ALLOMETRIC RELATIONSHIPS BETWEEN SAPWOOD AREA AND SHRUB DIMENSIONS FOR 6 COMMON SOUTHERN AFRICAN SAVANNA BUSH ENCROACHER SPECIES: UNIVERSAL OR SPECIES-SPECIFIC?

Roi Hendler[1], Tim Herkenrath[1], Rosemary Shikangalah[2], Niels Blaum[1], and Katja Geissler[1]

[1]Universitat Potsdam Arbeitsgruppe Vegetationsokologie und Naturschutz
[2]Namibia University of Science and Technology

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Abstract

Southern African savanna rangelands are facing a widespread degradation pattern called bush encroachment. This is associated with implications for various aspects of the water cycle and in particular canopy transpiration. At the individual-tree scale, it is estimated by scaling sap-flux density by sapwood area. However, the direct measurement of sapwood area is impracticable at landscape scale and general allometric equations of the West-Brown-Enquist (WBE) model relating sapwood area to primary size measures seem to fail for some species and climates. Therefore, we conducted intensive field measurements to establish species-specific allometric relationships between sapwood area and sizes (stem diameter, crown area) in six dominant shrub species involved in bush encroachment in Namibia (*Colophospermum mopane, Senegalia mellifera, Vachellia reficiens, Dichrostachys cinerea, Vachellia nebrownii, Catophractes alexandri*). We found strong allometric relationships between sapwood area and stem diameter as well as between sapwood area and crown area for all six species. These relations are largely in line with the WBE theory but still provide estimates that are more accurate. Only in *D. cinerea*, the sapwood area was significantly smaller than predicted by the WBE theory, which might be caused by a larger need for stabilizing heartwood. Our results are useful to estimate water loss via transpiration at a large scale using remote sensing techniques and can promote our understanding of the ecohydrological conditions that drive species specific bush encroachment in savannas. This is particularly important in the light of climate change, which is considered to have major implications on ecohydrological processes in savannas.

Roi Hendler1,2*, Tim Herkenrath 1, Rosemary Shikangalah 3, Niels Blaum 1, Katja Geissler 1,4

1) University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany

2) Anhalt university of Applied Sciences, Strenzfelder Allee 28, 06406 Bernburg (Saale), Germany

3) Namibia University of Science and Technology, Faculty of Engineering, Department of Mining and Process Engineering, Private Bag 13388, Windhoek

4) University of Potsdam, Biodiversity Research / Systematic Botany, Maulbeerallee 1, 14469 Potsdam, Germany

* Corresponding author: Katja Geissler: kgeissle@uni-potsdam.de,telephone: +493319771974, fax: +493319771930

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ABSTRACT

Southern African savanna rangelands are facing a widespread degradation pattern called bush encroachment. This is associated with implications for various aspects of the water cycle and in particular canopy transpiration. At the individual-tree scale, it is estimated by scaling sap-flux density by sapwood area. However, the direct measurement of sapwood area is impracticable at landscape scale and general allometric equations of the West-Brown-Enquist (WBE) model relating sapwood area to primary size measures seem to fail for some species and climates. Therefore, we conducted intensive field measurements to establish species-specific allometric relationships between sapwood area and sizes (stem diameter, crown area) in six dominant shrub species involved in bush encroachment in Namibia (*Colophospermum mopane, Senegalia mellifera, Vachellia reficiens, Dichrostachys cinerea, Vachellia nebrownii, Catophractes alexandri*). We found strong allometric relationships between sapwood area and stem diameter as well as between sapwood area and crown area for all six species. These relations are largely in line with the WBE theory but still provide estimates that are more accurate. Only in *D. cinerea* , the sapwood area was significantly smaller than predicted by the WBE theory, which might be caused by a larger need for stabilizing heartwood. Our results are useful to estimate water loss via transpiration at a large scale using remote sensing techniques and can promote our understanding of the ecohydrological conditions that drive species specific bush encroachment in savannas. This is particularly important in the light of climate change, which is considered to have major implications on ecohydrological processes in savannas.

INTRODUCTION

Bush encroachment is a prominent form of rangeland degradation in arid and semiarid regions worldwide (Stevens et al. 2016). In sub-Sahara Africa, where rangelands cover over two thirds of the land area, it leads to various problems, which are often linked through ecohydrological feedback loops (Trimble & van Aarde, 2014). Problems include faunal and floral biodiversity loss (Blaum et al., 2007, 2009; Chown, 2010; Dreber et al., 2018; Hering et al., 2019), decreased carrying capacities of rangelands (Angassa 2005; reviewed in Ayalew & Mulualem, 2018; De Klerk, 2004), lowered infiltration rates and related soil moisture depletion, and presumably changed evapotranspiration patterns (Chartier et al., 2011; Huxman et al., 2005; Geissler et al., 2019; Groengroeft et al., 2018; Wilcox et al., 2022). High temperatures and solar radiation make evapotranspiration the major form of water loss, which accounts for water loss amounting to over 90% of the annual precipitation (Haan et al., 1994). It includes water evaporating from the soil and from the plant foliage after being intercepted as well as water transpired by plants following soil water uptake. Thus, even relatively small changes of vegetation composition and structure could have important consequences, not only for soil moisture budgets but also for groundwater recharge, land-atmosphere energy exchange, local climate, and primary production including carbon accumulation (Huxman et al., 2005; Lubczynski, 2009). Hence, estimating evapotranspirative water loss is critical for managing the environmental effects of bush encroachment. A common constraint is, however, the difficulty in obtaining evapotranspiration estimates and its partitioning across widespread and sometimes inaccessible savannas. This difficulty is often closely associated with species-specific traits of water use of the woody species, which are involved in a particular bush encroachment process (Lubczynski et al., 2017).

It has become increasingly apparent that the estimation of evapotranspiration depends on sufficient understanding and accurate modelling, including validation, of the two main processes underlying evapotranspiration, namely transpiration and evaporation. While estimating evaporation is relatively straightforward, determining the rate of vegetation water use is far more complex (Sun et al., 2019). Transpiration is influenced by many factors including species-specific rooting depth, conductive sapwood area and canopy structure (Sohel, 2022).

A common method to estimate transpiration of woody vegetation relies on measurements of sap-flux density (SFD) across the active fluid-transporting tissue (the xylem), also known as sapwood. Multiplication of SFD with sapwood area provides the total water-use of an individual tree, while the multiplication with total sapwood area of all woody plants per ground area gives provides an estimate measure of woody stand transpiration at landscape scale. In general, the per-species SFD variability among trees of different size and age is relatively low (Jaskierniak, et al., 2016; Kumagai et al., 2007; Reyes-Acosta & Lubczynski, 2014). Therefore, tree water use depends mainly on the conductive sapwood area. A reliable estimate of sapwood area, therefore, is a key component in quantifying transpiration of the woody vegetation components in bush encroached savannas.

However, measuring sapwood area is time consuming, often destructive and impractical, both at the small scale of a plot or stand and at landscape level. This is particularly true for shrub stands occurring in semiarid savannas, which often comprise of multi-stemmed species. While some variability of sapwood patterns among species exists (Carrodus, 1972), fortunately, sapwood area scales reliably with various plant dimensions, such as leaf area, stem diameter and crown dimensions, which are easier to assess (Lubczynski et al., 2017; Mitra 2020; West et al., 1999). Particularly crown properties can later be detected and quantified at landscape scale using aerial imagery, light detection and ranging (LiDAR). Although previous attempts to establish allometric relationships between sapwood area and crown dimensions, such as crown area or crown diameter, have found that they can in fact be strong (Fregoso, 2002; Mitra et al., 2020), stem diameter achieves still the most accurate values of sapwood area. A convenient model for explaining characteristic allometric relations of different species between specific size measures, such as stem diameter, and traits, such as sapwood area, is the West-Brown-Enquist-model of West et al. (1999, hereafter WBE). It predicts that sapwood area scales with stem diameter with a third power law of 7/3 (2.33). Reasons for the constant scaling are geometric and hydrodynamic constraints that limit the size in living organisms (West et al., 1997). Despite many findings supporting the WBE model's predictions, empirical results showed that variations from the predicted scaling value do occur (Daba & Soromessa, 2019; Schoppach et al., 2021). Therefore, establishing species-specific relationships between sapwood area and stem diameter may be essential to accurately estimating transpiration rates (Ter-Mikaelian & Korzukhin, 1997; Yaemphum et al., 2022). This may be particularly important in savanna shrubs, which may increase sapwood area relative to the total wood area, avoiding cavitation-embolism under drought (Brodersen & McElrone, 2013).

Allometric equations for estimating sapwood area and eventually whole-tree and stand transpiration using tree size parameters have been developed for various woody ecosystems, such as tropical and temperate forests (Yaemphum et al., 2022; Wang et al., 2010), but only a few exist for arid and semiarid bush encroached savannas. Studies for Southern Africa are particularly rare (Lubczynski et al., 2017).

The primary goal of this study was therefore to test whether allometric relations between sapwood area and stem diameter or crown area exist for six dominant bush encroacher species of Namibia. Relying on extensive field measurements, we derived species-specific equations, which can later be used in combination with sap flux monitoring to estimate canopy transpiration for different bush encroachment scenarios at plot and landscape scale, with the latter based on remote sensing of crown area. Second, we tested whether the allometric relations between sapwood area and stem diameter agree with scaling predictions from the WBE model. We predicted that deviations from the model are attributed to drought induced species-specific changes of relative investments in the area of sapwood.

METHODS

2.1 STUDY AREA

The study took place in the Etosha Heights Private Reserve (EHPR) (19.2451 degS, 15.1921 degE), located in the Kunene region in northern Namibia, approximately 400 km north of the city of Windhoek. EHPR spreads over 480 km^2 and shares an approximately 65 km long border with the Etosha National Park. The research site is part of a large-scale wildlife area.

The climate in the region is semi-arid (Peel et al., 2007). It is characterized by high air and soil temperatures

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with mean annual temperatures above 22degC and high solar radiation. Annual rainfall amounts to 300 - 350 mm and precipitation is highly variable in time and space. Annual evaporation rate ranges 2,500 - 2,600 mm, and thus an order of magnitude higher than the average levels of rainfall received (Atlas of Namibia Team, 2022). Temperatures and precipitation are changing seasonally, with the highest average precipitation during the wet season (November - March) and lowest average precipitation during the dry season (April - October). The soil is rich in carbonate and consists of limestone and dolomite rocks as well as sand and calcrete (Nortje, 2019). The vegetation type in the area is a tree-and-shrub savanna with varying density, from large open grasslands with scattered trees up to dense, shrub-dominated landscapes (Atlas of Namibia Team, 2022). The most dominant shrub species in the region is *Colophospermum mopane* , which occurs in high abundance throughout the reserve (Bester, 1996). Other prominent species in the area include *Senegalia mellifera, Dichrostachys cinerea, Vachellia nebrownii, Catophractes alexandri* and *Vachellia reficiens* . The fauna within EHPR is rich and includes large populations of species from various taxonomic classes, including large mammalian grazers (Antelopes, Giraffes), browsers (Elephants, Rhinos), and predators (Lions, Leopards).

2.2 SHRUB SAMPLING AND MEASUREMENTS

We sampled all prominent shrub species, in total six species, in an area of approximately 164 km^2 in central-east EHPR during March and April 2021. Sampling was assigned to 60 blocks, with a minimal distance between blocks of 500 m to control for local effects and to avoid spatial autocorrelation. Measured individuals and stems reflect the full range of sizes for each species occurring within EHPR. To avoid biases in shrub dimensions due to browsing, we sampled only individuals with minimal apparent damage, such as recently broken branches or a large portion of missing foliage caused by e.g., rhinos or elephants.

To establish allometric relationships between canopy area and sapwood area via stem diameter, we measured canopy area (CA) and stem diameter (D_{Stem}) for one individual of each of the six species (360 individuals in total, 60 per species) in each block. CA estimates relied on the average crown spread method (ACS) (Blozan, 2004), using measuring poles with a 1 cm scale. As stems are not necessarily round, D_{Stem} was measured by averaging two perpendicular diameters using a vernier scale with an accuracy level of 1 mm. In the case of a multi-stemmed individual, we measured all stems. Although D_{Stem} is commonly measured at breast height (i.e., 130 cm above ground level), the morphology of most shrub species included in this study did not allow for this measure, as shrubs are often either smaller or far too branched at this height. Since species differ in size and morphology, we selected appropriate heights for each species as follows: 20 cm (*Catophractes alexandri, Vachellia nebrownii*), 50 cm (*Dichrostachys cinerea, Senegalia mellifera, Vachellia reficiens*), 130 cm (*Colophospermum mopane*). The validity and comparability of stem diameter measurements at different heights rely on the foundations of Leonardo da Vinci's area-preserving rule, which states that the total cross-section area across all stems in an individual plant remains constant along the height axis (Richter 1970). This area-preserving rule has been repeatedly supported by different studies and methods (Minamino & Tateno. 2014; Oppelt, 2001).

To study the relationship between stem diameter and sapwood area, we randomly selected between 20 and 23 individuals per species (visiting 25 blocks: 0-1 individual per block per species, 130 individuals in total). We removed one branch per individual using branch shears or a handsaw. To ensure that our data set for developing the allometries contained samples from the complete spectrum of D_{stem} values, we sampled a large range of branch sizes (3.9 mm – 111.4 mm). Measurements of stem diameter and sapwood area were achieved via staining of stem cross sections. Immediately after cutting, the ends were shaved with fresh razor blades, thus reducing the possibility that damage to the xylem during harvest would affect our results. The sample was immediately inserted into a tube containing a staining solution of methylene blue 0.5% (w/v) and distilled water with a concentration ratio of 1:20. The amount of diluted solution varied according to the diameter of the sample and the tubes used for staining, between 10 ml for very small samples (twigs) and 200 ml (large branches). Tubes were sealed to prevent evaporation and samples remained in the solution for at least 24 hours to allow uptake of the dye into the stem via active transpiration by the remaining foliage. After removing and drying the samples in the air, cross-sections were made approximately 1 cm above the

bottom of each sample using branch shears or an electric hand saw. The cross-sections were placed on a clear background adjacent to a ruler with 1 mm marks for consistent scaling. Images were taken using a digital Canon SX540 HS camera placed on a tripod. Visual analysis was done using ImageJ (Fiji is Just) version 2.1.0/1.53c (Abramoff, 2004; Schindelin et al., 2012). Representative examples for staining samples for each species are illustrated in Fig 1. In every sample, the borders of the following three areas were marked manually and the resulting areas measured digitally with an accuracy of 1 mm^2: A) total area (the entire area of the cross-section including bark), B) wood area, and C) heartwood area (Fig. 2). The outer limits of the heartwood were defined as the first innermost tree ring of the cross-section not containing traces of blue staining (Fig. 2). While our staining approach dyed the active part of the sapwood only, this procedure enabled us to identify the entire sapwood area that has been formed. Sapwood area was mathematically obtained by subtracting the heartwood area from the wood area. Stem diameter (D_{stem}) was derived based on total area (A_{tot}), assuming circularity of the cross-section.

2.3 DATA ANALYSIS

Species-specific allometric relationships were modeled using the power law equation (Niklas, 1994)

$Y \; = \; b \bullet X^a$, (1)

where X is the size measure (D_{stem} or CA), b a normalization constant, a the scaling exponent, and Y the estimated sapwood area (SA or SA_{tot}). We considered the total sapwood area (SA_{tot}) of each study shrub for the allometry between canopy area (CA) and SA. To obtain SA_{tot} we measured the D_{stem} of all stems, applied the corresponding species-specific allometric relationship between D_{stem} to SA to each stem, and summed up the estimates. To identify the scaling exponent and to enable a comparison with the WBE prediction, we applied log-transformation and fitted a linear model, as

$\ln(Y) = \; a \bullet ln \; (X) + ln(b)$. (2)

Models were assessed using both, R^2 and the regression coefficient a (the scaling exponent) and its significance ($P < 0.05$ of F-value). Additionally, 95% confidence intervals of the scaling exponent were calculated and plotted for each species-specific model.

The equations were back-transformed into their 'natural' exponential form to simplify the application of the allometric relationships. To prevent underestimation bias of the logarithmic regression estimate (Niklas, 1994), a back-correction factor CF was introduced based on Sprugel (1983), as

$CF \; = exp(\frac{SEE^2}{2})$ (3)

where SEE is the standard error of the scaling exponent estimate a.

The final equation for the prediction of sapwood area from the respective size measure will then have the following form:

$\ln(Y) = CF \bullet (\; \ln(b) + \; a \bullet ln \; (X)) \Rightarrow Y = b^{CF} \bullet X^{a \bullet CF}$, (4)

To identify species-specific structural characteristics of sapwood formation due to drought and their relation to plant age, we also calculated the relative sapwood area ($\frac{SA}{wood\ area}$) and fitted an additional linear model for the relationship between relative sapwood area and D_{stem} for each species.

Data processing, data visualization and statistical analysis were performed with R version 4.0.5 (2021-03-21) and R-Studio version 1.1.423 (R Core Team, 2019). Used packages included 'car' (Fox & Weisberg, 2019), 'dplyr' (Wickham et al., 2023a), 'FSA' (Ogle et al., 2023) 'ggplot2' (Wickham, 2016), 'ggpubr' (Kassambara, 2020), and 'tidyr' (Wickham, 2023b).

RESULTS

In total, we stained and measured 130 individual plants for sapwood area and stem diameter, and measured canopy area and total stem diameter of 360 individuals of six savanna bush encroacher species. A detailed summary of the measurements is found in Appendix Table A1.

In all six species, sapwood area was positively correlated with stem diameter. D_{stem} accounted for almost the entire variation in *C. alexandri* (99%), *C. mopane* (98%), *S. mellifera* (97%), *V. reficiens* (97%), *V. nebrownii* (97%) and *D. cinerea* (78%) (Fig. 3, Table 1). The very high values of R^2 for all species established D_{stem} as a strong independent variable to estimate sapwood area. Apart from *D. cinerea* , all species included the regression line predicted by the WBE model within the 95% confidence interval of the slope.

The relative sapwood area to D_{stem} relationship varied substantially between species (Fig. 4). While this ratio was constant in *C. mopane, S. mellifera* , and *V. reficiens* , a significant positive relationship was found in *C. alexandri* , *V. nebrownii* and a significant negative one in *D. cinerea* . On average, *D. cinerea* invested clearly the least of all species in water conducting sapwood compared to heartwood.

Moreover, sapwood area was positively correlated with canopy area. CA accounted for most of the variation of SA_{tot} in *C. alexandri* (82%), *C. mopane* (84%), *S. mellifera* (80%), *V. reficiens* (86%), *V. nebrownii* (81%) and a bit less again in *D. cinerea* (71%) (Fig. 5, Table 2). Although R^2 values were high for all species, they were lower than for the correlation between D_{stem} and SA (Fig. 3, Table 1).

DISCUSSION

Sapwood area is a key component in quantifying canopy transpiration and allometric equations for estimating sapwood area using tree size parameters have been developed for various woody ecosystems. And yet, in the case of Southern African savannas, only few exist (Lubczynski et al., 2017), although various allometric relationships have been extensively studied in recent years (Fregoso, 2002; Issoufou et al., 2015; Moncrieff et al., 2011; Tredennick et al., 2013). Scaling exponents of these size-correlated trends often rely on the universal value predicted by the West-Brown-Enquist model (West et al., 1999; Niklas, 1994). Nevertheless, the model itself is a point of dispute (Brown et. at., 2005; Kozlowski & Konarzewski, 2004) because it does not incorporate features specific for different plant taxa or for different environments. As sapwood formation is likely governed by low water availability, establishing species-specific relationships between sapwood area and tree dimension for Southern African savanna woody species may be essential to accurately estimating transpiration rates (Ter-Mikaelian & Korzukhin, 1997; Yaemphum et al., 2022). In this study, we established allometric relationships between tree dimension and sapwood area in six shrub species involved in savanna bush encroachment in Namibia.

Our results illustrate that sapwood area can be reliably predicted based on stem diameter in all six species tested. Comparing our results with the prediction of the WBE model (West et al., 1999) showed that the model holds true in most cases.

Various findings illustrate that despite the unique conditions in savannas and other drylands, the scaling relationships between stem diameter and sapwood area in drought resistant plants are similar to those of plants found in other climates (Fregoso, 2002; Gebauer et al., 2009; Patino et al., 1995; Wang et al., 2010). However, the relationship between stem diameter and sapwood area in *D. cinerea* revealed an exponent substantially lower than the other five bush species tested. This is not exclusive for the Etosha region. In the eastern Kalahari in Botswana, *D.cinerea* revealed the smallest slope of nine species (Lubczynski et al., 2017), although authors fitted a linear function rather than a power function (in accordance to the WBE model) to the relation between sapwood area and stem diameter. Petit and Anfodillo (2009) illustrate an anatomical reason why actual sapwood area fails to scale with the stem diameter raised to 2.33 sometimes. What we usually consider as sapwood does not actually correspond to the conductive tissues in the WBE model. Conduits (vessels and tracheids) are always embedded in a matrix of wood fibers (stabilization function) and parenchyma (storage and embolism repair function). If the general assumptions of the WBE theory regarding geometric and hydrodynamic constrains (West et al., 1997) are valid, smaller allometric exponents as in *D. cinerea* arise if there is more genuine conductive tissue and less parenchyma and wood fibers on the same surface. More genuine conductive tissue can arise either with wider conduits or with more conduits in total. Such a sapwood composition at the expense of parenchyma is, however, more vulnerable to cavitation and -embolism (Brodersen & McElrone, 2013), even if the same conductivity across the stem

is reached compared to species exhibiting the allometric exponent of 2.33 of the WBE theory. Parenchyma cells in sapwood serve as large water storage reservoirs and are linked to osmotically driven embolism repair mechanism (Broderson & McElrone, 2013). The vulnerability to cavitation and embolism might be partly compensated by a decrease in conduit size. The higher wood density of *D. cinerea* compared to other savanna species (Fernandez-Ortuno et al., 2015) supports indeed a smaller conduit size. That these vessels are small, although probably high in number, finds also support since *D. cinerea* has a low sap flow velocity relative to other savanna shrub species (Zziwa 2003), and estimations of transpiration rates of vegetation plots in areas predominated by *D. cinerea* were lower than areas with similar shrub density predominated by other common shrubs (Chavarro-Rincon, 2009). Although the size and number of conducting vessels per stem area of *D. cinerea* is unknown, the allometric exponent and sap flow velocity taken together indicate that the species might be relying on this to compensate for a reduced sapwood area. Thus, *D. cinerea* seems to be less efficient in water uptake and might be more water dependent than the other bush encroacher species in our study. Indeed *D. cinerea* does almost not increase in biomass and is less abundant in areas with less soil moisture and higher temperature (de Klerk, 2004; Shikangalah et al., 2021). Its main distribution in Namibia as bush encroacher extends to savannas with MAP > 550mm (de Klerk, 2004). Questions remain regarding the underlying causes of its dominance in these moister areas as well as the functional driver of the unusual small allometric exponent. In any case, *D. cinerea* 's striking anatomy is supported by our results on low relative sapwood area and by previous results showing that *D. cinerea* has an unusual small sapwood to heartwood ratio than other woody savanna species (Shikangalah et al., 2021; Zziwa, 2003). A large heartwood area might relate to an adaptation mechanism, which increases the stem stability, because heartwood is generally stiffer than sapwood. A strong argument for this view is our observation that relative sapwood area decreased with age (stem diameter as a proxy of age or growth). However, if central heartwood was to increase flexural stiffness, the heartwood would need to have a inordinately lower elasticity than sapwood (Niklas, 1997), a trait which we do not know. Moreover, high wind velocities as a driver of stability traits are not typical for the main distribution areas of *D. cinerea* (Atlas of Namibia Team, 2022).

An adaptation in flexural stiffness or any other reason for relatively more heartwood was not detected in *C. mopane* , *S. mellifera* and *V. reficiens* . Furthermore, the small shrubs *V. nebrownii* and *C. alexandri* even decrease the relative amount of central heartwood with stem age, promoting a higher flexibility instead of stiffness, which might be affordable if the increase in overall woody biomass contributes to stability already. If sapwood area is correlated with storage capacity for water (Scholz et al., 2008), lower water availability could be a driver distinguishing their local occurrence. While definitive conclusions regarding *C. mopane* , *S. mellifera* and *V. reficiens* based on these findings are currently hard to make, our results could help understanding what conditions drive which shrub species during bush encroachment.

Based on the overall strong relationship between stem diameter and sapwood area, we were also able to establish strong relationships between crown area and sapwood area in all six species. This result is meaningful because it supplies further support for the potential of estimating sapwood area based on aerial imagery (Mitra et al., 2020). Whereas previous studies found a linear relationship between crown size and properties of water conductance (Ahongshangbam et al., 2020; Quinonez-Pinon & Valeo, 2019; Tziaferidis, 2021), the relationships detected in our study were slightly exponential, presumably due to the inclusion of smaller samples. Another reason for a divergent allometric relationship might be the time of sampling. We carried out data collection and measurements at the end of the rainy season. Deciduous phenology of savanna trees and shrubs has been shown to be strongly influenced by seasonality (Dahlin, 2016), meaning that the relationships between crown area and total sapwood area may vary seasonally. Continuous measurements of crown area and stem diameter as a base for total sapwood area are therefore necessary to adapt the relationship described above to different seasons and years.

In addition, since our measurements of plant dimensions were taken within a nature reserve, where browsing pressure by large African mammals such as Giraffes, Elephants, and Rhinos is present, a comparison of crown area across different land-use types with different browsing pressures might be required to understand to what degree crown area is affected by the presence of large browsers. Nevertheless, we believe that our allometric relations are sufficiently reliable and universal due to our selection of apparently unharmed

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individuals, as well as due to the sampling of shrubs from multiple plots covering a large area with many different local conditions.

CONCLUSIONS

The assessments of six main bush encroacher species of Namibia proposed here indicate that sapwood area can be reliably predicted based on stem diameter, crown dimensions and the universal WBE model. Our allometric equations offer the prospect of vastly increasing our knowledge about transpirational water losses in semiarid bush-encroached savannas. Robust species-specific models predicting individual shrub sapwood area from shrub size are, however, critical for accurate estimating of stand- and landscape-scale transpiration in shrub encroached regions, in particular when *D. cinerea* is involved. A subsequent extension of our research may apply these species-specific total sapwood area-crown area or sapwood area-stem diameter allometric equations to estimate woody transpiration for different bush encroachment scenarios in the studied region. Such analysis remains highly relevant for all Southern African savannas given the widespread shift in vegetation composition via bush encroachment by different species but also considering climate change, in particular as droughts are projected to become longer and more frequent (IPBES, 2018; IPCC, 2023).

References

Abramoff, M., Magalhaes, P. & Ram, S. J. (2003). Image Processing with ImageJ. Biophotonics International. 11. 36–42.

Ahongshangbam, J., Roll, A., Ellsasser, F., Hendrayanto, H., & Holscher, D. (2020). Airborne Tree Crown Detection for Predicting Spatial Heterogeneity of Canopy Transpiration in a Tropical Rainforest.*Remote Sens.* , 12, 651. https://doi.org/10.3390/rs12040651

Angassa, A. (2005). The ecological impact of bush encroachment on the yield of grasses in Borana rangeland ecosystem. *African Journal of Ecology,* 43, 14–20. https://doi.org/10.1111/j.1365-2028.2005.00429.x

Atlas of Namibia Team, 2022, Atlas of Namibia: its land, water and life, Namibia Nature Foundation, Windhoek

Ayalew, S., & Mulualem, G. M. (2018). A Review on Bush Encroachment Effect on Cattle Rearing in Rangelands. *J. Rangel. Sci.* , 8, 403–415.

Bester, FV. 1996. Bush encroachment — A thorny problem. In: Tarr, Peter W., ed. 1996. op. cit. pp. 175–177.

Blaum, N., Rossmanith, E., Popp, A. & Jeltsch, F. (2007). Shrub encroachment affects mammalian carnivore abundance in arid rangelands.*Acta Oecologica,* 31, 86–92. https://doi/10.1016/j.actao.2006.10.004

Blaum, N., Seymour, C., Rossmanith, E., Schwager, M., & Jeltsch, F. (2009). Changes in arthropod diversity along a land use driven gradient of shrub cover in the southern Kalahari: Identification of suitable indicators. *Biodivers Conserv* , 18, 1187–1199. https://doi.org/10.1007/s10531-008-9498-x

Blozan, W. (2004). Tree measuring guidelines of the eastern native tree society. History Research Science, 13-17.

Brodersen, C. R. & McElrone, A. J. (2013). Maintenance of xylem Network Transport Capacity: A Review of Embolism Repair in Vascular Plants. *Frontiers in Plant Science* , 4, 1–11.

Brown, J. H., West, G.B. & Enquist, B. J. (2005), Yes, West, Brown and Enquist"s model of allometric scaling is both mathematically correct and biologically relevant. *Functional Ecology* , 19, 735–738. https://doi.org/10.1111/j.1365-2435.2005.01022.x

Carrodus, B. B. (1972). Variability in the Proportion of Heartwood Formed in Woody Stems. *New Phytol.* , 71, 713–718. http://www.jstor.org/stable/2434722

Chartier, M. P., Rostagno, C. M., & Pazos, G. E. (2011). Effects of soil degradation on infiltration rates in grazed semiarid rangelands of northeastern Patagonia, Argentina. *Journal of Arid Environments* , 75, 656–661. doi: 10.1016/j.jaridenv.2011.02.007

Chavarro-Rincon, D. (2009). Tree transpiration mapping from upscaled sap flow in the Botswana Kalahari (Unpublished doctoral dissertation). International Institute for Geo-information Science and Earth Observation, Enschede.

Chown, S. L. (2010). Temporal biodiversity change in transformed landscapes: a southern African perspective. *Phil. Trans. R. Soc. B,* 365, 3729–3742. https://doi/10.1098/rstb.2010.0274 Add to Citavi project by DOI).

Daba, D. E., & Soromessa, T. (2019). The accuracy of species-specific allometric equations for estimating aboveground biomass in tropical moist montane forests: case study of *Albizia grandibracteata* and *Trichilia dregeana* . *Carbon Balance Manage* , 14, 18. https://doi.org/10.1186/s13021-019-0134-8

Dahlin, K. M., Del Ponte, D., Setlock, E., & Nagelkirk, R. (2016). Global patterns of drought deciduous phenology in semi-arid and savanna-type ecosystems. *Ecography* , 40, 314–323. https://doi.org/10.1111/ecog.02443

de Klerk, J. N. (2004). Bush Encroachment in Namibia. ISBN 0–86976–620–1

Dreber, N., van Rooyen, S.E., & Kellner, K. (2018). Relationship of plant diversity and bush cover in rangelands of a semi-arid Kalahari savannah, South Africa. Afr. J. Ecol., 56: 132–135. https://doi.org/10.1111/aje.12425

Fernandez-Ortuno, D., Grabke, A., Li, X., & Schnabel, G. (2015). Independent Emergence of Resistance to Seven Chemical Classes of Fungicides in Botrytis cinerea. Phytopathology, 105, 424–432. https://doi.org/10.1094/PHYTO-06-14-0161-R

Fox J, Weisberg S (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fregoso, A. D. (2002). Dry-season transpiration of savannah vegetation - Assessment of tree transpiration and its spatial distribution in Serowe, Botswana (Unpublished master's. thesis). The International Institute for Geo-Information Science and Earth Observation (ITC), University of Twente

Gebauer, T., Horna, V., & Leuschner, C. (2009). Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species. *Tree Physiol,* 28, 1821–1830. https://doi.org/10.1093/treephys/28.12.1821

Geissler, K., Hahn, C., Joubert, D., & Blaum, N. (2019): Functional responses of the herbaceous plant community explain ecohydrological feedbacks of savanna shrub encroachment. *Perspect. Plant Ecol. Evol. Syst* , 39. https://doi.org/10.1016/j.ppees.2019.125458

Groengroeft, A., de Blecourt, M., Classen, N., Landschreiber, L. & Eschenbach, A. (2018) Acacia trees modify soil water dynamics and the potential groundwater recharge in savanna ecosystems. In: Climate change and adaptive land management in southern Africa – assessments, changes, challenges, and solutions

(ed. by Revermann, R., Krewenka, K.M., Schmiedel, U., Olwoch, J.M., Helmschrot, J. & Jurgens, N.), pp. 177-186, Biodiversity & Ecology, 6, Klaus Hess Publishers, Gottingen & Windhoek. doi:10.7809/b-e.00321

Haan, C. T., Barfield, B. J., & Hayes, J. C. (1994). Rainfall-Runoff Estimation in Storm Water Computations. In Design Hydrology and Sedimentology for Small Catchments; Haan, C.T., Barfield, B.J., Hayes, J.C., Eds.; Academic Press: San Diego, CA, USA, 1994 (pp 37–103)

Hering, R., Hauptfleisch, M., Geissler, K., Marquart, A., Schoenen, M., & Blaum, N. (2019). Shrub encroachment is not always land degradation: Insights from ground-dwelling beetle species niches along a shrub cover gradient in a semi-arid Namibian savanna. *Land Degrad Dev* , 30, 14–24. https://doi.org/10.1002/ldr.3197

Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T. and Jackson, R.B. (2005). Ecohydrological Implications of Woody Plant Encroachment.*Ecology* , 86, 308–319. https://doi.org/10.1890/03-0583

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (2018): The IPBES assessment report on land degradation and restoration. Montanarella, L., Scholes, R., and Brainich, A. (eds.). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany

International Panel on Climate Change (IPCC) (2023) Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge and New York: Cambridge University Press

Issoufou, H. B & Rambal, S., Le Dantec, V., Oi, M., Laurent, J., Saadou, M. & Seghieri, J. (2015). Is the WBE model appropriate for semi-arid shrubs subjected to clear cutting?. Tree physiology. 35. 10.1093/treephys/tpv002.

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

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

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), 272–284Jaskierniak, 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

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

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

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, 272–284. https://doi.org/10.1093/jpe/rtv056

Kassambara A. 2020. ggpubr: "ggplot2" based publication ready plots. R package, version 0.3.0.

Kozlowski, J. & Konarzewski, M. (2004). Is West, Brown and Enquist's Model of Allometric Scaling Mathematically Correct and Biologically Relevant? *Function Ecology* , 18, 283-289. https://doi.org/10.1111/j.0269-8463.2004.00830.x

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, 161–168. https://doi.org/10.1093/treephys/27.2.161

Lubczynski, M. W. (2009). The hydrogeological role of trees in waterlimited environments. *Hydrogeology Journal* , 17, 247–259.

Lubczynski, M. W., Chavarro-Rincon, D. C., & Rossiter, D. G. (2017). Conductive sapwood area prediction from stem and canopy areas—allometric equations of Kalahari trees, Botswana.*Ecohydrology,* 10, e1856. https://doi.org/10.1002/eco.1856

Minamino, R., Tateno, M. (2014). Tree Branching: Leonardo da Vinci's Rule versus Biomechanical Models. *PLoS ONE* 9, e93535. https://doi.org/10.1371/journal.pone.0093535

Mitra, B., Papuga, S. A., Alexander, M. R., Swetnam, T. L., & Abramson, N. (2020). Allometric relationships between primary size measures and sapwood area for six common tree species in snow-dependent ecosystems in the Southwest United States. *J. For. Res. 31, 2171–2180*https://doi.org/10.1007/s11676-019-01048-y

Moncrieff, G. R., Chamaille-Jammes, S., Higgins, S. I., O'Hara, R. B. & Bond, W. J. (2011). Tree allometries reflect a lifetime of herbivory in an African savanna. *Ecology* , 92, 2310–2315. https://doi.org/10.1890/11-0230.1

Niklas, K. J. (1994). Plant Allometry: The Scaling of Form and Process. Chicago: University of Chicago Press.

Niklas, K. J. (1997). Size- and age-dependent variation in the proper-ties of sap- and heartwood in black locust (Robinia pseudoacaciaL.). *Annals of Botany,* 79, 473–478.

Nortje, G. (2019). A Game Drive Optimisation Strategy for Etosha Heights Game Safaris, Etosha Heights, Namibia. 10.13140/RG.2.2.19246.56643.

Ogle, D. H., Doll, J. C., Wheeler, A. P., Dinno, A. (2023). FSA: Simple Fisheries Stock Assessment Methods. R package version 0.9.4, https://CRAN.R-project.org/package=FSA.

Oppelt, A. L., Kurth, W., Godbold, D. L. (2001). Topology, scaling relations and Leonardo's rule in root systems from African tree species.*Tree Physiology,* 21, 117–128.

Patino, S., Tyree, M. T., & Herre, E. A. (1995). Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to free standing and hemi-epiphytic Ficus species from Panama. *New Phytol,* 129, 125–134. https://doi.org/10.1111/j.1469-8137.1995.tb03016.x

Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Koppen-Geiger climate classification. *Hydrology and Earth System Sciences,* 11, 1633e1644.

Petit, G., & Anfodillo, T. (2009). Plant physiology in theory and practice: An analysis of the WBE model for vascular plants.*Journal of Theoretical Biology,* 259, 1-4. https://doi.org/10.1016/j.jtbi.2009.03.007

Quinonez-Pinon, & M. R., Valeo, C. (2019). Scaling Approach for Estimating Stand Sapwood Area from Leaf Area Index in Five Boreal Species. *Forests* , 10, 829. https://doi.org/10.3390/f10100829

Reyes-Acosta, J. L., & Lubczynski, M. W. (2014). Optimization of dry-season sap flow measurements in an oak semi-arid open woodlandin Spain. *Ecohydrology* , 7, 258–277.

Richter, J. (1970). The notebooks of Leonardo da Vinci. Dover, New York.

Schindelin, J., Arganda-Carreras, I., Frise, E. et al. (2012). Fiji: an open-source platform for biological-image analysis. *Nature Methods* , 9, 676–682. https://doi.org/10.1038/nmeth.2019

Scholz, F. G., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., & Miralles- Wilhelm, F. (2008). Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. *Tree Physiol* . 28, 469–480. doi: 10.1093/treephys/28.3.469

Schoppach, R., Chun, K. P., He, Q., Fabiani, G., & Klaus, J. (2021). Species-specific control of DBH and landscape characteristics on tree-to-tree variability of sap velocity. *Agricultural and Forest Meteorology* , 307, 108533. https://doi.org/10.1016/j.agrformet.2021.108533

Shikangalah, R., Musimba, A., Mapaure, I., Mapani, B., Herzschuh, U., Tabares, X. & Kamburona-Ngavetene, C. (2021). Growth rings and stem diameter of Dichrostachys cinerea and Senegalia mellifera along a rainfall gradient in Namibia. *Trees, Forests and People* , 3, 100046. https://doi.org/10.1016/j.tfp.2020.100046

Sohel, Md. S. (2022). Systematic review and meta-analysis reveals functional traits and climate are good predictors of tropical tree water use. *Trees Forests and People* . 8. 10.1016/j.tfp.2022.100226

Sprugel, D. G. (1983). Correcting for Bias in Log-Transformed Allometric Equations. *Ecology* , 64, 209–210. https://doi.org/10.2307/1937343

Stevens, N., Lehmann, C. E., Murphy, B. P., & Durigan, G. (2016). Savanna woody encroachment is widespread across three continents.*GlobalChange Biology* , 23, 235–244. https://doi.org/10.1111/gcb.13409

Sun, X., Wilcox, B. P., & Zou, C. B. (2019). Evapotranspiration partitioning in dryland ecosystems: A global meta-analysis of in situ studies. *Journal of Hydrology* , 576, 123–136. https://doi.org/10.1016/j.jhydrol.2019.06.022

Ter-Mikaelian M.T., & Korzukhin M. D. (1997). Biomass equations for sixty-five North American tree species. *For Ecol Manag,* 97. 1–24. https://doi.org/10.1016/S0378-1127(97)00019-4

Tredennick, A. T., Bentley, L. P., & Hanan, N. P. (2013). Allometric convergence in savanna trees and implications for the use of plant scaling models in variable ecosystems. *PloS one* , 8(3), e58241. https://doi.org/10.1371/journal.pone.0058241

Trimble, M. J., & Van Aarde, R. J. (2014). Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemicity. *Anim Conserv,* 17, 441–453. https://doi.org/10.1007/s10531-014-0716-4

Tziaferidis, S. R., Spyroglou, G., Fotelli, M., & Radoglou, K. (2021). Allometric models for the estimation of leaf area and dry weight from sapwood and heartwood area in black locust (R. pseudacacia), EGU General Assembly 2021, online, 19–30 Apr 2021, EGU21-3999, https://doi.org/10.5194/egusphere-egu21-3999

Wang, X,. Wang, C., Zhang, Q., & Quan, X. (2010). Heartwood and sapwood allometry of seven Chinese temperate tree species. *Ann. For. Sci.,* 67, 410. https://doi.org/10.1051/forest/2009131

West, G. B., Brown, J. H., & Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* . 276, 122–126. https://doi.org/10.1126/science.276.5309.122

West, G. B., Brown, J. H., & Enquist, B. J. (1999). A general model for the structure and allometry of plant vascular systems. *Nature* . 400, 664–667. https://doi.org/10.1038/23251

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.

Wickham, H., Francois, R., Henry, L., Muller, K., & Vaughan, D. (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.0, <https://CRAN.R-project.org/package=dplyr>.

Wickham, H., Vaughan, D., & Girlich, M. (2023). tidyr: Tidy Messy Data. R package version 1.3.0, <https://CRAN.R-project.org/package=tidyr>.

Wilcox, B. P., Basant, S., Olariu, H., & Leite, P. A. M. (2022). Ecohydrological connectivity: A unifying framework for understanding how woody plant encroachment alters the water cycle in drylands.*Front. Environ. Sci* . 10:934535. doi: 10.3389/fenvs.2022.934535

Yaemphum, S., Unawong, W., & Torngern, P. (2022). Sapwood area~DBH allometries for 14 common tree species in a successional tropical forest in Thailand. *Forestry* , 95, 562–571. https://doi.org/10.1093/forestry/cpab054

Zziwa, N. C. (2003). Assessment of water fluxes in semi-arid environments (Serowe case study (Botswana). (Unpublished master's thesis). International Institute for Geo-information Science and Earth Observation, Enschede.

Tables

TABLE 1. Allometric exponents with 95% confidence interval,their test statistics, and the back-correction factor CF for the relationship between stem diameter and sapwood area for six main shrub encroacher species in a semiarid savanna of Namibia. CF is needed for prediction of SA from SD applying back-transformation of the allometric relationship at ln-scale (see Eq. 5 and Fig. 3).

	C. alexandri	D. cinerea	V. nebrownii	V. reficiens	S. mellifera	C. mopane
Allometric constant (intercept)	-1.07	0.70	-1.67	-1.51	-0.47	-1.04
exponent	2.13	1.26	2.31	2.17	1.93	2.07
Exponent 95% LCI/UCI	2.02/2.24	0.95/1.57	2.19/2.42	1.99/2.34	1.76/2.10	1.92/2.20
Correction Factor	1.016	1.116	1.013	1.032	1.025	1.018

TABLE 2. Species-specific allometric exponents with 95% confidence interval, their test statistics, and the back-correction factor CF for the relationship between crown area and total sapwood area of six main shrub encroacher species in a semiarid savanna of Namibia. CF is needed for prediction of total sapwood area from SAtot applying back-transformation of the allometric relationship at ln-scale (see Eq 5 and Fig 5).

	C. alexandri	D. cinerea	V. nebrownii	V. reficiens	S. mellifera	C. mopane
Normalization constant	1.51	2.41	0.45	0.98	2.12	1.18
Exponent	1.09	0.94	1.17	1.24	1.10	1.34
Exponent 95% LCI/UCI	0.96/1.24	0.78/1.10	1.03/1.33	1.11/1.37	0.96/1.26	1.20/1.50
Correction Factor	1.14	1.18	1.15	1.09	1.17	1.24

TABLE A1 **(supplementary material).** Summary statistics of single shrub dimensions of the six main bush encroacher species in a semiarid savanna of Namibia. Values for stem diameter, sapwood area (per stem) and canopy area are based on real measurements; values for total sapwood area (per individual shrub) are estimated using allometric equations (see formula 4).

	C. alexandri	D. cinerea	V. nebrownii	V. reficiens	S. mellifera	C. mopane
Canopy area (m^2)						
N	60	60	60	60	60	60

	C. alexandri	D. cinerea	V. nebrownii	V. reficiens	S. mellifera	C. mopane
Min.	0.1	0.3	0.2	0.7	1.1	0.3
Max.	8.9	17.7	21.5	69.4	99.4	117.4
Mean	2.1	3.9	5.1	15.9	18.8	19.1
SD	2	3.8	4.2	11.2	18.3	20.8
Stem diameter (mm)						
N	23	22	23	21	20	21
Min.	3.9	6.5	7.2	12.3	14.5	9.6
Max.	62.8	54.5	58.3	109	107.4	111.4
Mean	21.7	23.6	23.2	50.4	46.5	43.8
SD	14.4	15.6	13.9	31.4	26.2	26.5
Sapwood area per stem (mm²)						
N	23	22	23	21	20	21
Min.	7	19.3	15.4	34.1	120.8	26.5
Max.	2165.3	385.2	2116.2	7190	56655.8	4747.8
Mean	370.9	131.1	410.8	1558.1	1397.6	1129.1
SD	509	123.7	517.2	1890.1	1567.2	1235.7
Bark thickness per stem (mm)						
N	23	22	23	21	20	21
Min.	0.19	0.11	0.42	0.93	0.72	1.22
Max.	2.45	2.38	2.8	5.73	3.85	7.65
Mean	1.06	1.21	1.1	2.53	1.8	3.69
SD	0.57	0.62	0.59	1.42	0.91	1.83
Total sapwood area (mm²)						
N	60	60	60	60	60	60
Min.	0.2	2.1	0.2	1.6	4.5	0.8
Max.	95.4	222.6	79.4	580.9	1441.8	1527.4
Mean	12.6	44.1	12.2	98.5	250.4	219.7
SD	17.5	44.5	12.5	116.4	302.5	290
Total stem area (mm²)						
N	60	60	60	60	60	60
Min.	0.64	0.6	1	5.1	5.6	1.8
Max.	161.8	299	170	964.1	1761.2	1963.5
Mean	24.2	43	34	199.4	307.3	345.7
SD	30.1	62	28.7	190.1	369.9	406.3

Figure legends

FIGURE 1: Representative samples of sapwood area staining for six main shrub encroacher species in a semiarid savanna in Namibia. A) *Catophractes alexandri* , **B)** *Colophospermum mopane* **, C)** *Dichrostachys cinerea* , **D)** *Senegalia mellifera* , **E)** *Vachellia nebrownii* ,**F)** *Vachellia reficiens* **.**

FIGURE 2: Delineation of sapwood area based on sapwood staining in *C. alexandri.* The following areas are outlined by 3 white lines: A) total area, B) wood area, and C) heartwood area.

FIGURE 3. Allometric relationship between stem diameter (D_{stem}) and sapwood area (SA) and relationship between stem diameter (D_{stem}) for six main shrub encroacher species in a semiarid savanna in Namibia. Solid black lines are the regression lines calculated by the models, dashed black lines are the 95% confidence intervals, and the grey line is the predicted relationship according to the WBE model (slope = 2.33) (West 1999) with species-specific intercepts.

FIGURE 4. relative sapwood area (relative SA) for six main shrub encroacher species in a semiarid savanna in Namibia. Relative sapwood area is sapwood area divided by the wood area of the cross-section.

FIGURE 5. Relationship between crown area (CA) and total sapwood area (SAtot) for six main shrub encroacher species in a semiarid savanna of Namibia. Solid lines are the regression lines calculated by the models; dashed black lines are the 95% confidence intervals.

C. alexandri

ln(SA) = 2.13× ln(Dstem) + -1.07

R^2_{adj} = 0.99

$F_{1,21}$ = 1.62e+03

P < 0.001

C. mopane

ln(SA) = 2.07× ln(Dstem) + -1.04

R^2_{adj} = 0.98

$F_{1,19}$ = 931.

P < 0.001

D. cinerea

ln(SA) = 1.26× ln(Dstem) + 0.7

R^2_{adj} = 0.77

$F_{1,20}$ = 72.3

P < 0.001

S. mellifera

ln(SA) = 1.93× ln(Dstem) + -0.47

R^2_{adj} = 0.96

$F_{1,18}$ = 518.

P < 0.001

V. nebrownii

ln(SA) = 2.31× ln(Dstem) + -1.67

R^2_{adj} = 0.99

$F_{1,21}$ = 1.73e+03

P < 0.001

V. reficiens

ln(SA) = 2.17× ln(Dstem) + -1.51

R^2_{adj} = 0.97

$F_{1,19}$ = 712.

P < 0.001

ln Sapwood Area (cm^2)

ln Stem Diameter (cm)

18