method, cut and dye method, Kalahari, linear regression models

1 | INTRODUCTION

The quantification of vegetation water use in semiarid climates, where trees make use of not only shallow but also deep soil moisture and even groundwater reserves, is essential for determining water balances of open savannas and agricultural systems (Dye, Soko, & Poulter, 1996; Hultine, Williams, Burgess, & Keefer, 2003; Lubczynski, 2009). Such quantification is particularly important in dry environments such as the Kalahari, where replenishment of groundwater resources by

recharge is one of the lowest in the world, that is, in order of only few millimeters per year (De Vries, Selaolo, & Beekman, 2000), and the roots of Kalahari trees are deepest in the world, reaching lengths of more than 60 m, thus being very efficient in water uptake across the thick (>60 m) unsaturated zone of the Kalahari Sand mantle (Obakeng, 2007).

Numerous studies have shown that measurement of sap flow is an efficient method for determining whole tree water use (Lorant, Mackay, Ewers, Adelman, & Kruger, 2008; Vertessy, Hatton, Reece, O'Sullivan, & Benyon, 1997; Wilson, Hanson, Mulholland, Baldocchi, & Wullschlegel, 2001; Wullschlegel, Hanson, & Todd, 2001). The most common methods are thermal (Čermák, Kučera, & Nadezhdina, 2004;

*Formerly at Faculty of Geo-Information Science and Earth Observations, University of Twente, Enschede, the Netherlands.

Smith & Allen, 1996; Steppe, De Pauw, Doody, & Teskey, 2010). The majority of these methods estimate sap flow (Q) by measuring sap flux density (J_p) across the conductive sapwood (xylem) area (A_x), where Q is a product of J_p and A_x . In general, the per-species J_p variability among trees of different size and age is relatively modest or even low (Jaskierniak, Kuczera, Benyon, & Lucieer, 2016; Kumagai, Aoki, Shimizu, & Otsuki, 2007; Reyes-Acosta & Lubczynski, 2013, 2014). Therefore, spatial tree water uptake depends mainly on the conductive sapwood area of trees. This study is therefore dedicated to the research of A_x of Kalahari trees, as support for future Kalahari tree transpiration mapping, following the method proposed by Reyes-Acosta and Lubczynski (2013).

There is scant research on A_x found in the scientific literature. This is likely due to the complexity of conductive sapwood, but also because invasive methods of A_x assessment are often not permitted and logistically difficult, but noninvasive, are cumbersome, quite uncertain, and mostly not portable. The methods of A_x assessment focus on defining a boundary between conductive sapwood and centrally positioned, nonconductive heartwood. The most frequently used method is a point method of invasive extraction of wood cores with an increment borer to determine sapwood depth, further used to estimate A_x . The increment cores can be assessed by visual analysis, by staining or by microscopic analysis. The visual analysis is applicable if obvious changes in color and texture between sapwood and heartwood boundary are apparent, although color contrast does not always represent the boundary between conductive and nonconductive wood (Lu, Urban, & Zhao, 2004 and also this study, see below). An alternative method is to stain wood cores to reveal the difference in chemical composition (e.g., pH difference) between sapwood and heartwood. Staining solutions commonly used include methyl orange, benzidine, sodium nitrite, safranin, astra, and Eosin-B. Although successful in many studies, according to Pfautsch, Macfarlane, Ebdon, and Meder (2012), the staining of sapwood cores is not always accurate because of insufficient color contrast and because it is species dependent; therefore, they advised to cross-validate the assessment accuracy by microscopy of light transmission to identify open vessels. Another assessment approach is the resistance to penetration method (Rust, 1999), which uses a rotating needle inserted into the wood to detect the hardness difference between softer sapwood and harder heartwood. The power needed to penetrate sapwood is calibrated, to detect the depth at which the change in tissue resistance occurs. This method is applicable where wood hardness difference between soft and hard zones indeed represents boundary between conductive sapwood and heartwood.

An interesting method of sapwood assessment is to use sufficiently long sap flow probes equipped with J_p sensors distributed along the length of a probe to cover the entire sapwood depth. An example of such probe is the Heat Field Deformation device (Nadezhdina, Vandegehuchte, & Steppe, 2012), equipped with eight thermistors at 1 cm separation distance. If any of the thermistors reaches heartwood, then it is expected to indicate $J_p = 0$. The advantage of this method is that it provides not only sapwood depth but also radial J_p profiles, whereas disadvantages relate to discrepancy related to eventual heat conduction along the probes (typically made of heat-conductive stainless steel material), leading to overestimates of A_x (Pfautsch et al., 2012), large costs, and fragility.

All the methods discussed above represent point assessment methods, so their common disadvantage is that to be accurate, they require a number of samplings around the perimeter of a stem. The most accurate and versatile, but also the most destructive, is the method of cutting whole tree and staining it by dye (so called *cut-and-dye* method) to determine A_x from stem discs by visual, microscopic, and/or by dye staining assessment (Lu & Chacko, 1998; Lu et al., 2004). In many countries, however, this method is not permitted due to environmental protection of trees.

Noninvasive, in vivo methods seem to be ideal for the spatial assessment of A_x , provided they are accurate and that instruments are portable, which is not the case yet. The largest experience in wood testing is so far with computed tomography (CT), which has been widely used to determine wood anatomy (Fromm et al., 2001; Rust, 1999; Steppe et al., 2004). CT measures the attenuation of beam radiation with increasing wood density and moisture, either or both of which can be used to define the boundary between heartwood and sapwood. Unfortunately, a portable CT is costly. Further, the CT outcome with respect to quantitative assessment of A_x is not always unique, as also experienced in this study (see below). Another method of nondestructive sapwood assessment is by using electric resistivity tomography (ERT), which uses the difference in electric resistivity between the water-rich conductive sapwood and the water-poor resistive heartwood to find the boundary. The opinions about ERT performance in evaluation of A_x are quite different. For example, the application of ERT on *Pinus silvestris* L. trees by Bieker and Rust (2010) resulted in an unreliable estimate of sapwood width, lower than by staining. In contrast, Wang, Guan, Guyot, Simmons, and Lockington (2016) claimed to obtain a good agreement between ERT and increment cores in eucalyptus, assessed on the basis of natural color difference, stating that ERT sapwood–heartwood differentiation was successful except in wet conditions. However, their conclusions were debated by Pfautsch and Macfarlane (2016), who stated that the results of Wang et al. (2016) were not sufficiently accurate, due to ERT overestimation of sapwood depth; further they stated, that it is unlikely that ERT will ever be able to provide accurate measures of sapwood depth in eucalyptus, as their moisture contents of sapwood and heartwood, including the one of the species tested by Wang et al. (2016), were very similar or even the same. The most sophisticated and the most suitable for the noninvasive assessment of A_x seems to be nuclear magnetic resonance (NMR) method, as in contrast to CT and ERT, it can uniquely distinguish hydrogen nuclei while testing plants in vivo, not only determining A_x but also velocity, distinguishing between flowing and nonflowing water (Windt, 2007). However, the costly medical NMR device implemented as magnetic resonance imaging is not portable due to the large size of the magnets, whereas the available portable instruments (Jones, Aptaker, Cox, Gardiner, & McDonald, 2012; Windt & Blümmler, 2015) are still rare, heavy, costly, and not commercially available. Besides, to our knowledge, the current portable NMR devices can only image thin stems of up to 10 cm diameter.

All of the above methods, either destructive or nondestructive, lead to quantification of the A_x of an individual tree and, if J_p of that tree is measured, then the product of the two, that is, sap flow, provides estimate of whole tree water use (Wullschlegel, Meinzer, & Vertessy, 1998). At the small scale of a plot (or stand), with a limited

number of trees, the plot tree transpiration can be estimated by A_x and J_p measurements of all trees. In large plots, where A_s of each stem can be estimated, the A_x can be scaled from limited amount of per-species A_s and A_x measurements applying $A_s \sim A_x$ allometric equations and applying per-species J_p estimated as the mean of different sizes or ages of trees if their variability is low or otherwise categorized as function of A_x (Reyes-Acosta & Lubczynski, 2013). However, if the assessment of tree water use has to be done over large areas, for example, at the catchment scale with many trees of different tree species and different sizes, the direct measurement of A_s at each tree is impractical. To handle that problem, Reyes-Acosta and Lubczynski (2013) proposed an efficient, automated method of tree transpiration mapping, tested over sparse oak woodland area in Western Spain, applying remote sensing (RS) upscaling of A_x from A_c . Following that method and the principle of allometric proportionality (Picard, Saint-Andre, & Henry, 2012), the cumbersome tree measurements of A_x can be obtained from species-specific allometric equations relating A_x with A_c , the A_c automatically definable for all tree canopies on air photos or high-resolution satellite images.

The allometric equations relating sapwood area with stem area (A_x vs. A_s) have been developed in numerous studies at numerous ecosystems and for numerous tree species (Cienciala, Kucera, & Malmer, 2000; Kumagai et al., 2005; Parolin, Müller, & Junk, 2008; Roberts, Vertessy, & Grayson, 2001; Vertessy, Benyon, O'Sullivan, & Gribben, 1995; Wulschleger et al., 2001). The allometric equations relating canopy areas with sapwood areas (A_x vs. A_c), to our knowledge, have only been developed for oaks of Spanish *dehesa* (Reyes-Acosta & Lubczynski, 2013). However, neither of the two equation types has been defined for the Kalahari tree species till date, only the allometric equations using A_s as predictor of biomass (Meyer et al., 2014).

The objective of this study, which is a follow-up of the PhD project of (Chavarro Rincon, 2009), is focused mainly on defining species-specific allometric equations relating A_x with A_s and A_x with A_c for nine abundant Kalahari tree woody species (local names are in brackets): *Acacia erioloba* (Mogothlo), *Terminalia sericea* (Mgonono), *Burke Africana* (Monato), *Dichrostachys cinerea* (Moseletsele), *Ochna pulchra* (Monyeleneye), *Acacia fleckii* (Mohahu), *Acacia luederitzii* (Mokha), *Lonchocarpus nelsii* (Mahata), and *Boscia albitrunca* (Motopi), as presented in Figure 1 and characterized in van Wyk and van Wyk (2013). These equations are meant to facilitate future study on RS upscaling of tree transpiration of Kalahari trees.

The main novelties of this study is in the recognition of the four categories of the conductive sapwood patterns (C1–C4) and in development of reliable (high R^2) linear allometric equations $A_x \sim A_s$ and $A_x \sim A_c$, for the nine abundant Kalahari tree species based on the assessment of 195 Kalahari, world's deepest root trees.

2 | MATERIALS AND METHODS

2.1 | Study area

The Kalahari is a large ecosystem with scarce water resources, extensive droughts, and therefore severe competition for water between vegetation, livestock, and humans. This study was carried out within a representative 10 × 10-km experimental area centered at S 22°20', E 26°20' and located in the Central District of Botswana, at the

eastern fringe of the Kalahari (Obakeng, 2007), approximately 40 km west of Serowe. The study area is a gently undulating sand plateau, gradually sloping towards the west, without prominent drainage. It is covered by the >60-m-thick, unsaturated, permeable, and homogeneous Kalahari Sand mantle. That sand, due to its homogeneity (Obakeng, 2007), creates nearly uniform tree water uptake conditions. The climate is semiarid with mean annual temperature ~20°C and two distinct seasons, long dry winter, and rainy summer responsible for the whole annual precipitation of ~400 mm. Streams in the study area are scarce and ephemeral and shallow moisture is available only during and shortly after the rainy season, so the deep moisture of the Kalahari Sand unsaturated zone, or even groundwater, are the main sources of tree water uptake during dry seasons. The Kalahari vegetation is a mosaic of open savanna, composed of grassland and low thorny trees, many of them with a marked seasonal variation in leaf cover (Chavarro Rincon, 2009).

2.2 | Biometric stem and canopy measurements

Biometric tree measurements were carried out during the dry season (July–September). The selection of the tree species and their stem sizes was based on the earlier study by Mapanda (2003) in the same as this study, 10 × 10-km area. Mapanda (2003) sampled 1,334 trees in circular plots of 19.94 m radius, within regular grid of 1-km distance. For each tree species, in this study, groups of 18 to 24 trees of various biometric dimensions (in total 195 trees) were sampled to derive allometric equations correlating sapwood area (A_x) with stem area (A_s) and with canopy area (A_c). All A_s and A_c were estimated by two diameter measurements in two cardinal directions N–S and E–W. The stem diameters were measured ~50 cm above the ground. The canopy diameters were estimated as the horizontal measurements of the ground-projected silhouette of a canopy.

2.3 | Sapwood measurements—cut and dye method

The use of the increment borer method was impossible in Kalahari, due to extraordinary wood hardness as many attempts done with different brands of increment borers resulted in their breakages. Further, in situ CT, ERT, or NMR methods were not feasible, due to the lack of portable versions of these instruments, remoteness of the study area, and, above all, large number of trees to be measured. Thus, after receiving official approval from Botswana Government, the cut and dye method was applied to all 195 sampled trees. Each of these trees was felled by cutting it with sharp chainsaw and immediately after immersing the cut end of the stem in a bucket filled with Eosin-B® (Merck) staining solution, to allow the tree to transpire for several hours during which the sap conductive area was stained red. The cut tree stumps were visually investigated with a magnifying glass, after which thin nonstained discs were sliced from the stumps.

After removal of trees from the stain, the tree wood was given several hours to dry up in order to avoid radial spreading of the stain during disc cutting. Then thin discs were cut with a sharp chainsaw from the stained stems, at least 20 cm above the stem base, thereby avoiding the stem portion stained by capillarity rather than sap flow. All discs were photographed against scales, and one representative stained disc per tree (~20 cm above tree cut) was selected and scanned over a scaled photograph to quantify its sapwood area A_x . Stem areas

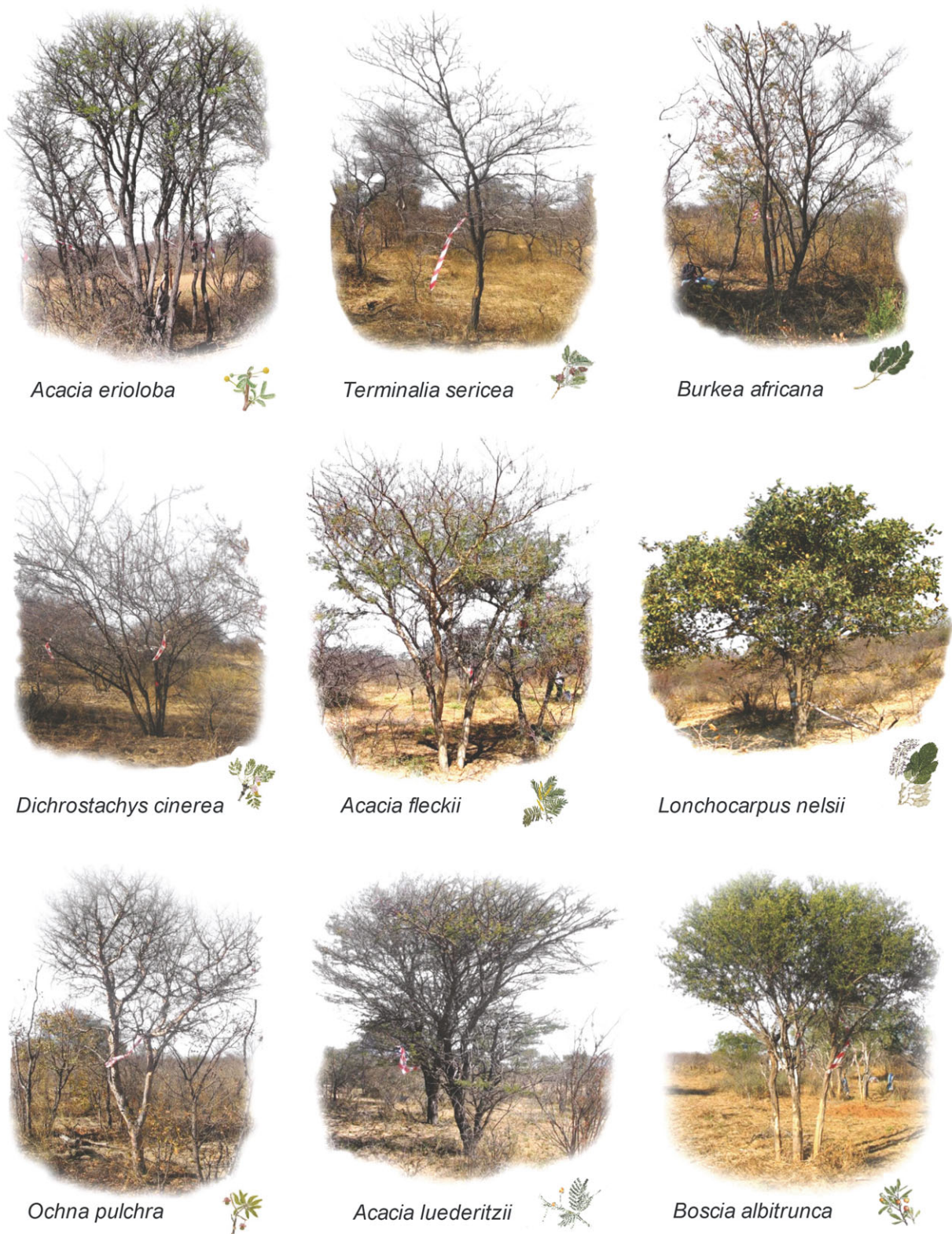


FIGURE 1 Investigated nine Kalahari tree species (appearance during dry season)

(As) were measured the same way, as a check and to eventually improve field estimates of As.

2.4 | CT tree disc scanning

CT scanning was carried out as an additional measurement. Ideally, CT scanning should be done in situ, with a portable instrument to take

advantage of natural contrast in density and moisture content between heartwood and sapwood tissues. Because such equipment was not available for our Kalahari campaigns, selected disc samples were sent to the Netherlands and scanned there at the Medical Spectrum Twente in Enschede with a SOMATOM PLUS X-ray system (Siemens). In CT scanning, differences in density, rather than in moisture, provided qualitative interpretation of CT brightness following

the principle that the attenuation of the radiation beam is linearly correlated to bulk density of a material and calibrated in Hounsfield units (HU), that is, $HU = 0$ for water, $HU = -1,000$ for air, and $HU > 0$ for materials with densities above 1 g/cm^3 (Fromm et al., 2001).

CT scanning was carried out on six discs, one each from *B. africana*, *D. cinerea*, *A. luederitzii*, *A. fleckii*, *L. nelsii*, and *B. albitrunca*. Only six discs were investigated because of restriction on the CT equipment usage, so only the species with less certain conductive sapwood area determination from the cut and dye method were selected. However, the main aim of that experiment was to evaluate the potential of the CT contribution to A_x determination on Kalahari tree species, by comparing the CT results with the results of the cut and dye method. To enhance the power of CT interpretation, each CT image was stretched between its lowest and highest HU limits, so that denser tissue appeared white and less dense black.

2.5 | Statistical analysis

Exploratory data analysis and regression modeling of allometric functions A_x versus A_s and A_x versus A_c were carried out in the R Environment for statistical computing (Ihaka & Gentleman, 1996) to predict

A_x from easily measured biometric parameters such as A_s and A_c applying the following linear regression models: $A_x = m \cdot A_s$ and $A_x = n \cdot A_c$, where m and n are the equation slopes. These are both area-to-area models, so a linear model form is suggested. These were fit by ordinary least squares with the "lm" method of the standard "stats" R package. Models were first fit with intercepts, for example, $A_x = a' + m \cdot A_s$ and $A_x = a'' + n \cdot A_c$. The null hypothesis that the intercept is 0 (suggested in theory because a tree with no stem area would have no sapwood and one with no canopy would have no stem area) could not be rejected for any of the models, so they were refit as shown above. Models were checked for compliance with the assumption of independent and identically (i.i.d.) linear model residuals, as required by the ordinary least squares method of fitting linear model parameters.

3 | RESULTS

3.1 | Cut and dye method

The cut discs of the 195 stained trees showed species-specific patterns of conductive sapwood areas (A_x) as presented in Figure 2. Based on

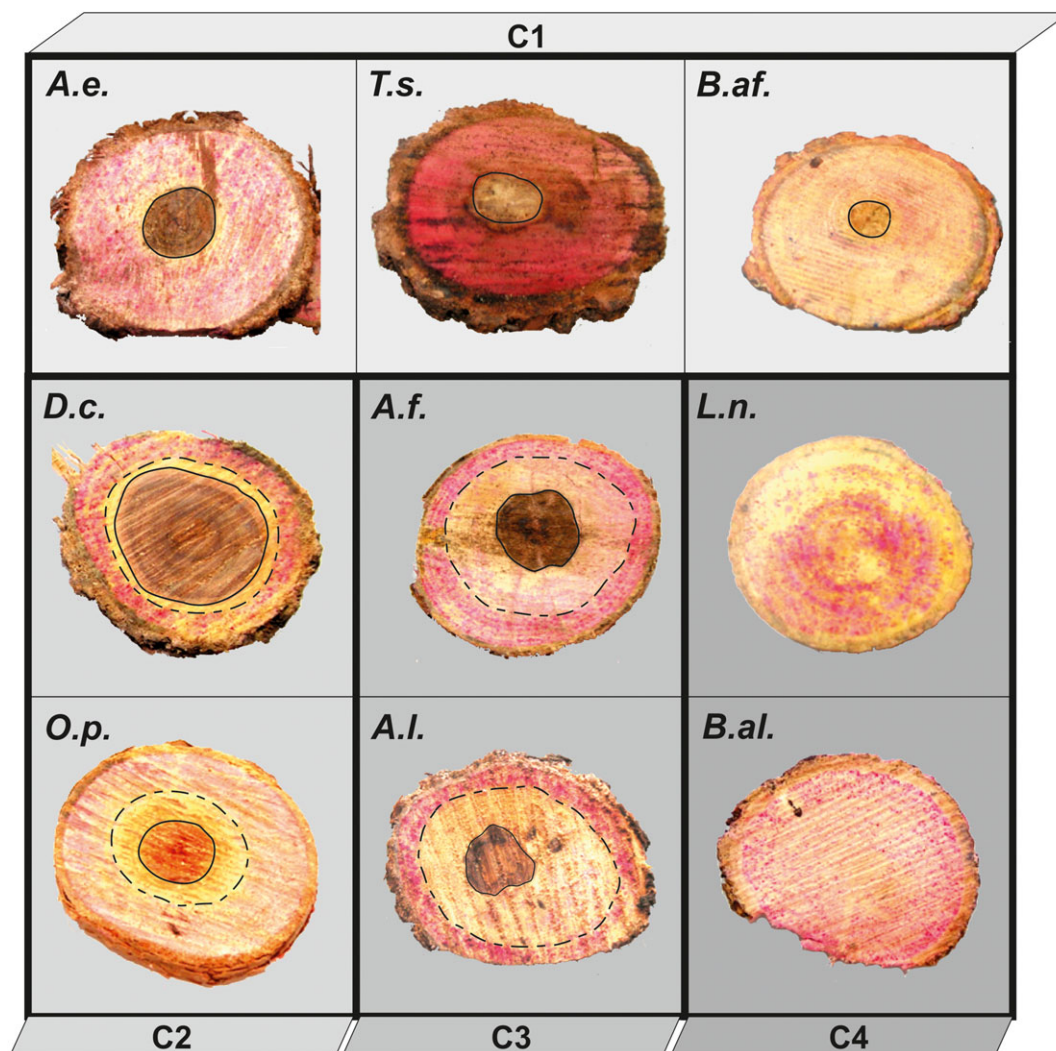


FIGURE 2 Selected nine representative stem photos of 195 disc samples of the nine species after staining experiment: *B.af.* (*Burke Africana*), *D.c.* (*Dichrostachys cinerea*), *O.p.* (*Ochna pulchra*), *A.l.* (*Acacia luederitzii*), *A.f.* (*Acacia fleckii*), *L.n.* (*Lonchocarpus nelsii*), and *B.al.* (*Boscia albitrunca*); C1–C4 are conductive sapwood categories differing by disc zonation pattern identified by visual analysis as explained in the manuscript

visual and staining analysis of these patterns, four sapwood categories (C1–C4) were identified. (C1) Species with Ax that can be visually identified by natural color differences between conductive sapwood and hardwood tissues. In these species, staining matches visual identification (*A. erioloba*, *T. sericea*, and *B. africana*). (C2) Species where dark color of heartwood can be clearly identified but the originally light and uniform sapwood is partly conductive (external annuli stained) and partly nonconductive (internal annuli nonstained). Using only visual macroscopic inspection, it is impossible to separate these two different sapwood zones (*D. cinerea* and *O. pulchra*). (C3) Species where dark color of heartwood can be clearly identified but the originally light and uniform sapwood is sharply divided into two annuli zones differing by staining intensity, the external with more intense, darker staining, and the internal with lighter staining (*A. luederitzii* and *A. fleckii*). (C4) Species where heartwood is not detected, neither visually nor by staining, as staining is observed indiscriminately all over the stem cross section (*B. africana* and *L. nelsii*).

3.2 | CT scanning

Figure 3 presents the CT panchromatic images next to the photographs of the corresponding stained discs (different discs than in

Figure 2). The *B. africana* disc of category C1 is characterized by a clear color boundary difference between conductive sapwood and heartwood confirmed by staining experiment. However, the CT image does not reproduce that boundary. After the light color (high HU) of the dry bark, there is a medium-dense, gray sapwood zone with interchanging lighter and darker rings but no lighter, centrally positioned spot resembling nonstained heartwood. Instead, there is a dark, less dense annulus zone with lightest, so densest, centrally positioned spot around the pith, which however is much smaller than the nonconductive heartwood. In the case of the *D. cinerea* category C2 tree disc, the heartwood together with thin annulus of nonconductive sapwood, visually nondistinguishable from conductive sapwood, represents most of the stem area. They together are well represented in the CT image by the light color of dense tissue in contrast to darker, so less dense, conductive sapwood annulus. The problem with Ax assessment of C2 species is that the nonconductive sapwood annulus is not distinguishable by visual analysis from conductive sapwood, although in the CT image, it is not distinguishable from the heartwood, so only the staining procedure seems to provide the appropriate estimate of Ax. In the two tree species of C3 category, *A. luederitzii* and *A. fleckii*, the conductive sapwood clearly differs from heartwood, having naturally lighter color. That difference is also well seen on the CT images by lighter, so denser,

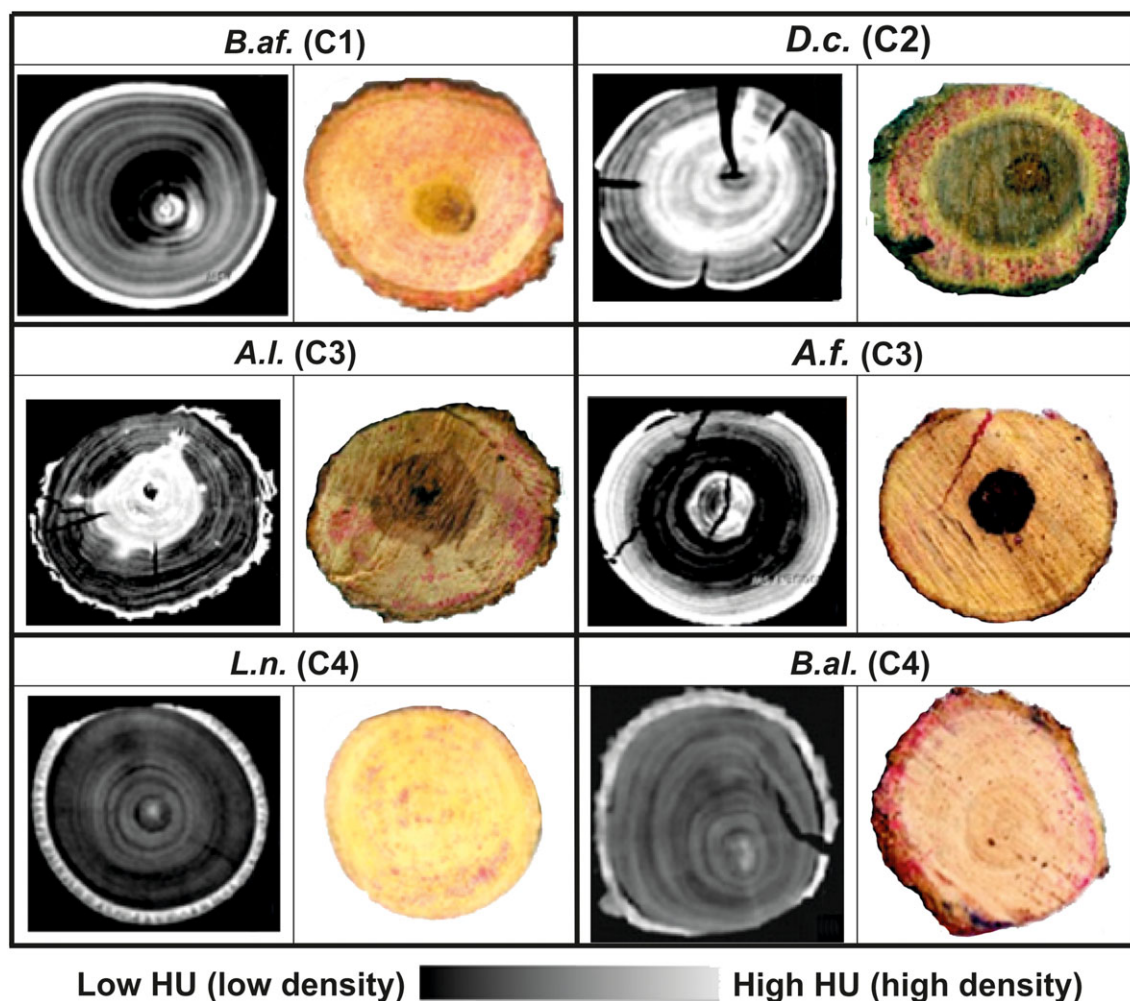


FIGURE 3 Computed tomography scanning of the selected stem discs of *B.af.* (*Burke Africana*), *D.c.* (*Dichrostachys cinerea*), *O.p.* (*Ochna pulchra*), *A.l.* (*Acacia luederitzii*), *A.f.* (*Acacia fleckii*), *L.n.* (*Lonchocarpus nelsii*), and *B.al.* (*Boscia albitrunca*); C1–C4 are conductive sapwood categories differing by disc zonation pattern identified by visual analysis as explained in the manuscript; HU = Hounsfield unit

color of heartwood in the central part of the stem. The sapwood of C3 species is divided into two annuli, although the two presented in Figure 3 stained disc samples do not show these boundaries as clear as the discs in Figure 2. However, even if not well seen by staining, these boundaries are quite well depicted in CT images, although it is remarkable that in *A. luederitzii*, the external annulus is slightly CT darker and so less dense, whereas in *A. fleckii*, the external annulus is CT lighter and so denser. The category C4 species *L. nelsii* and *B. africana* have no heartwood, and the whole sapwood area is conductive. This is in good agreement with CT images, which do not show any well-defined boundary with centrally located light color zone that could be interpreted as heartwood. Only for *L. nelsii*, an increase in wood density inward can be noticed.

Based on the features observed by visual analysis and staining experiment, with additional feedback of CT, the conductive sapwood area A_x was determined as in Figure 2 and computed for the 195 trees from scaled digital photographs. The A_x was obtained by subtracting the area corresponding to the bark and to the heartwood from the total stem area A_s .

3.3 | Statistical analysis

Figure 4 shows per-species box plots of the three measured biometric variables. Several of the distributions are skewed. *A. luederitzii* represents the largest size tree species of all trees measured, and it also has the largest variability. For most species, a larger A_s or A_c is associated with a larger A_x , although there are exceptions; for example, *D. cinerea* has larger A_c than *O. pulchra* but lower A_x .

Figure 5 shows scatterplots of A_x versus A_s and the corresponding 0-intercept linear regression equation. These models explained almost all the variance in A_x by the measured value of A_s . However, the slopes of these species-specific linear models differed widely, from 0.39 for *D. cinerea* (category C1) characterized by the lowest proportion of A_x to A_s (Figure 2), to 0.79 and 0.71 for *L. nelsii* and *B. africana* (both category C4) respectively, with the steepest slopes because of no heartwood and therefore full occupation of the central part of the stem by conductive sapwood. The presented results imply that A_x can be very well predicted from A_s by applying the species-specific allometric equations shown in Figure 5.

Figure 6 shows scatterplots of A_x versus A_c and the corresponding 0-intercept linear regression equations. These models explain well the

variance in A_x by the measured value of A_c , although not as well as by A_s . A remarkable feature of Figure 6 is the huge difference between slopes of the regression equations, ranging from 1.48 for *D. cinerea* to 17.04 for *O. pulchra*. This is because of a large difference in tree morphology among Kalahari species. The presented results imply that A_x can be well predicted from A_c applying species-specific allometric equations shown in Figure 6. The final outcome of the statistical regression analysis resulting in two sets of allometric equations is summarized in Table 1 as below.

4 | DISCUSSION

This study was carried out in extremely rough conditions of Kalahari Desert, located ~3 hours by "sand-driving" from the nearest village (Serowe, Botswana). This made the task of the cut and dye experiments on 195 Kalahari trees very difficult logistically and therefore unique. However, the science-sacrificed trees and effort involved to determine the presented allometric equations led to valuable information, because with these equations published, no more tree cutting of these particular tree species is needed for tree transpiration mapping or other applications requiring estimate of A_x in Kalahari.

We selected the environmentally unfriendly cut and dye method for defining A_x because (a) increment coring did not work on Kalahari trees due to extraordinary wood hardness; (b) we did not have access to sufficiently long sap flow measurement probes; besides intensive radial and circumferential measurements of ~200 trees in rough condition of Kalahari would be very difficult and logistically nearly impossible; (c) we also did not have access to the equipment evaluating resistance to penetration; besides, that method most likely would not work in Kalahari, as some of the Kalahari trees had less dense zones deeper inside stems (Figure 3), so likely softer, as, for example, indicated by CT of *B. africana* and *A. fleckii*; (d) the noninvasive, in vivo, spatial assessment methods, such as portable versions of CT, ERT, or NMR, were not considered, because of unavailability of such equipment for this project, limited CT contribution for sapwood area determination (Fromm et al., 2001 and this study), controversial ERT results (e.g., Pfautsch & Macfarlane, 2016), and restriction of maximally 10-cm stem diameter on the investigated by portable NMR stem size (Jones et al., 2012), but the most important, because the use of these noninvasive methods in rough conditions of the Kalahari study area

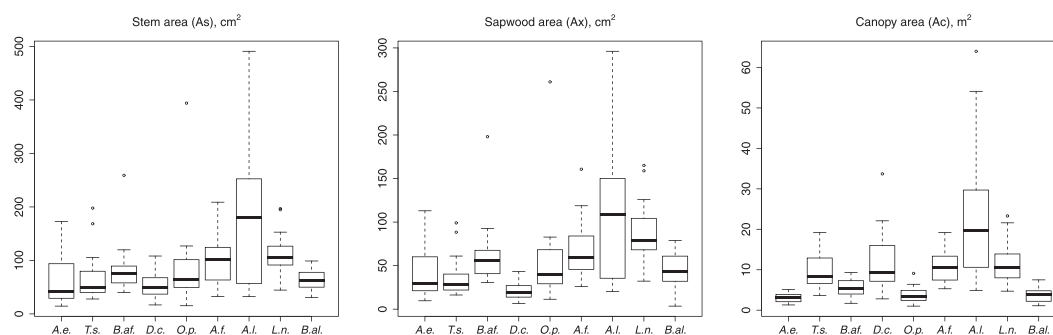


FIGURE 4 Distribution of biometric variables at nine tree species investigated: *B.af.* (*Burke Africana*), *D.c.* (*Dichrostachys cinerea*), *O.p.* (*Ochna pulchra*), *A.l.* (*Acacia luederitzii*), *A.f.* (*Acacia fleckii*), *L.n.* (*Lonchocarpus nelsii*), and *B. al.* (*Boscia albitrunca*)

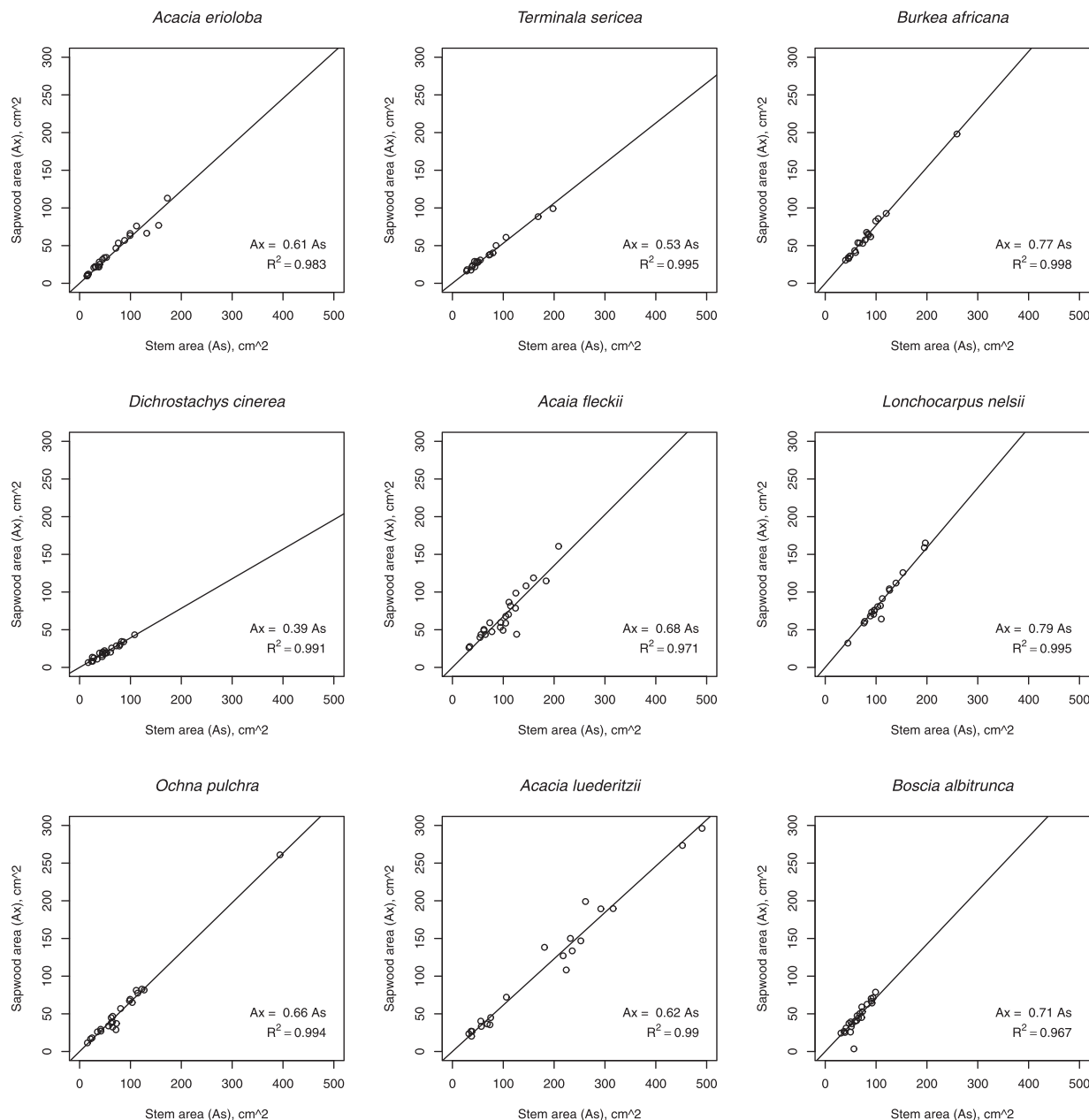


FIGURE 5 Fitted, species-specific linear regression models representing allometric equations of sapwood area (A_x) predicted by stem area (A_s)

seems to be nearly impossible considering the large amount of trees to be tested, complexity of those methods, extensive time required for a single tree test, and challenging logistics in such rough Kalahari conditions; (e) the cut and dye method in combination with visual assessment is the most accurate among possible methods (Lu et al., 2004); and (f) once allometric equations are developed for certain Kalahari species, no further tree cutting of that species is needed.

The distribution of conductive sapwood in stems, as disclosed by cut and dye method (Figure 2), has critical implication for eventual sap flux density (J_p) measurements in Kalahari trees, as J_p varies radially, typically from large in the outer rings, to smaller in inner rings, towards heartwood (Granier et al., 1994; Nadezhkina, Čermák, & Ceulemans, 2002; Phillips, Oren, & Zimmermann, 1996; Reyes-Acosta & Lubczynski, 2014; Wullschlegel & King, 2000). Therefore, if, for example, a measured section of J_p probe is substantially shorter than the conductive sapwood depth, such J_p measurement is prone to

overestimation. For C1 and C2 species, it is important to have sufficiently long probes to cover the whole thickness of sapwood depth. For C2 species, the nonconductive sapwood should be then detected as the $J_p = 0$ zone. For C3 species, the J_p rates are likely quite different in the external than in the internal sapwood zones, therefore, it is also critical that the probes penetrate the whole sapwood depth. For C4 species, the whole stem transpires water so the probe must cover the entire radius of the stem. As the radial J_p patterns vary not only between trees of different species but also between trees of different sizes of the same species, and also temporally (Delzon, Sartore, Granier, & Loustau, 2004; Gebauer, Horna, & Leuschner, 2008; Ghimire, Lubczynski, Bruijnzeel, & Chavarro-Rincón, 2014), these complexities also need to be taken into account when mapping tree transpiration (Reyes-Acosta & Lubczynski, 2013).

The laboratory CT applied to six discs provided radially varying, mainly wood density-dependent HU zones, as the investigated discs

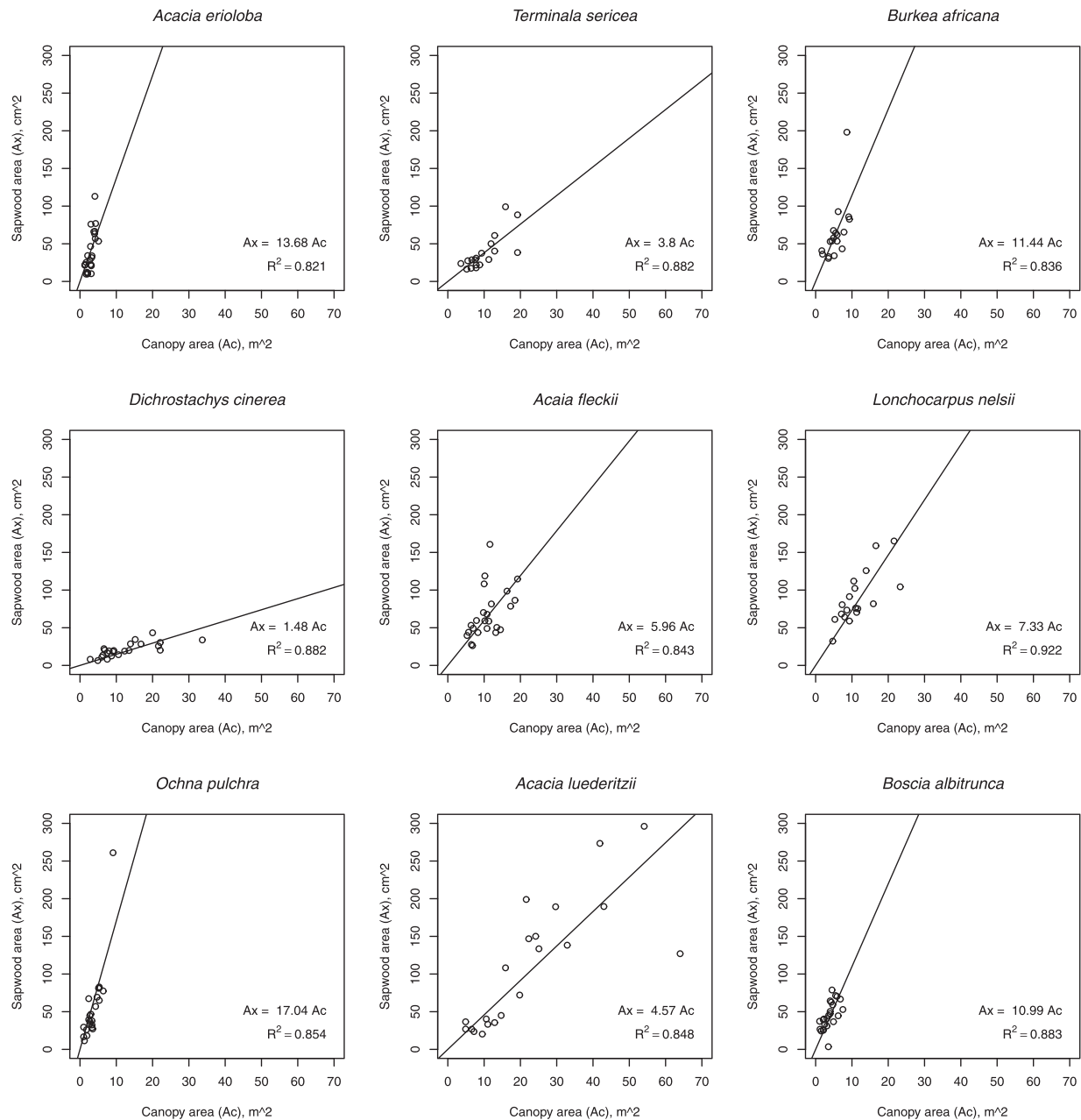


FIGURE 6 Fitted, species-specific linear regression models representing allometric equations of sapwood area (Ax) predicted by canopy area (Ac)

TABLE 1 Per-species linear regression models of sapwood area (Ax, in cm²) predicted from stem area (As, in cm²) and from canopy area (Ac, in m²)

Tree species	C	No	Ax = slope As			Ax = slope Ac		
			Slope	SE	R ²	Slope	SE	R ²
<i>Acacia erioloba</i>	C1	24	0.613	0.016	0.983	13.678	1.300	0.821
<i>Terminalia sericea</i>		18	0.532	0.009	0.995	3.803	0.327	0.882
<i>Burkea africana</i>		18	0.769	0.009	0.998	11.436	1.189	0.836
<i>Dichrostachys cinerea</i>	C2	23	0.392	0.008	0.991	1.477	0.112	0.882
<i>Ochna pulchra</i>		23	0.658	0.011	0.994	17.044	1.463	0.854
<i>Acacia fleckii</i>	C3	24	0.676	0.024	0.971	5.958	0.523	0.843
<i>Acacia luederitzii</i>		21	0.615	0.013	0.990	4.574	0.420	0.848
<i>Lonchocarpus nelsii</i>	C4	18	0.794	0.013	0.995	7.326	0.500	0.922
<i>Boscia albitrunca</i>		24	0.712	0.027	0.967	10.987	0.813	0.883

Note. SE = standard error.

undergone long transport from Africa to the Netherlands drying up and therefore losing their natural soil moisture status. The expected sharp boundary between dense heartwood and less dense sapwood was not always well depicted as, for example, in the case of *B. africana*, where nonstained heartwood was larger than indicated by CT. Also, CT differentiation of sapwood into conductive and nonconductive was questionable. For example, in most cases, denser annuli were found towards the center of discs, that is, in the direction of likely declining sap transport, whereas in the case of *A. fleckii*, the denser sapwood, according to CT, was at the external annuli. These somewhat confusing CT results with respect to evaluation of A_x are likely because the CT primarily evaluates wood density differences, not necessarily correlated with sap transportation ability. Besides, the CT output depends also on the moisture distribution, which unfortunately could not be taken into account in our experiments, as CT scanning was not done in situ but in a hospital in the Netherlands, so the discs had time to dry up during long transportation from Africa. On the basis of the six CT laboratory experiments, we conclude that CT disc scanning can provide complementary, useful information to detect conductive sapwood area by other method but cannot be used as standalone method to define A_x .

The results presented in Figures 5 and 6 are summarized in Table 1. For the nine Kalahari tree species investigated in this study, the A_x can be very well predicted from A_s by applying the derived species-specific allometric equations. The A_x can also be quite well predicted from A_c , although that prediction is slightly poorer than the prediction from A_s because of the following: (a) conductive sapwood area is dependent mainly on 3-D canopy volume rather than on 2-D canopy area used in this study as reference for RS identification of canopies; (b) the biometric measurements of this study were carried out in dry season, so that, accurate determination of canopy edges was difficult.

The field-developed, species-specific $A_x = m \cdot A_s$ allometric equations are optimal for scaling A_x from A_s for mapping tree transpiration in small study areas such as plots or stands, as these equations typically provide very accurate (high R^2 as in this study) prediction of A_x from $m \cdot A_s$ on trees, where only the easy and quick measurement of A_s , rather than the cumbersome A_x measurement, is performed.

In large study areas, such as for example catchments, where measurement of A_s of each tree is not feasible, field-developed,

species-specific $A_c = n \cdot A_c$ allometric equations, such as developed in this study, can contribute to automated tree transpiration mapping by applying RS identification of tree canopies next to field-developed species-specific J_p patterns (Reyes-Acosta & Lubczynski, 2013). The RS identification of individual tree canopies typically involves (a) recognition (classification) of tree species type (unless there is only one tree species in a study area) and (b) RS assessment of individual canopies A_c by automated delineation of their edges on the high-resolution multispectral images, further attributed to per-species $A_x \sim A_c$ allometric equations to determine A_x of each tree in the analyzed area. Both RS steps always involve uncertainty, which in the case of the multispecies Kalahari environment can be quite significant mainly due to difficulties in species classification (Adelabu & Dube, 2015; Chavarro Rincon, 2009; Kimani, Hussin, Lubczynski, Chavarro-Rincon, & Obakeng, 2007).

It is the large biodiversity of the Kalahari environment and similarity in spectral reflection patterns between different *Acacia* species that make Kalahari tree species classification difficult, although overlapping canopies makes their delineation even more difficult. However, with the newest RS techniques such as image segmentation and new earth observation products such as very high-resolution multispectral images, hyperspectral images, LIDAR, or combination of techniques (e.g., Ferreira, Zortea, Zanotta, Shimabukuro, & de Souza, 2016; Leckie, Walsworth, & Gougeon, 2016; Pham, Brabyn, & Ashraf, 2016), uncertainty in the RS tree canopy identification is continuously reduced.

If an investigated tree species is recognized as one of the listed in the Table 1, an appropriate equation can be used. However, it often happens that tree species cannot be easily recognized on the ground or even more frequently in RS images. To address that problem, additional statistical trial tests were carried out to determine combined, all-species $A_x = a' + m \cdot A_s$ and $A_x = a'' + n \cdot A_c$ Kalahari statistical models by modelling all 195 Kalahari trees together. Figure 7 shows scatterplots of A_x versus A_s (left) and A_x versus A_c (right) along with the best linear models using all trees. The prediction of A_x from A_s ($A_x = 0.65 A_s$) was surprisingly good ($R^2 = 0.973$), despite some increasing spread for large trees, in contrast to prediction of A_x from A_c ($A_x = 27.5 + 3.32 A_c$, with A_x in centimeter but A_c in meter), which was quite poor ($R^2 = 0.378$), especially for medium-sized and large trees. Note also that if for the former, the intercept was 0, for the latter, the intercept was

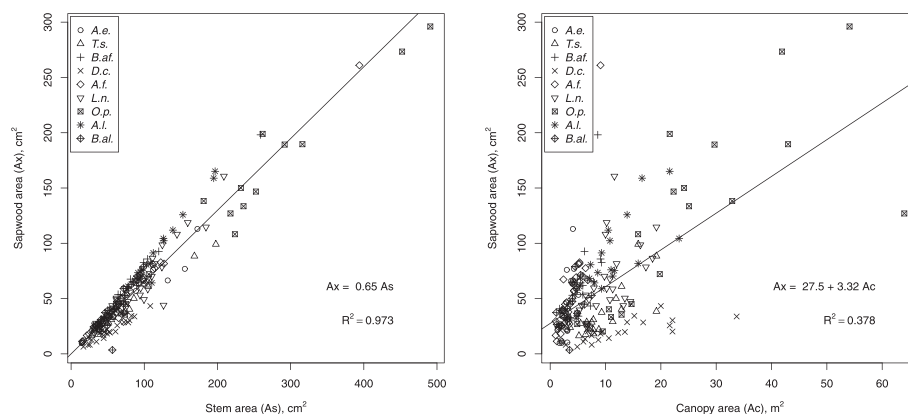


FIGURE 7 Fitted, linear regression models representing allometric equations of sapwood area (A_x) predicted by stem area (A_s —left panel) and by the canopy area (A_c —right panel), for all 195 trees

significantly different from 0, and in addition, removing that intercept resulted in a large change in the allometric slope and lower R^2 ; therefore, that equation has both, an intercept and a slope. It has to be emphasized that the combined, all-species equations are meant only to be used for rough estimates if Kalahari tree species cannot be identified. Otherwise, equations listed in Table 1 are recommended for A_x prediction, along with the confidence intervals computed from the reported standard error of the regression coefficient.

Meinzer, Bond, Warren, and Woodruff (2005) suggest that power functions may be more appropriate than linear models for allometric equations. Consequently, power functions were fitted as log-linear models to the relation of sapwood area to both stem and canopy areas. The fits were substantially worse than for the linear models: from stem area, $R^2 = 0.854$ versus 0.973; from canopy area, 0.25 versus 0.378 for the all-trees models with similar results for the nested-by-species model. Thus, it is concluded that for each of the nine investigated Kalahari species, linear rather than power allometric functions are justified. Further, the power fit by the all-species model from sapwood area was only slightly more than one (1.047 ± 0.0312) and was not significantly different from one at $p = 0.066$; thus, we could not reject the null hypothesis that the power is one, that is, that the relation is in fact linear. The power fit by the all-species model from canopy area was 0.4607 ± 0.0572 , which was substantially less than one, and in fact suggested a square root relation. However, this was mostly fit to the many small trees, and when extrapolated to the relatively few trees with a canopy area greater than 10 m^2 , the power model fitted much worse than a linear relation, and a scatterplot showed no suggestion of a square root relation in this range. There was a great spread and in fact seemed to be no relation between sapwood area and canopy area for medium-sized and large trees; this is clear from Figure 7b. Thus, it is concluded that for all-species, a linear allometric equation, rather than a power model, is justified in Kalahari.

The reliably defined, per-species allometric equations, covering a large spectrum of tree sizes of a given species, are valid for tree transpiration assessment in the environment, in which they were derived, in this study for the Kalahari. The main environmental factors that restrict extrapolation of derived equations to other locations are as follows: (a) different soil conditions, in particular water-holding capacity in the rooting zone; (b) different water table depths; and (c) different climatic (mainly solar) conditions. Considering soil characteristic, as confirmed by more than two hundreds of soil samples (Obakeng, 2007), the Kalahari sandy soil represents highly homogeneous region of the world. The groundwater table in Kalahari, is generally deep $>60 \text{ m}$, which forces trees' adaptation to such conditions. In this regard, Obakeng (2007) proved that different Kalahari tree species investigated in this study area have roots exceeding 20–30 m but some of them, including *B. albitrunca*, even could tap water table at more than 60 m depth. Considering this, and also field evidence, for example, tree blossom at the end of dry season before first rains (Chavarro Rincon, 2009) and hydrological monitoring results (Obakeng, 2007), it can be safely assumed that Kalahari trees are negligibly dependent on shallow moisture availability, having access to deep water resources, that is, deep soil moisture and/or groundwater. Spatial differences in solar energy have also a large effect on plant behavior, which is reflected by differences in plant phenology; if these differences were distinct within Kalahari

region, they probably could affect sapwood distribution (and J_p pattern), particularly when comparing distant areas. However, the Kalahari region is known for its uniform climatic conditions. For example, the solar radiation climate map of Africa (Diabate, Blanc, & Wald, 2004) classifies the whole Kalahari region as one, uniform, solar zone (class XVI). Based on the above arguments, that is, relative uniformity of soil, water table depth, and climate, it can be hypothesized that developed allometric equations (Table 1), are applicable for the whole Kalahari region, although this statement requires further verification and evaluation of its uncertainty.

5 | CONCLUSIONS

1. To our knowledge, none of the presented $A_x = m'A_s$ and $A_x = n'A_c$ allometric equations, for any of the nine Kalahari tree species investigated in this study, has ever been presented in scientific literature.
2. This study sacrificed 195 trees for the benefit of science, that is, for development of Kalahari allometric equations, which allow estimation of A_x from A_s or A_c , without tree cutting.
3. The applied cut and dye method of staining cut tree trunks combined with visual analysis was well able to determine conductive sapwood areas of stained trees.
4. The population of approximately 20 trees per species provided a data set large enough for developing reliable $A_x = m'A_s$ and $A_x = n'A_c$ allometric equations.
5. The CT method was not diagnostic with regard to conductive sapwood area but was helpful supplying supplementary information, mainly on tissue density differences, which, however in general, were not correlated with stain transport, so likely also not with sap transport.
6. The nine analyzed Kalahari tree species, exhibited different sapwood patterns, which were categorized into four categories, C1–C4.
7. Tree species of category C1 (*A. erioloba*, *T. sericea*, and *B. africana*) could be well detected by visual analysis; their conductive sapwood area differed by color from heartwood, which was confirmed by staining experiment; also in trees of category C4 (*L. nelsii* and *B. albitrunca*), the visual analysis matched the staining results as the whole sapwood was conductive.
8. The trees of category C2 (*D. cinerea* and *O. pulchra*) and C3 (*Acacia fleckii* and *A. luederitzii*) are characterized by abrupt radial heterogeneity of the sapwood area not detectable by visual analysis. In the C2 trees, the external annulus is conductive and internal not, whereas in the C3, both annuli are conductive although the external show larger stain intensity suggesting larger sap transport.
9. For spatial upscaling, in relatively small areas (e.g., plots) where A_s of every tree can be estimated, the $A_x = m'A_s$ allometric equations are recommended considering their superior accuracy; however, in large areas (e.g., catchments) where A_s estimate of every tree is not feasible, $A_x = n'A_c$ allometric equations should be used.

10. The application of the $Ax = nAc$ allometric equations, in combination with RS identification of canopies at high-resolution images and with species-specific sap flux density measurements, has great promise in hydrology for automated tree transpiration mapping at the catchment scale, also because, the error in statistical $Ax = nAc$ prediction is small as compared to errors of other water balance estimates.
11. Considering large uniformity of soil, climate, and deep water table in Kalahari, we hypothesize that for the nine species investigated, the allometric equations developed in this study are valid for whole Kalahari region, although further research on that hypothesis is needed to strengthen its credibility.

ACKNOWLEDGEMENTS

This study was partly funded by the Netherlands Organization for Scientific Research through a WOTRO grant. The authors want to thank the Medical Spectrum Twente in Enschede, for conducting CT examinations, and the Botswana Geological Survey for arranging the logistics during the field campaign. Many thanks to Jean Roy for his invaluable contribution to the field experiments and two anonymous reviewers who provided constructive and valuable comments.

REFERENCES

- Adelabu, S., & Dube, T. (2015). Employing ground and satellite-based QuickBird data and random forest to discriminate five tree species in a Southern African Woodland. *Geocarto International*, 30(4), 457–471.
- Bieker, D., Rust, S., (2010). Non-destructive estimation of sapwood and heartwood width in scots pine (*Pinus sylvestris* L.), 44.
- Čermák, J., Kučera, J., & Nadezhdina, N. (2004). Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands. *Trees*, 18, 529–546.
- Chavarro Rincon, D. C. (2009). *Tree transpiration mapping from upscaled sap flow in the Botswana Kalahari*, ITC (pp. 141). Enschede: University of Twente.
- Cienciala, E., Kucera, J., & Malmer, A. (2000). Tree sap flow and stand transpiration of two *Acacia mangium* plantations in Sabah, Borneo. *Journal of Hydrology*, 236, 109–120.
- De Vries, J., Selaolo, E., & Beekman, H. (2000). Groundwater recharge in the Kalahari, with reference to paleo-hydrologic conditions. *Journal of Hydrology*, 238(1–2), 110–123.
- Delzon, S., Sartore, M., Granier, A., & Loustau, D. (2004). Radial profiles of sap flow with increasing tree size in maritime pine. *Tree Physiology*, 24(11), 1285–1293.
- Diabate, L., Blanc, P., & Wald, L. (2004). Solar radiation climate in Africa. *Solar Energy, Elsevier*, 76, 733–744. HAL-00361362. <https://hal.archives-ouvertes.fr/hal-00361362/document>
- Dye, P. J., Soko, S., & Poulter, A. G. (1996). Evaluation of the heat pulse velocity method for measuring sap flow in *Pinus patula*. *Journal of Experimental Botany*, 47(7), 975–981.
- Ferreira, M. P., Zortea, M., Zanotta, D. C., Shimabukuro, Y. E., & de Souza, C. R. (2016). Mapping tree species in tropical seasonal semi-deciduous forests with hyperspectral and multispectral data. *Remote Sensing of Environment*, 179, 66–78.
- Fromm, J. H., Sautter, I., Matthies, D., Kremer, J., Schumacher, P., & Ganter, C. (2001). Xylem water content and wood density in spruce and oak trees detected by high-resolution computed tomography. *Plant Physiology*, 127, 416–425.
- Gebauer, T., Horna, V., & Leuschner, C. (2008). Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species. *Tree Physiology*, 28(12), 1821–1830.
- Ghimire, C. P., Lubczynski, M. W., Bruijnzeel, L. A., & Chavarro-Rincón, D. (2014). Transpiration and canopy conductance of two contrasting forest types in the lesser Himalaya of Central Nepal. *Agricultural and Forest Meteorology*, 197, 76–90.
- Granier, A., Anfodillo, T., Sabatti, M., Cochard, H., Dreyer, E., Tomasi, M., ... Bréda, N. (1994). Axial and radial water flow in the trunks of oak trees: A quantitative and qualitative analysis. *Tree Physiology*, 14, 1383–1396.
- Hultine, K., Williams, D., Burgess, S., & Keefer, T. (2003). Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia*, 135, 167–175.
- Ihaka, R., & Gentleman, R. (1996). R: A language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, 5(3), 299–314.
- Jaskierniak, D., Kuczera, G., Benyon, R. G., & Lucieer, A. (2016). Estimating tree and stand sapwood area in spatially heterogeneous southeastern Australian forests. *Journal of Plant Ecology*, 9(3), 272–284.
- Jones, M., Aptaker, P. S., Cox, J., Gardiner, B. A., & McDonald, P. J. (2012). A transportable magnetic resonance imaging system for in situ measurements of living trees: The tree hugger. *Journal of Magnetic Resonance*, 218, 133–140.
- Kimani, J., Hussin, Y., Lubczynski, M., Chavarro-Rincon, D., & Obakeng, O. T. (2007). Mapping savannah trees in Kalahari using high resolution remote sensing images and object-oriented classification. *International Journal of Geoinformatics*, 3(2), 29–39.
- Kumagai, T., Anfodillo, T., Sabatti, M., Cochard, H., Dreyer, E., Omasi, M., ... Bréda, N. (2005). Sources of error in estimating stand transpiration using allometric relationships between stem diameter and sapwood area for *Cryptomeria japonica* and *Chamaecyparis obtusa*. *Forest Ecology and Management*, 206, 191–195.
- Kumagai, T., Aoki, S., Shimizu, T., & Otsuki, K. (2007). Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiology*, 27(2), 161–168.
- Leckie, D. G., Walsworth, N., & Gougeon, F. A. (2016). Identifying tree crown delineation shapes and need for remediation on high resolution imagery using an evidence based approach. *ISPRS Journal of Photogrammetry and Remote Sensing*, 114, 206–227.
- Lorant, M. M., Mackay, D. S., Ewers, B. E., Adelman, J. D., & Kruger, E. L. (2008). Environmental drivers of spatial variation in whole-tree transpiration in an aspen-dominated upland-to-wetland forest gradient. *Water Resources Research*, 44(2), W02441.
- Lu, P., & Chacko, E. K. (1998). Evaluation of Granier's sap flow meter in mango (*Mangifera indica* L.) trees. *Agronomie*, 18, 461–471.
- Lu, P., Urban, L., & Zhao, P. (2004). Granier's thermal dissipation probe (TDP) method for measuring sap flow in trees: Theory and practice. *Acta Botanica Sinica*, 46(6), 631–646.
- Lubczynski, M. W. (2009). The hydrogeological role of trees in water-limited environments. *Hydrogeology Journal*, 17, 247–259.
- Mapanda, W. (2003). *Scaling - up tree transpiration of eastern Kalahari sandveld of Botswana using remote sensing and geographical information systems* (pp. 117). Enschede: ITC.
- Meinzer, F. C., Bond, B. J., Warren, J. M., & Woodruff, D. R. (2005). Does water transport scale universally with tree size? *Functional Ecology*, 19(4), 558–565.
- Meyer, T., D'Odorico, P., Okin, G. S., Shugart, H. H., Caylor, K. K., O'Donnell, F. C., ... Dintwe, K. (2014). An analysis of structure: Biomass structure relationships for characteristic species of the western Kalahari, Botswana. *African Journal of Ecology*, 52(1), 20–29.
- Nadezhdina, N., Čermák, J., & Ceulemans, R. (2002). Radial patterns of sap flow in woody stems of dominant and understory species: Scaling errors associated with positioning of sensors. *Tree Physiology*, 22, 907–918.

- Nadezhkina, N., Vandegehuchte, M. W., & Steppe, K. (2012). Sap flux density measurements based on heat field deformation method. *Trees*, 26, 1439–1448.
- Obakeng, O.T., (2007). Soil moisture dynamics and evapotranspiration at the fringe of the Botswana Kalahari. PhD Thesis, Vrije Universiteit, Amsterdam, NL.
- Parolin, P., Müller, E., & Junk, W. J. (2008). Sapwood area in seven common tree species of Central Amazon floodplains. *Pesquisas, Botânica*, 59, 277–286.
- Pfautsch, S., & Macfarlane, C. (2016). Comment on Wang et al. 'quantifying sapwood width for three Australian native species using electrical resistivity tomography'. *Ecohydrology*, 9(5), 894–895.
- Pfautsch, S., Macfarlane, C., Ebdon, N., & Meder, R. (2012). Assessing sapwood depth and wood properties in eucalyptus and *Corymbia* spp. using visual methods and near infrared spectroscopy (NIR). *Trees*, 26(3), 963–974.
- Pham, L. T. H., Brabyn, L., & Ashraf, S. (2016). Combining QuickBird, LiDAR, and GIS topography indices to identify a single native tree species in a complex landscape using an object-based classification approach. *International Journal of Applied Earth Observation and Geoinformation*, 50, 187–197.
- Phillips, N., Oren, R., & Zimmermann, R. (1996). Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell & Environment*, 19(8), 983–990.
- Picard, N., Saint-Andre, L., Henry, M., (2012). Manual for building tree volume and biomass allometric equations. www.fao.org/docrep/018/i3058e/i3058e.pdf. CIRAD et FAO, 2012.
- Reyes-Acosta, L. J., & Lubczynski, M. W. (2013). Mapping dry-season tree transpiration of an oak woodland at the catchment scale, using object-attributes derived from satellite imagery and sap flow measurements. *Agricultural and Forest Meteorology*, 174–175, 184–201.
- Reyes-Acosta, J. L., & Lubczynski, M. W. (2014). Optimization of dry-season sap flow measurements in an oak semi-arid open woodland in Spain. *Ecohydrology*, 7(2), 258–277.
- Roberts, S., Vertessy, R., & Grayson, R. (2001). Transpiration from *Eucalyptus sieberi* (L. Johnson) forests of different age. *Forest Ecology and Management*, 143(1–3), 153–161.
- Rust, S. (1999). Comparison of three methods for determining the conductive xylem area of scots pine (*Pinus sylvestris*). *Forestry*, 72(2), 103–108.
- Smith, D. M., & Allen, S. J. (1996). Measurement of sap flow in plant stems. *Journal of Experimental Botany*, 47(305), 1833–1844.
- Steppe, K., Cnudde, V., Girard, C., Lemeur, R., Cnudde, J. P., & Jacobs, P. (2004). Use of X-ray computed microtomography for non-invasive determination of wood anatomical characteristics. *Journal of Structural Biology*, 148(1), 11–21.
- Steppe, K., De Pauw, D. J. W., Doody, T. M., & Teskey, R. O. (2010). A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agricultural and Forest Meteorology*, 150(7–8), 1046–1056.
- van Wyk, B., & van Wyk, P. (2013). *Field guide to trees of Southern Africa*. Published by Struik Nature, Cape Town. ISBN9781770079113.
- Vertessy, R. A., Benyon, R. G., O'Sullivan, S. K., & Gribben, P. R. (1995). Relationships between stem diameter, sapwood area, leaf area and transpiration in a young mountain ash forest. *Tree Physiology*, 15(9), 559–567.
- Vertessy, R. A., Hatton, T. J., Reece, P., O'Sullivan, S. K., & Benyon, R. G. (1997). Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology*, 17(12), 747–756.
- Wang, H., Guan, H., Guyot, A., Simmons, C. T., & Lockington, D. A. (2016). Quantifying sapwood width for three Australian native species using electrical resistivity tomography. *Ecohydrology*, 9(1), 83–92.
- Wilson, K. B., Hanson, P. J., Mulholland, P. J., Baldocchi, D. D., & Wullschlegel, S. D. (2001). A comparison of methods for determining forest evapotranspiration and its components: Sap-flow, soil water budget, eddy covariance and catchment water in poplar, castor bean, tomato and tobacco. Plant cell and balance. *Agricultural and Forest Meteorology*, 106(2), 153–168.
- Windt, C. W. (2007). Nuclear magnetic resonance imaging of sap flow in plants. PhD Thesis, Wageningen University. www.wageningenur.nl/en/show/Nuclear-Magnetic-Resonance-imaging-of-sap-flow-in-plants.htm
- Windt, C. W., & Blümle, P. (2015). A portable NMR sensor to measure dynamic changes in the amount of water in living stems or fruit and its potential to measure sap flow. *Tree Physiology*, 35(4), 366–375.
- Wullschlegel, S. D., Hanson, P. J., & Todd, D. E. (2001). Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. *Forest Ecology and Management*, 143(1–3), 205–213.
- Wullschlegel, S. D., & King, A. W. (2000). Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiology*, 20, 511–518.
- Wullschlegel, S. D., Meinzer, F. C., & Vertessy, R. A. (1998). A review of whole-plant water use studies in tree. *Tree Physiology*, 18(8–9), 499–512.

How to cite this article: Lubczynski MW, Chavarro-Rincon DC, Rossiter DG. Conductive sapwood area prediction from stem and canopy areas—allometric equations of Kalahari trees, Botswana. *Ecohydrology*. 2017;10:e1856. <https://doi.org/10.1002/eco.1856>