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An analysis of structure: biomass structure relationships for characteristic species of the western Kalahari, Botswana

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Abstract

Savannah ecosystems are important carbon stocks on the Earth, and their quantification is crucial for understanding the global impact of climate and land-use changes in savannahs. The estimation of aboveground/belowground plant biomass requires tested allometric relationships that can be used to determine total plant biomass as a function of easy-to-measure morphological indicators. Despite recent advances in savannah ecology, research on allometric relations in savannahs remains confined to a few site-specific studies where basal area is typically used as the main morphometric parameter with plant biomass. We investigate allometric relations at four sites along a 950-km transect in the Kalahari across mean rainfall gradient 170 mm yr^{-1}–550 mm yr^{-1}. Using data from 342 harvested trees/shrubs, we relate basal area, height and crown diameter to aboveground biomass. These relationships are strongest in trees and weakest in small shrubs. Strong allometric relationships are also determined for morphologically similar groups of woody vegetation. We show that crown diameter can be used as an alternative to basal area in allometric relationships with plant biomass. This finding may enhance the ability to determine aboveground biomass over large areas using high-resolution aerial or satellite imagery without requiring ground-based measurements of basal area.

Key words: allometry, biomass estimations, Kalahari, savannah

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Résumé

Les écosystèmes de savane sont d'importants stocks de carbone terrestres, et leur quantification est cruciale pour comprendre l'impact global des changements du climat et de l'utilisation des sols en savane. L'estimation de la biomasse végétale au-dessus et en dessous de la surface exige des relations d'allométrie éprouvées qui puissent servir à déterminer la biomasse végétale totale en fonction d'indicateurs morphologiques faciles à mesurer. Malgré de récentes avancées en matière d'écologie des savanes, la recherche sur les relations d'allométrie en savane reste confinée à quelques études localisées où la surface terrière est habituellement utilisée comme paramètre morphométrique principal pour la biomasse végétale. Nous avons étudié les relations d'allométrie sur quatre sites le long d'un transect de 950 km dans le Kalahari, sur un gradient de pluviosité moyen allant de 170 mm à 550 mm/an. En utilisant les données provenant de 342 arbres/arbustes récoltés, nous relions la surface terrière, la hauteur et le diamètre de la couronne à la biomasse aérienne. Ces relations sont plus fortes chez les arbres et moins chez les petits arbustes. De fortes relations d'allométrie sont aussi déterminées pour des groupes de végétation ligneuse de morphologie semblable. Nous montrons que le diamètre de la couronne peut servir d'alternative à la surface terrière dans les relations d'allométrie avec la biomasse végétale. Cette découverte peut améliorer la capacité de déterminer une biomasse aérienne sur de grandes surfaces au moyen d'images aériennes ou satellitaires de haute résolution sans nécessiter de mesures au sol de la surface terrière.

Introduction

Savannah ecosystems cover about 20% of the Earth's land surface, including about 40% of Australia and Africa (Scholes & Walker, 1993). They provide important services such as rangeland for livestock production, firewood, carbon sequestration and protection against soil erosion. It has been estimated that savannahs contribute about 15% (Taylor & Lloyd, 1992) to 29% (Mohamed *et al.*, 2004) of the global terrestrial net primary productivity. Despite their important role in the global carbon balance, the contribution of savannahs to the global stocks of organic carbon remains poorly quantified. It is unclear (i) how much biomass is stored in savannahs; (ii) how it is partitioned between above- and belowground stocks; and (iii) how these stocks are expected to change under different land-use and climate change scenarios. This lack of a quantitative assessment of carbon stocks in savannah vegetation is a major limitation to the understanding of whether changes in climate, land management or disturbance regime might turn savannahs into important sources or sinks of atmospheric CO_2 (Williams *et al.*, 2007; Wang *et al.*, 2009a).

Possible changes in vegetation structure and composition induced by shifts in rainfall regime can be inferred through a 'space-for-time' substitution along a rainfall gradient. Thus, we focus on savannah ecosystems located along the Kalahari Transect (KT), where a rainfall gradient exists on the relatively uniform soil substrate of the Kalahari's sand sheet. The consistent soils of the Kalahari combined with a documented rainfall gradient provide an excellent 'open air laboratory' to study the effects of climate change on vegetation patterns, the distribution and production of biomass, and the region's carbon storage capacity (Scholes *et al.*, 2003). Previous research has assessed changes in vegetation cover, composition and structure along the KT and elucidated the relations existing between vegetation structure and abiotic factors such as nutrient (Wang *et al.*, 2010) and water availability (Caylor *et al.*, 2006). Empirical relations to determine the aboveground biomass of woody species in the Kalahari have been established by TIETEMA (1993), who provided allometric relationships for fuel wood–relevant hardwood species but did not consider other woody species. In this study, we aim to determine a set of allometric relations for woody plants in the Kalahari, which has been limited by an inadequate set of empirical allometric relations capable of providing a relatively accurate estimate of plant biomass based on some easy-to-measure quantities such as basal diameter, plant height or the size of the canopy footprint.

Although basal diameter (BD) is commonly used as the independent variable in allometric relationships, this approach is difficult to implement for smaller multi-stemmed shrubs that often characterize entire landscapes throughout the western and central parts of the Kalahari and savannahs in general. In these landscapes, it is impractical to determine woody biomass using allometric relationships with basal area (BA) because each shrub may have numerous and hard-to-reach stems. The basal area approach is more suitable for defined stands where DBH (diameter at breast height) or the basal diameter can be accurately measured. To this end, this study also investigates the suitability of crown area as a predictor for aboveground woody biomass. Unlike stems, which can only be measured in the field, woody crowns have the potential to be remotely sensed through a variety of methods, and the empirical relations determined in this study could pave the road to remote methods for the estimation of woody biomass.

Materials and methods

Research sites

We focus on the Botswana segment of the Kalahari Transect, which stretches 950 km in the north–south direction across the western part of the country along a rainfall gradient ranging from 550 mm yr^{-1} in the north to 170 mm yr^{-1} in the south. Along this transect, four sites were selected in areas with different average annual rainfalls. According to the Botswana Department of Meteorology, the 1971–2206 Mean Annual Precipitations (MAP) from the northernmost and wettest to southernmost and driest sites are as follows: just short of the Namibian border, Shakawe has a MAP of 539 mm, Kuke has 439 mm and Tshane has 358 mm; and just short of the South African border, Bokspits has 177 mm. All sites are dominated by Aeolian sand, with Bokspits being the only site with dune fields. While all sites have Kalahari Thornveld vegetation, northernmost Shakawe also has Miombo vegetation and is a transition between the two vegetation types.

The Shakawe site had some woody areas with dominant tree species over 15 m including *Baikiaea plurijuga, Burkea africana* and *Pterocarpus angolensis*. Multistemmed tree/shrub (8 m) species included *Burkea africana, Ochna pulchra* and *Terminalia sericea*, and the multistemmed shrub (2 m) *Grewia flavescens* was common as well. Moving south 330 km, the Kuke site is vertically more homogenous, with multistemmed shrubs (2 m) of *Croton gratissimus, Boscia albitrunca, Bauhinia petersiana, Grewia flavescens* and *Philenoptera nelsii.* Another 275 km south, the Tshane site has slightly taller multistemmed shrubs (3 m) of *Boscia albitrunca, Grewia flava, Lycium hirsutum, Rhigozum brevispinosum* and *Rhus tenuinervis,* and under 7 m-tall *Acacia luederitzii var. luederitzii* trees. Another 340 km south to the edge of the South Africa border, the Bokspits site has widely spaced trees up to 15 m of *Acacia erioloba, Acacia haematoxylon* and *Boscia albitrunca*, up to 4 m multistemmed *Acacia mellifera* shrubs, and shorter (1.5 m) multistemmed *Lycium bosciifolium* and *Rhigozum trichotomum*.

Sampling protocol

At each site, three 20 m × 20 m plots were cleared, and all woody vegetation was identified following the nomenclature of Coates-Palgrave (2002). Before clearing, structural parameters such as height (H), crown diameter (CD) and basal (stem) diameter (BD) of each individual were determined.

While harvesting the woody vegetation, the aboveground biomass of all trees and shrubs in the 20 m × 20 m plots was weighted using spring scales. Height (H) was measured as maximum height of the top of the canopy using a measuring tape if maximum height could be reached and using a clinometer in the case of taller trees.

To avoid bias and to account for structural variety, the crown diameter was measured twice, along the east–west and north–south directions. The average was recorded CD and formed the basis for canopy area (CA) calculations ($CA = \pi/4\ CD^2$). The BD was measured just above the basal swell at roughly ankle height, because most woody vegetation grows in multistemmed forms at all sites (Dayton, 1978). For multistemmed individuals, the total basal area (BA) was calculated as the sum of the basal areas of all stems:

$$BA = \pi/4 \sum_i BD_i^2 \qquad (1)$$

Calculation of regression curves

Regression curves were determined to relate aboveground wet biomass to the three structural parameters. Power-law relationships of biomass versus height, crown diameter and basal area were plotted using a logarithmic scale to account for changes in magnitude. The bias introduced by compressing values of different magnitudes onto a logarithmic scale (i.e. by giving them less weight in comparison with small values) was corrected using the approach described by Beauchamp & Olson (1973) and Sprunger (1983).

The power-law relationships between biomass and the three structural parameters height, crown diameter and basal area were derived for four cases: (i) all individuals at all sites; (ii) all individuals at each site; (iii) each species of which more than 15 individuals were sampled (please note that due to high similarities, species of the same genera might have been combined into a species group, while other species of the same genera have not, for example *Grewia spp*. vs. *Lycium hirsutum* and *L. boscifolium*) and (iv) all species in each of five distinct morphological classes: i) *Acacia* spp.; ii) tall (>2 m) dense canopy species; iii)small ($\leq$ 2 m) dense canopy species; iv) tall (>2 m) open canopy species and v) small ($\leq$ 2 m) open canopy species. The coefficients of determination (R^2) values were calculated as well as the root mean squared error (RMSE) of log-transformed values. The regressions derived for all woody species across the entire transect indicate that height, basal diameter or canopy size can all be used in allometric relationships with plant biomass.

Results

Table 1 lists all the species sampled along the transect. The total number of individuals included in the assessment across the four sites was 342 with 55 individuals at Shakawe, 125 at Kuke, 122 at Tshane and 40 at Bokspits (Table 2). A total of 23 different woody species were measured during the study.

All individuals at all sites

Plant biomass was related to the three structural parameters: basal area (BA), crown area (CA) and height (H) (Fig. 1). This analysis included all the 342 trees and shrubs sampled regardless of species, site or growth form. The R^2 values (Table 2) indicate that the regression of biomass versus basal area performs better than the regressions using the other parameters (H and CA), with R^2 values of 0.82 for BA, 0.73 for H and 0.75 for CA. However, the calculated RMSE indicates only minor

Table 1 Species, number of individuals sampled, site (B = Bokspits, T = Tshane, K = Kuke, S = Shakawe) and morphological category (1 Acacias, 2 tall dense canopy spp, 3 small dense canopy spp, 4 tall open canopy spp, 5 small open canopy spp)

Scientific name	Total number	Site ID	Morphological category
Acacia erioloba	4	B	I
Acacia luederitzii	12	T	I
Acacia mellifera	42	T, B	I
Acacia tortilis	2	K	I
Bauhinia petersiana	3	K	IV
Boscia albitrunca	16	K, T	II
Burkea africana	17	S	II
Cadaba aphylla	2	T	V
Combretum collinum	1	S	II
Combretum molle	5	K	II
Combretum zeyheri	15	K	II
Croton gratissimus	65	K	III
Grewia flava	15	T	III
Grewia flavescens	17	K	III
Lycium bosciifolium	5	B	V
Lycium cinereum	56	T	V
Ochna pulchra	20	S	II
Philenoptera nelsii	1	K	III
Rhigozum brevispinosum	1	T	IV
Rhigozum trichotomum	4	B	IV
Rhus tenuinervis	10	T	IV
Spirostachys africana	9	K	II
Terminalia sericea	20	S, K	II
Total	342		

differences between the three regressions with values of 0.87 for BA, 1.05 for H and 1.01 for CA (Table 2).

All individuals at each site

The results of an analysis of all individuals at each site are shown in Fig. 2, which provides the power-law fitting parameters for the relationships between plant biomass and the three structural parameters BA, H and CA for the four different field sites. The corresponding R^2 values (i.e. R^2_{H}, R^2_{BA} and R^2_{CA}, respectively) and the RMSE values are reported in Table 2. These results indicate that basal area is a good predictor of biomass at all sites, with R^2 ranging from 0.82 at Shakawe, Tshane and Bokspits, and 0.79 at Kuke. Height is overall the worst predictor with R^2 values dropping to 0.51 at Kuke. The canopy area performs well at all sites and at Kuke even better than the basal area, reaching an R^2 value of 0.89.

All individuals of each species or genus

Species-specific analysis was conducted only on species with more than 15 sampled individuals. Due to morphological similarity, *A. erioloba A. luederitzii* and *A. tortilis* have been combined in one group representing species characterized by bipinnate leaf structures.

Results from this analysis are presented in Fig. 3, and the corresponding R^2 values are summarized in Table 2. These results present a mixed picture: while the regression using basal area provides the best results for large woody species, the biomass of small shrubs such as *Lycium* and *Grewia spp* is better estimated using height or crown diameter. Crown area performs well overall as a predictor of plant biomass throughout the entire range of species. The best R^2 value of 0.97 was observed for *Burkea africana*, while R^2 values for *Ochna pulchra* are the lowest among all species for all three structural parameters used. The RMSE (ln) values that represent the same outcome suggest that crown area is a useful indicator. Overall, the best results have been achieved for *A. mellifera* with high R^2 values for all parameters (BA = 0.90, H = 0.76, CA = 0.92).

All individuals of each morphological class

All species were grouped into five categories, representing different growth forms and patterns. The categories are based on wood density, leaf form and growth patterns. The category associated with each plant species is presented in Table 1. The allometric relations for these grouped species with similar morphological characteristics indicate that crown area is an overall good predictor of biomass, with R^2 values ranging from 0.9 for morphological group I to 0.62 for morphological group V. While, in some cases, other parameters might perform better than crown diameter, the R^2 values suggest that the differences are relatively small (<11%) and that canopy area consistently performs well for all of these morphological groups. While, for tall trees and shrubs, basal area is a good predictor of plant biomass, it shows weak allometric relationships when applied to small, open and mainly multistemmed vegetation represented in categories IV and V with R^2 values as low as 0.45 for category IV (Table 2, Fig. 4).

Discussion

The regressions derived for all woody species across the entire transect indicate that height, basal diameter or

Table 2 Regression analysis results

Grouping	# of samples (n)	Slope	R^2	RMSE (ln)
All individuals	342			
Basal area (BA)		$0.1046 \times BA^{1.1400}$	0.82	0.87
Height (H)		$0.9399 \times H^{2.7454}$	0.73	1.05
Crown area (CA)		$1.3175 \times CA^{1.2183}$	0.75	1.01
Site Shakawe	55			
Basal area (BA)		$0.1000 \times BA^{1.1141}$	0.82	0.69
Height (H)		$0.7189 \times H^{3.4273}$	0.69	1.00
Crown area (CA)		$2.7414 \times CA^{0.8678}$	0.72	0.87
Site Kuke	125			
Basal area (BA)		$0.1179 \times BA^{1.0765}$	0.79	0.51
Height (H)		$0.6104 \times H^{3.2868}$	0.51	0.84
Crown area (CA)		$1.5535 \times CA^{1.0782}$	0.67	0.64
Site Tshane	122			
Basal area (BA)		$0.1046 \times BA^{1.1488}$	0.82	1.11
Height (H)		$0.9643 \times H^{2.8118}$	0.73	1.02
Crown area (CA)		$1.3175 \times CA^{1.2299}$	0.75	1.12
Site Bokspits	40			
Basal area (BA)		$0.2835 \times BA^{1.0559}$	0.82	0.83
Height (H)		$2.7809 \times H^{4.0156}$	0.75	0.99
Crown area (CA)		$1.8323 \times CA^{1.2688}$	0.89	0.77
Acacia spp	18			
Basal area (BA)		$0.1415 \times BA^{1.1801}$	0.81	1.00
Height (H)		$0.9321 \times H^{3.0604}$	0.80	1.18
Crown area (CA)		$1.0251 \times CA^{1.5185}$	0.78	1.10
Acacia mellifera	42			
Basal area (BA)		$0.2382 \times BA^{1.1040}$	0.90	0.55
Height (H)		$2.7115 \times H^{4.0373}$	0.76	1.05
Crown area (CA)		$1.2369 \times CA^{1.4668}$	0.92	0.48
Boscia albitrunca	16			
Basal area (BA)		$0.0931 \times BA^{1.2492}$	0.75	0.82
Height (H)		$2.5703 \times H^{2.8129}$	0.67	1.49
Crown area (CA)		$3.3214 \times CA^{1.3621}$	0.86	1.08
Burkea africana	17			
Basal area (BA)		$0.0574 \times BA^{1.2101}$	0.93	0.35
Height (H)		$0.5967 \times H^{3.6868}$	0.71	1.05
Crown area (CA)		$2.6452 \times CA^{1.2218}$	0.97	1.04
Combretum spp	21			
Basal area (BA)		$0.2182 \times BA^{0.9897}$	0.77	0.64
Height (H)		$0.2713 \times H^{14.2216}$	0.68	7.41
Crown area (CA)		$1.9200 \times CA^{1.1421}$	0.68	0.74
Croton gratissimus	65			
Basal area (BA)		$0.0625 \times BA^{1.2259}$	0.88	0.40
Height (H)		$0.5722 \times H^{3.6455}$	0.53	1.04
Crown area (CA)		$1.3862 \times CA^{1.1490}$	0.77	0.55
Grewia spp	32			
Basal area (BA)		$0.1486 \times BA^{1.0335}$	0.50	0.94
Height (H)		$0.7526 \times H^{2.6886}$	0.70	0.77
Crown area (CA)		$0.8205 \times CA^{1.0487}$	0.71	0.71

Table 2 *(continued)*

Grouping	# of samples (n)	Slope	R^2	RMSE (ln)
Lycium cinereum	56			
Basal area (BA)		$0.1019 \times BA^{0.9761}$	0.52	1.08
Height (H)		$0.6525 \times H^{2.6421}$	0.79	0.71
Crown area (CA)		$0.4834 \times CA^{1.1581}$	0.63	0.95
Ochna pulchra	20			
Basal area (BA)		$0.1939 \times BA^{0.7515}$	0.59	0.48
Height (H)		$0.7831 \times H^{3.7578}$	0.48	0.77
Crown area (CA)		$2.1224 \times CA^{0.5601}$	0.55	0.48
Terminalia sericea	20			
Basal area (BA)		$0.3790 \times BA^{0.9348}$	0.84	0.57
Height (H)		$1.9731 \times H^{4.4869}$	0.55	2.30
Crown area (CA)		$2.3588 \times CA^{1.0577}$	0.69	0.81
Morphological group I				
Basal area (BA)		$0.1672 \times BA^{1.1672}$	0.90	0.73
Height (H)		$2.0518 \times H^{3.5310}$	0.75	1.19
Crown area (CA)		$1.1403 \times CA^{1.4806}$	0.90	0.72
Morphological group II				
Basal area (BA)		$0.0978 \times BA^{1.1447}$	0.83	0.68
Height (H)		$1.0429 \times H^{2.6806}$	0.64	1.00
Crown area (CA)		$2.7155 \times CA^{0.9304}$	0.72	0.86
Morphological group III				
Basal area (BA)		$0.1034 \times BA^{1.0860}$	0.75	0.64
Height (H)		$0.7124 \times H^{2.6730}$	0.64	0.79
Crown area (CA)		$1.1580 \times CA^{1.1415}$	0.73	0.68
Morphological group IV				
Basal area (BA)		$0.1780 \times BA^{1.1825}$	0.45	1.48
Height (H)		$0.7722 \times H^{3.8619}$	0.73	1.30
Crown area (CA)		$1.2509 \times CA^{1.3333}$	0.78	0.93
Morphological group V				
Basal area (BA)		$0.1042 \times BA^{1.0128}$	0.56	1.05
Height (H)		$0.7230 \times H^{2.6370}$	0.76	0.79
Crown area (CA)		$0.5242 \times CA^{1.1328}$	0.62	0.97

canopy size can all be used in allometric relationships to determine plant biomass. Basal area measurements are often considered the best indicators of woody biomass in allometric relations for shrubs (Brown, 1976) and trees (Ter-Mikaelian & Korzukhin, 1997). Basal area has also been found to perform better than height measurements in multiple stem growth forms in the Kalahari (TIETEMA, 1993). TIETEMA (1993) found that several woody species in Botswana exhibit great similarity in allometric relations between aboveground biomass and basal area, especially *Acacia* and *Combretum* spp. In addition to providing allometric relationships for each species, TIETEMA (1993) also developed a combined regression for important fuel wood species (e.g. *Acacia*, *Combretum*, *Terminalia spp.* and others) that dominate the upper canopy. Other species, such as *Grewia*, *Lyzium* and *Rhigozum*, have not been considered in his study, because these have very little to no relevance with regard to fuel wood. However, these species should be considered when determining the ecosystem's aboveground biomass and carbon storage. In our study, we have included multiple small shrub, low-wood-density species to see whether findings presented by TIETEMA (1993) are still valid.

Our application of power-law regression analysis, combined for all species and sites, indicates that the relationship between biomass and basal area generally becomes weaker compared with TIETEMA's study (1993) when shrubs are included. This is represented as an R^2 drop of

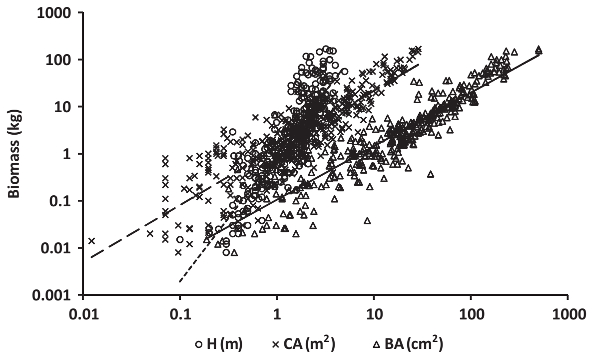

Fig 1 Regression for all species and sizes. (BA–solid line, CA–dashed line, H–dotted line)

13% when shrubs are included. Yet for the combined curve, basal area proves to be the better predictor of plant biomass than the other structural parameters. The lower performance of height and crown area might be the result of difficulties to measure height or crown diameter (as the determining factor of CA) of shrubs as accurately, while stem diameter is measurable with higher accuracy.

The regression analyses performed in this study indicate a slightly weaker relationship for all species and sizes combined, with an R^2 value of 0.81 for basal area. This decline in explained variance may be ascribed to the addition of smaller shrub species that generally perform worse than trees, as indicated by the per species analysis. However, the regression presented in Fig. 1 is still acceptable to determine biomass using a regression based on basal area for all species and sizes.

Looking at site-specific differences, basal area performs better than height and canopy area at the two northernmost sites, Shakawe and Kuke. Best performance was reached using height at Tshane and crown diameter at the Bokspits site. It should be noted, however, that the differences in R^2 values observed between basal area and crown diameter are minimal. The results also reflect the great variety in structural patterns generally observed in savannah areas (Caylor & Shugart, 2006). A change in slope of all regressions is noticeable comparing the two northern to the two southern sites, indicating stronger increase in biomass accumulation with increasing plant size (expressed by either one of these three structural parameters) in the north. This difference might be attributed to differences in plant community composition.

The growth form of woody species in the Kalahari is variable, ranging from single stemmed trees to multi-stemmed large shrubs of the same species (e.g. *Terminalia sericea*), to dense canopy shrubs (e.g. *Combretum spp.*), dense bipinnate leafed (e.g. *Acacia luederitzii*) to small shrubs with dense or open canopies seldom exceeding heights of 2 m

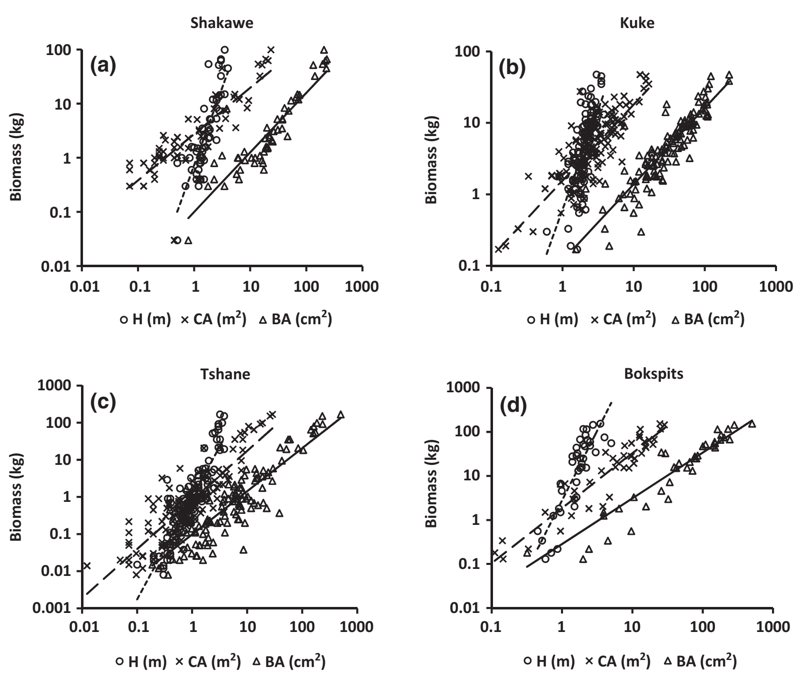

Fig 2 Site-specific regression of all species and sizes. (BA–solid line, CA–dashed line, H–dotted line)

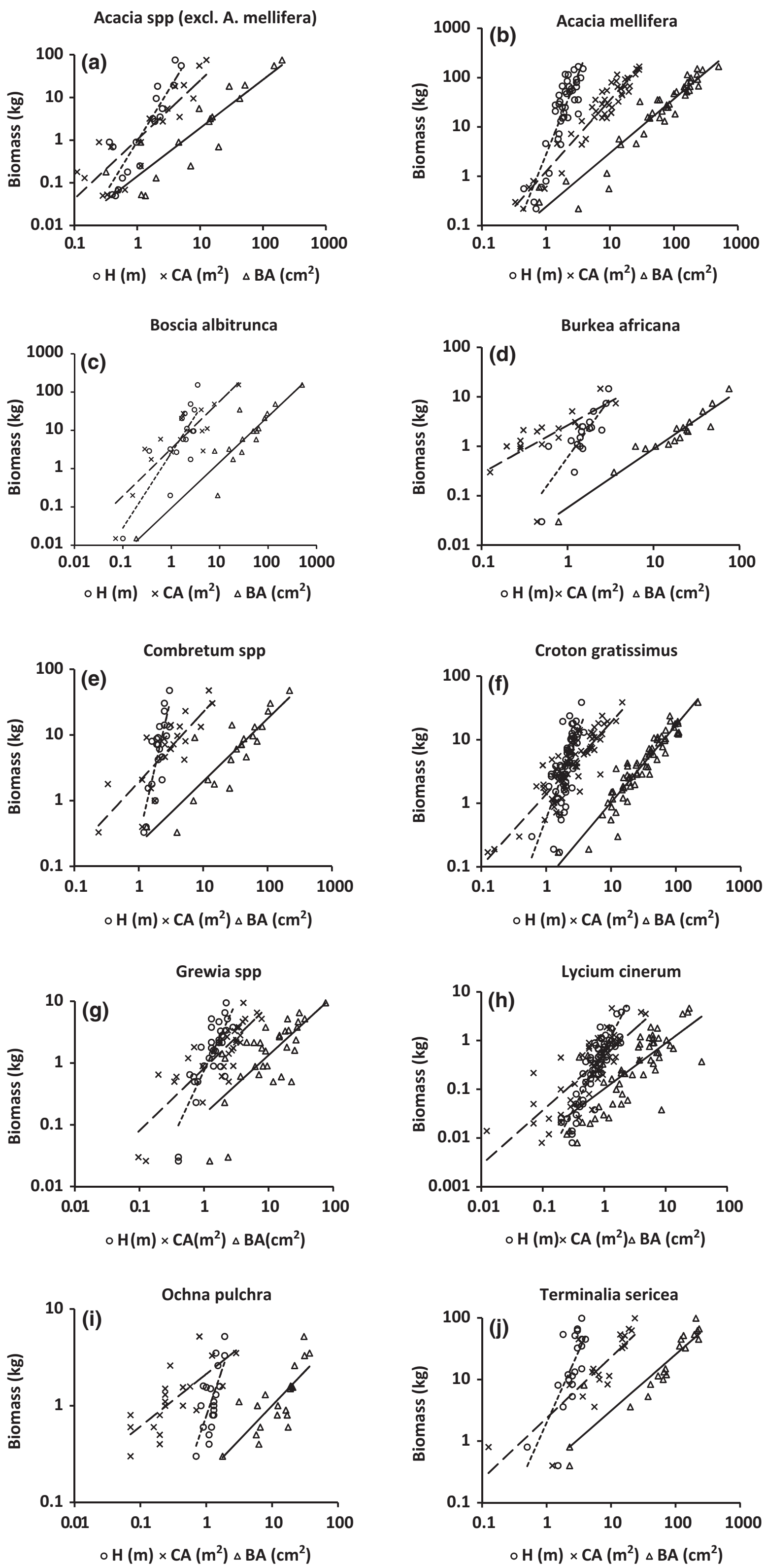

Fig 3 Species-specific regression. (BA–solid line, CA–dashed line, H–dotted line)

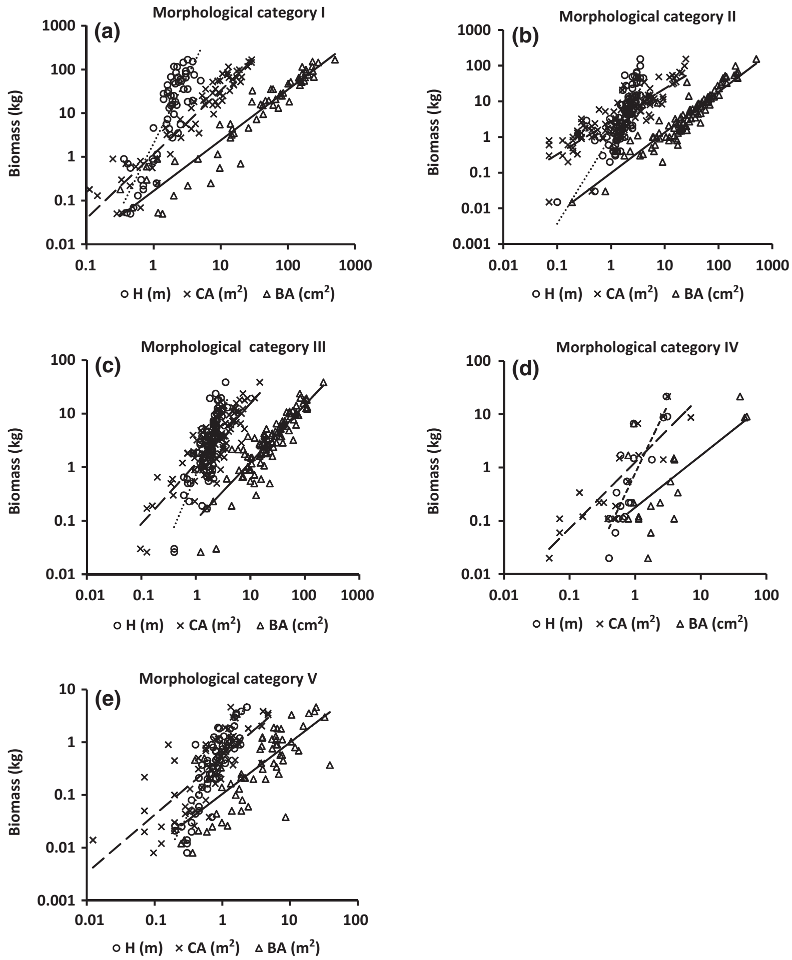

Fig 4 Categorized regression. (BA–solid line, CA–dashed line, H–dotted line)

(e.g. *Grewia spp. and Lycium spp.*). To determine aboveground biomass across the Kalahari ecosystem, these morphological characteristics should be taken into consideration. Our species analysis reveals that species exhibiting multistemmed and low (under 2 m) growth forms (categories IV and V) show low R^2 values of 0.45 and 0.56 for relationships between basal area and biomass. Basal area is therefore not well predicted. As a result of the multistemmed characteristics of these species, basal area is obtained as the sum for all stems (often more than 50); thus, measurement inaccuracies are squared for each diameter while converting to basal area, and errors can be amplified when this is repeated for each stem and all basal areas. For smaller, multistemmed shrub species, height and crown area are better indicators of plant biomass in allometric relationships. Our study indicates that depending on the morphological characteristic of a species, the best parameter to determine biomass may vary between basal area, crown diameter and height (Table 2). Strongest relationship was observed using BA for category I, II and III, using CA for category IV, and using H for category V.

Allometric relations are commonly developed in ecology and forestry to provide an empirical framework for the quantification of biomass based on nondestructive measurements of suitable structural or morphological parameters. To simplify the use of these relations for the quantification of aboveground biomass, easily measurable parameters should be preferably selected. A number of species in the Kalahari occur in multistemmed shrub life form. Therefore, the measurement of the basal area of each stem can be a challenging task, particularly in thorny species such as *A. mellifera*, which typically exhibits numerous and hard-to-reach stems. While basal area is the accepted standard independent variable for univariate regression-based allometric studies, the measurement of basal area and height in the field, especially in remote regions and across large areas, remains a challenge with regard to logistics, manpower and costs. This limits their usefulness in the determination of woody biomass in the Kalahari.

This study shows that crown diameter is a good indicator that can be used to determine biomass. In fact, the differences between biomass estimates based on crown diameter and basal area are minimal for large species that dominate the upper canopy levels, while canopy area performs better than basal area for small dense shrubs (category IV) and small brush-like species with open canopy and lower stem density. The view emerging from this study is that crown diameter provides an acceptable alternative to basal area in plant allometric relationships for the woody species in these savannahs particularly in the case of multistemmed individuals. Because ground measurements of basal area and height are impractical or impossible to perform for landscapes covered by multi-stemmed shrubs, canopy area should be considered as a reasonable and easy-to-measure alternative to basal areas that provides robust estimates of aboveground plant biomass. The crown diameter or crown area of savannah vegetation can be extracted across entire landscapes by leveraging high-resolution optical remote-sensing products. In particular, space and airborne LIDAR systems seem to be promising for the determination of woody biomass. These equations not only provide valuable information for land managers, as indicated by Wang *et al.*, 2009b; but could further be used to elaborate large-scale carbon estimation of aboveground and belowground carbon and soil carbon.

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