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Assessments
Changes
Challenges
and Solutions

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Assessments, changes, challenges, and solutions

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Patterns of above-ground biomass and its environmental drivers: an analysis based on plot-based surveys in the dry tropical forests and woodlands of southern Africa

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Abstract: In this paper we present an estimate of above-ground biomass (AGB) in the dry tropical forests and woodlands of southern Angola, western Zambia, northern Namibia and northern Botswana. Furthermore, we investigated the environmental variables influencing the spatial distribution of AGB. We compiled data from 498 vegetation plots and forest inventories covering seven vegetation types. The dataset contained measurements of 8803 individual trees belonging to 167 different species. The frequency of the trees per diameter at breast height (DBH) classes indicated healthy community structures with all vegetation types of miombo (Zambia and Angola), *Baikiaea* (Angola and Namibia), *Baikiaea-Combretum*, mopane, and *Terminalia* showing high number of trees in the smaller classes. We used two regional allometric equations developed for the miombo woodlands by Ryan (2011) and Chidumayo (2013) to calculate AGB. The highest AGB was recorded in the miombo woodlands of Zambia (median = 82.2 t/ha), followed by the dense *Baikiaea-Combretum* woodlands in Angola (median = 61 t/ha) and the Angolan miombo woodlands (median = 60.4 t/ha). Using generalized linear models, we analysed the relationship of AGB and environmental variables. Mean annual precipitation had the highest predictive power, explaining almost two thirds of the variance. Our conclusion was that, at regional scale, climate is a key driver of vegetation patterns, and biomass is no exception. There is a high local variability, however, that cannot completely be explained by gridded environmental datasets.

Resumo: Neste artigo, apresentamos uma estimativa da biomassa acima do solo (AGB) em florestas tropicais secas e bosques do Sul de Angola, Oeste da Zâmbia, Norte da Namíbia e Norte do Botswana. Além disso, investigamos as variáveis que influenciam a distribuição espacial da AGB. Compilámos dados de 498 parcelas de vegetação e inventários florestais, cobrindo sete tipos de vegetação. O conjunto de dados continha medições de 8803 árvores individuais, pertencentes a 167 espécies diferentes. A frequência das classes de árvores por diâmetro à altura do peito (DBH) indicou estruturas comunitárias saudáveis com todos os tipos de vegetação de miombo (Zâmbia e Angola), *Baikiaea* (Angola e Namíbia), *Baikiaea-Combretum*, mopane e *Terminalia*, mostrando um grande número de árvores nas classes mais pequenas. Utilizámos duas equações alométricas regionais, desenvolvidas para bosques de miombo por Ryan (2011) e Chidumayo (2013), para calcular a AGB. A mais elevada AGB foi registada nos bosques de miombo da Zâmbia (mediana = 82,2 t/ha), seguida pelos bosques densos de *Baikiaea-Combretum* em Angola (mediana = 61 t/ha) e os bosques de miombo angolano (mediana = 60,4 t/ha). Com recurso aos modelos lineares generalizados, analisamos a relação entre a AGB e variáveis ambientais. A precipitação média anual teve o maior poder preditivo, explicando quase dois terços da variância. A nossa conclusão foi que, à escala regional, o clima é um factor importante para os padrões da vegetação, e a biomassa não é excepção. Existe uma elevada variabilidade local, no entanto, esta não pode ser completamente explicada pelo elevado conjunto de dados ambientais.

Introduction

Dry tropical forests and woodlands cover large parts of southern Africa and are present in all five SASSCAL countries. They occur mainly in the northern, more mesic parts of the region that have a marked dry season lasting for several months per year but still receive sufficient precipitation during the wet season to support the growth of broad-leafed trees, reaching canopy heights well above ten meters (De Cauwer et al., 2018). From a floristic perspective, most of the woodlands in southern Africa fall into the Zambebian Phytoregion (White, 1983). Most of the dominant species of the tree layer belong to the Fabaceae family, but species of the Rubiaceae and Combretaceae play an important role too (Chidumayo & Gumbo, 2010). Ecosystem services from these woodlands provide important contributions to the livelihoods of over 100 million rural people and 50 million urban dwellers, mitigating some of the symptoms of the chronic poverty in the region (Deweese et al., 2010). As such, the woodlands provide the local population with several products ranging from timber and fuelwood to charcoal, honey, construction materials, and medicine. Furthermore, they are crucial for carbon storage, the water cycle, and climate regulation (Chidumayo, 1997; Frost, 1996; Ryan et al., 2011). As such, woodlands play a broad, twofold role: first, providing valuable ecosystem services such as increasing resilience through protecting watersheds and stream-flows, controlling erosion, enhancing soil fertility, regulating the climate, and protecting biodiversity; and, second, serving as a diverse source of jobs and livelihoods for African economies and citizens.

Understanding the spatial patterns of biomass in the Zambebian Phytoregion is important for providing insight into biomass variation and the influence of the environment, providing information on the carbon emissions related to land use change, establishing carbon mapping schemes, and modelling responses of the woodlands to their changing environment. African tropical forests and woodlands have been characterised by previous studies (Brown, 1997; Chave et al.,

2005) as holding relatively high carbon stocks.

The decrease in dry tropical forests and woodlands in Africa is alarmingly severe as a result of overutilization and land use changes (Deweese et al., 2010). The protection and sustainable management of forest carbon stocks, particularly in the tropics, is a key factor in mitigating global change effects. Nevertheless, our knowledge of how the environment affects carbon stocks in tropical ecosystems needs to be improved. For a sustainable management of woodlands and forests, spatial and temporal information on ecosystem structure, species composition, and biomass (carbon stocks) is indispensable (Thompson et al., 2012). Ground-based information is sparse to absent for vast

ground measurements to predict biomass for the entire tropics.

Estimates of forest AGB are approximations relying on a combination of land cover type and corresponding mean carbon derived from field surveys, instead of spatially explicit biomass maps (Carreiras et al., 2013). In the field, the AGB of woodlands can be estimated based on allometric equations that relate the breast height diameter (DBH) of a tree, a common measurement used in forest inventories, to its biomass. These equations are based on destructive harvesting and subsequent weighing of the biomass of the tree and are thus very labour-intensive. However, the established relationship between DBH and AGB allows the rapid quantification of AGB for forest stands

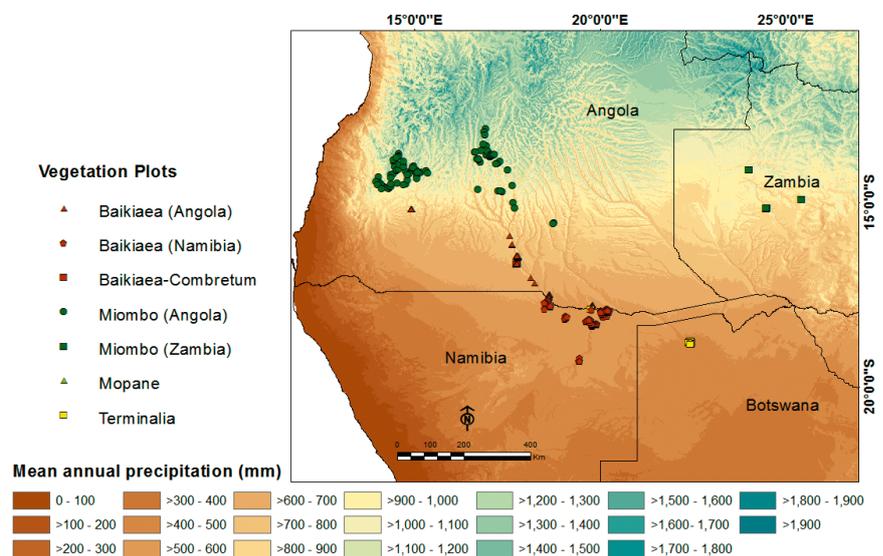


Figure 1: Map of the study sites and the seven vegetation types.

parts of south-central Africa, however. In contrast to tropical rainforests, dry tropical forests and woodlands have not been the focus of research (Bodart et al., 2013) and ground-based studies and forest inventories are scarce (Tewari, 2016).

Instead, several studies have tried to estimate the above-ground biomass (AGB) of forests in tropical regions using modelling and remote sensing approaches. Saatchi et al. (2011) developed a benchmark map of forest carbon stocks in the tropical regions across three continents. This study used a combination of data from in situ inventory plots and remote sensing to extrapolate from a spatially biased and limited number of

solely based on measurements of the DBH of the individual trees. A number of comprehensive allometric models for biomass estimation have been developed for the major forests and woodlands in Europe, the Americas, and Asia (Chave et al., 2014). In countries of sub-Saharan Africa, most studies estimating biomass or carbon stocks have also used allometric models together with forest inventory data (Mate et al., 2014; Mwakalukwa et al., 2014; Halperin et al., 2016). Ideally, allometric equations are developed for the specific woodland type in question, as the relationship is sensitive to species, and also the prevailing environmental conditions at the sites.

The objectives of this paper are:

1. to provide an estimate of AGB of the dry tropical forests and woodlands of southern Africa based on tree measurements in the field using two allometric equations, and
2. to investigate the environmental drivers of AGB on a regional scale.

Methods

The study was carried out in dry tropical forests and woodlands of Angola, Botswana, Namibia, and Zambia (Fig. 1, Tab. 1). The sampled area covers a strong

precipitation gradient ranging from the semi-arid Kalahari Desert in northern Botswana, with mean annual precipitation of 500 mm, to the semi-humid areas in north-western Zambia and central Angola, which receive up to 1,400 mm of yearly precipitation. Differences in mean annual temperature are less pronounced, ranging from 21 to 23°C. The study area is mostly covered by Kalahari sands, making arenosols with low nutrient content the dominant soil types. The western parts of the study area in Angola's Huila and Bie provinces, however, have a different underlying geology, and the common soil types are ferrasols.

Central Angola and Zambia are covered by brevi-deciduous miombo woodlands, which are dominated by *Brachystegia* species and *Julbernardia paniculata* (Tab. 1). The canopy is more or less closed and reaches heights well above 10 meters, and in Zambia even above 20 m (De Cauwer et al., 2018; Revermann et al., 2018). With decreasing precipitation southwards, the miombo woodlands give way to *Baikiaea* woodlands characterised by an interrupted canopy closure (De Cauwer et al., 2016; Revermann et al., 2018). The most southerly and driest part included in this study is north of the Okavango Delta, where mopane woodlands

Table 1: Most frequent species of the vegetation types and prevailing environmental conditions at the plot locations; mean values are given and the standard deviation in brackets; the temperature range was presented as the mean of the monthly range of the minimum and maximum temperatures.

Woodland type	Most frequent species	Total annual precipitation (mm)	Temperature range (°C)	Silt content topsoil (%)	Coarse fragments topsoil (%)	Fire frequency (number of years)	Human impact index
Miombo (Angola)	<i>Julbernardia paniculata</i> , <i>Brachystegia spiciformis</i> , <i>Brachystegia longifolia</i> , <i>Brachystegia</i> spp. 2	1123 (129)	10.7 (0.9)	11.2 (3.4)	4 (3)	0.8 (1.6)	17 (3)
Miombo (Zambia)	<i>Julbernardia paniculata</i> , <i>Brachystegia boehmii</i> , <i>Diospyros batocana</i> , <i>Guibourtia coleosperma</i>	999 (38)	9.6 (0.1)	26.5 (4)	0.8 (1.2)	0 (0)	14 (2)
Baikiaea (Angola)	<i>Baikiaea plurijuga</i> , <i>Burkea africana</i> , <i>Combretum collinum</i> , <i>Erythrophleum africanum</i>	689 (76)	11.1 (0.4)	10.3 (3.4)	4.6 (3.8)	2.4 (2.1)	12 (2)
Baikiaea-Combretum	<i>Baikiaea plurijuga</i> , <i>Philenoptera nelsii</i> , <i>Commiphora tenuiptulata</i> , <i>Acacia ataxacantha</i>	739 (6)	10.9 (0)	16 (2)	0.6 (0.5)	0 (0)	9 (0)
Baikiaea (Namibia)	<i>Baikiaea plurijuga</i> , <i>Philenoptera nelsii</i> , <i>Commiphora tenuiptulata</i> , <i>Acacia ataxacantha</i>	572 (24)	11.2 (0.1)	9.6 (2.7)	4.9 (3.6)	1.7 (1.6)	12 (5)
Mopane	<i>Colophospermum mopane</i> , <i>Baikiaea plurijuga</i> , <i>Acacia erioloba</i> , <i>Philenoptera nelsii</i>	476 (5)	11.2 (0.1)	8.8 (1.3)	1.9 (0.9)	0.4 (0.5)	10 (2)
Terminalia	<i>Terminalia sericea</i> , <i>Combretum collinum</i> , <i>Acacia erioloba</i> , <i>Burkea africana</i>	478 (22)	11.2 (0)	8.9 (3)	1.8 (1.5)	0.2 (0.4)	12 (6)

and *Terminalia* shrublands dominate. Trees in dense woodland or more open savanna woodland may reach heights of 10 m to 15 m in deep alluvial soils, and attain 25 m in the ‘cathedral mopane’ of Zambia (Ben-Shahar, 1998). Mopane tends to be stunted and shrubby (1–3 m) where it occurs in impermeable alkaline soils (Vermeulen, 1996).

Sampling design

For this analysis, we compiled data on tree measurements from different plot-based surveys. We included data from the Vegetation Database of the Okavango Basin (Revermann, 2016) from SASSCAL biodiversity observatories (Zambia: S51 Luampa, S52 Dongwe, S53 Kafue National Park; Angola: S74 Cussaque, S75 Bicuar National Park), from the Vegetation Survey of Huíla Province (Chisingui et al., 2018), and from the forest inventory in northern Namibia (De Cauwer et al., 2016). Vegetation plots of the surveys and on the biodiversity observatories were sized 20 m × 50 m. The sample plots of forest inventory in Namibia and in southern Angola followed a circular, nested design with a maximum radius of 30 m, as suggested for Namibia forest inventories by Burke et al. (2001). In every plot, all trees above a certain diameter at breast height (DBH) threshold were measured for height and DBH. As the threshold varied in the different surveys, we considered only trees with a DBH > 10 cm. Based on these measurements, the AGB was estimated using allometric equations. As results obtained by different equations calibrated at different locations can vary substantially (Ciais et al., 2011), we used two equations from the miombo region, to obtain an idea of the uncertainty caused by the use of different allometric equations. Equation 1 was calibrated in Mozambique by Ryan et al. (2011) and provides an estimate of the carbon content of the stem. We used the generally accepted ratio of the carbon fraction in woody dry matter of 0.47 (Eggleston et al., 2006) to convert carbon to AGB. Equation 2 was calibrated in the miombo woodlands of Zambia (Chidumayo, 2013). Finally, the aggregated biomass in kilograms per plot was converted to tonnes per hectare.

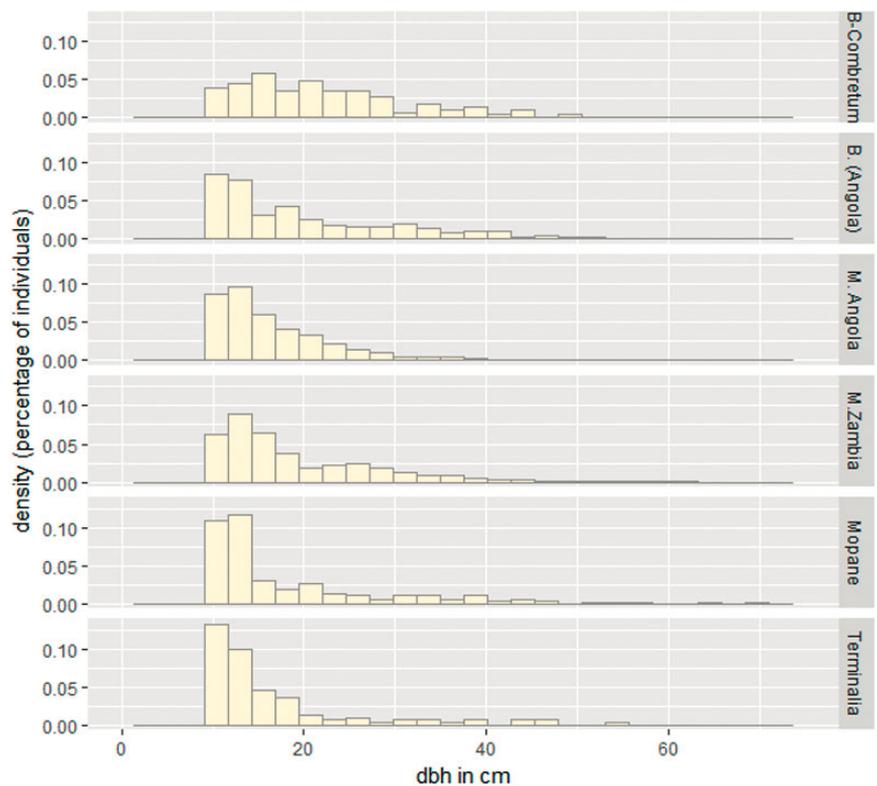


Figure 2: Size class distribution of the measured trees in each major vegetation type *Baikiaea-Combretum*, *Baikiaea* (Angola), miombo (Angola), miombo (Zambia), mopane, and *Terminalia*; only trees with DBH > 10 cm were considered (no diagram for *Baikiaea* woodlands in Namibia is displayed).

$$\text{Eq. 1: } \ln(B_{\text{stem}}) = 2.601 \ln(\text{DBH}) - 3.629$$

$$\text{Eq. 2: } \ln(\text{AGB}) = 2.5553 \ln(\text{DBH}) - 2.5265$$

where *DBH* is the stem diameter at breast height in cm, *ln* is the natural logarithm; *AGB* is the above-ground dry biomass in kg, and B_{stem} is the AGB of the stem in kg C.

Statistical analyses

To provide figures for the different sub-regions of the study area, the plots were grouped into seven major vegetation types: miombo woodlands in Angola and Zambia, *Baikiaea* woodlands in Angola and Namibia, *Baikiaea-Combretum* woodlands with thicket-like understorey (this vegetation type mainly occurs in certain parts of southern Cuando Cubango Province in Angola; for a description of this rare woodland type see Wallenfang et al., 2015), mopane woodlands, and *Terminalia* shrublands (Fig. 1). To visualize the structure and population status of the different vegetation types, we calculated size class distribution curves.

To investigate the environmental drivers of spatial patterns of AGB, we compiled environmental data from various sources

covering the entire region. Bioclimatic data were derived from CHELSA Climate Database (Karger et al., 2017); information on soil nutrients, soil texture, soil pH, and conductivity in the top- and subsoils were calculated for each plot location based on the data from the global soils database (Hengl et al., 2017; soilgrids.org). As disturbance and land use history are crucial factors influencing vegetation patterns, we furthermore included information on fire frequency and fire season derived from the MODIS burned area product (Stellmes et al., 2013). These variables along with the major vegetation types (see above) were used as predictor variables in a general linearized model (GLM) with AGB as the response variable assuming a gamma distribution. Predictor variables were checked for collinearity among pairs of predictor variables using the Pearson coefficient of correlation. In the case of high collinearity, one of a pair of highly correlated variables was removed from the set of variables (Dormann et al., 2013). The minimum adequate model was identified based on backward variable selection and the Akaike information criterion.

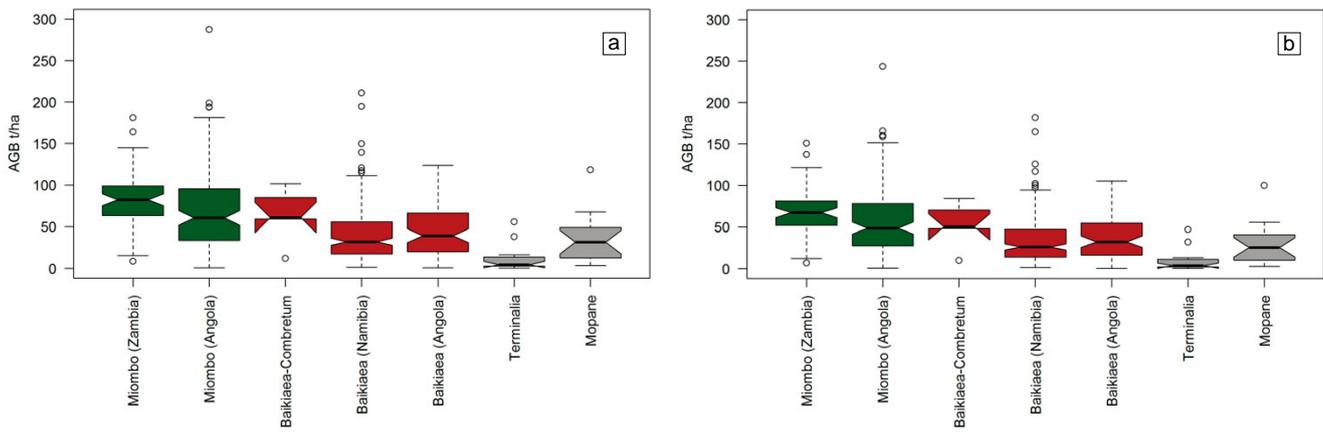


Figure 3: Estimated AGB (t/ha) according to the major vegetation types in the study area based on DBH measurements of individual trees and allometric equations by Ryan et al. (2011) (a) and Chidumayo (2013) (b).

Results

In total, 8803 individual trees were measured. A cumulative total of 167 woody species, 7 of which had not been identified to the genus level, were recorded. The species that were most abundant in the miombo woodlands were *Julbernardia paniculata*, *Brachystegia boehmii*, *B. spiciformis*, *B. longifolia*, and *Cryptosepalum exfoliatum* subsp. *pseudotaxus*. Common trees of the *Baikiaea* woodlands besides the species *Baikiaea plurijuga* were *Burkea africana*, *Combretum collinum*, *Erythrophleum africanum*, and *Philenoptera nelsii*. At the study site in Botswana, *Colophospermum mopane*, *Terminalia sericea*, *Acacia erioloba*, and *Philenoptera nelsii* were dominant (Tab. 1).

Though the *Baikiaea* woodlands had the thickest trees, tree densities were much lower; indeed, the miombo with the highest tree density in Zambia was five times denser than the *Baikiaea* woodlands with the lowest tree density in southern Angola (De Cauwer et al., 2018). The frequency of trees per DBH class for the seven major vegetation types showed a higher number of trees in the smaller classes in all vegetation types (Fig. 2).

Both allometric equations resulted in similar relative patterns of the distribution of AGB within vegetation types (Fig. 3, Tab. 2). AGB_{Ryan} provided a constant lower estimate compared to $AGB_{Chidumayo}$. The highest AGB was found in the miombo woodlands of Zambia, followed by the *Baikiaea-Combretum*

bretum woodlands in south Angola and the Angolan miombo woodlands. The AGB in the Angolan *Baikiaea* woodlands was slightly higher than that of the *Baikiaea* woodlands in Namibia and the mopane woodlands in Botswana. *Terminalia* shrublands had the lowest values in the entire study (Fig. 3, Tab. 2). It needs to be highlighted that there was high variation within the dataset, indicated by the high median absolute deviation (MAD) for all vegetation types.

Environmental drivers of above-ground biomass

Many of the climate variables showed strong collinearity, so one variable from each highly correlated pair had to be removed as a predictor variable. The same held true for the soil variables. The final models, with $AGB_{Chidumayo}$ and AGB_{Ryan} as response variables, contained the same predictor variables and displayed very similar model coefficients (Tab. 3). They both showed fairly low performance, with 16.1% and 15.3% explained deviance respectively. In the following, we will present results only for the model based on $AGB_{Chidumayo}$.

The variable with the highest predictive power was mean annual precipitation, explaining almost two thirds of the variance (Tab. 3). Generally, regions with higher precipitation showed higher AGB (Fig. 4). Mean annual precipitation exhibited a strong negative correlation with mean annual temperature. The second most important variable was silt content of the topsoil, explaining one fifth of the variance. Each of the remaining predictor

Table 2: Summary of above-ground biomass (AGB) in tonnes per ha according to the four major vegetation types and for the two allometric equations (Eq. 1 × 0.47, Ryan et al. [2011]; Eq. 2, Chidumayo [2013]). The median per vegetation type is given, and the variation is depicted by the median absolute deviation (MAD).

Major vegetation type	AGB _{Ryan} (t/ha)		AGB _{Chidumayo} (t/ha)	
	Median	MAD	Median	MAD
Miombo woodlands (Zambia)	67.2	20.7	82.2	24.6
Miombo woodlands (Angola)	48.8	37.2	60.4	45.5
<i>Baikiaea-Combretum</i> woodlands	50.2	29.8	61.0	35.6
<i>Baikiaea</i> woodlands (Angola)	32.5	27.8	39.2	33.5
<i>Baikiaea</i> woodlands (Namibia)	26.3	20.1	32.1	24.2
<i>Mopane</i> woodlands	25.6	22.9	31.5	28.2
<i>Terminalia</i> shrublands	3.7	3.4	4.6	4.2
total	35.3	32.6	42.9	39.5

variables contributed less than 10% to the explained variance (Tab. 3, Fig. 4).

Discussion

Stand structure and above-ground biomass

Tree size distributions are a simple yet effective tool for describing tree populations and woodland stands, and the distribution of diameters is the most potent simple factor for depicting the properties of a stand of trees (Ferreira de Lima et al., 2014). The community structure — the shape of the diameter distribution for all the vegetation types in our study — was typical for self-regenerating communities: the highest numbers of individuals were found in the smallest class. This so-called inverse J-shaped distribution is an indication of healthy population structure in which recruitment rates are higher than mortality (Sop et al., 2011).

Both allometric equations used in this study provided similar figures. However, the equation by Ryan et al. (2011) from Mozambique provided consistently lower estimates. As this equation is calibrated for the stem biomass and not the entire above ground biomass of the tree, this makes sense. The highest median estimated for miombo (Zambia) in Chidumayo’s was about 82 t/ha. These results match well with the modelled AGB based on remote sensing data supplied by Saatchi et al. (2011). Interestingly, the largest trees did not occur in the vegetation types with the highest AGB, the miombo woodlands, but in the *Baikiaea* woodlands. The *Baikiaea* woodlands are characterized by a more open canopy than the miombo woodlands and feature thick individual trees with large canopies. However, tree densities are low and there are large gaps in between the individual tree canopies, resulting in a grassy matrix in the inter-canopy area (Revermann et al., 2018). Thus, the much higher density of trees in the miombo woodlands compensates for, in the mean, smaller individuals (De Cauwer et al., 2018). The highest estimated AGB in the miombo woodlands of Zambia could be explained by the equally high density of stems per hectare as well as the presence of more individuals from

Table 3: Model coefficients of the GLM with AGB (t/ha) as response variable (calculated based on the allometric equation by Chidumayo [2013]); variable importance calculated via hierarchical partitioning is given as explained variance in a percentage. Explained deviance of the model is 16.1%.

Predictor	Estimate	p-value	Proportion of variance explained (%)
Intercept	1.1652	0.136	–
Mean annual precipitation	0.0013	< 0.001	65.3
Silt content topsoil	0.0227	< 0.001	21.7
Temperature range	0.0130	0.042	8.4
Coarse fragments topsoil	−0.0205	0.046	2.8
Fire frequency	0.0622	0.002	1.7

the larger size classes than in Angolan miombo woodlands (Fig. 2).

The estimation of AGB using allometric equations comes with its own uncertainty when one considers either pantropical models that differ significantly in the estimation of AGB from regional models (see Sichone et al., unpublished) or site-specific models applied to local inventories (Mauya et al., 2014). Though the IPCC 2006 guidelines (Eggleston et al., 2006) point towards the advantages of using spe-

cies-specific allometric equations. Given the absence of species-specific allometric equations, this study settled for regional ones. The allometric equations considered in this study were developed for miombo woodlands with the most frequently occurring genera, such as *Brachystegia*, *Julbernardia*, and *Cryptosepalum*. Even though the majority of sample sites were in miombo woodlands, other woodland types with a different species composition were analysed using the same allometric

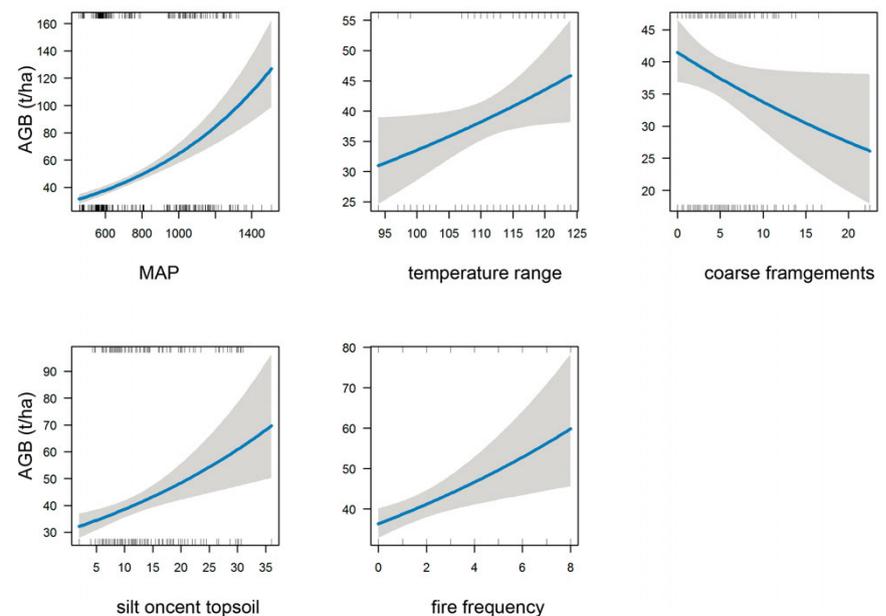


Figure 4: Visualisation of the predictor variables of the final GLM with AGB according to Chidumayo (2013). MAP = mean annual precipitation (mm); temperature range (°C); coarse fragments in the topsoil (%); silt content of the topsoil (%); fire frequency = number of fires in last 15 years.

equations in the absence of more suitable ones. Hence, it would be useful to develop equations for these woodland types to match the variability in tree biomass across all ecological zones and vegetation types. Furthermore, the inherent variability in growing conditions within a single biome such as miombo woodlands will obviously affect how well an allometric model applies to all locations in that zone. Within the geographical range of the study, there are different conditions in terms of climate, soil, and fire frequency (Tab. 1), all factors that affect allometry and thus the relationship between the independent variables and biomass.

However, new technologies currently still in the experimental stage might offer new solutions to estimate biomass on the local scale. As such, Strohbach (2018) and Knox et al. (2018) utilize unmanned aerial vehicles to investigate stand structure and height of woodlands. A study by Mathieu et al. (2018) makes use of the combination of airborne LiDAR data and freely available satellite data to calculate maps on woody cover on a regional scale. Additionally, Kankare et al. (2013) suggested the use of stem curve and crown size geometric measurements from terrestrial laser scanning data as a basis for allometric models.

Environmental drivers of AGB

On a regional scale, climate has long been identified as the main driver of vegetation patterns, and as such also of biomass. Generally, climate as the main driver was confirmed in this study, and AGB showed a positive relationship with mean annual precipitation and a negative one with mean annual temperature. Locally, however, the observed patterns of AGB deviated from this general finding. As such, miombo woodlands sampled in Angola received higher precipitation (annual mean 1123 mm) than the miombo woodlands in Zambia (annual mean 999 mm), but AGB was higher in the latter. This could be attributed in part to higher soil fertility in Zambia, represented by higher silt content in the topsoil in the GLM (Tab. 3). The share of fine material in the soil is responsible for nutrient retention, an important factor in a region where soils are predominantly sandy and very nutrient poor. Another factor could be higher anthropogenic

pressure on the woodlands, as population density is higher in the Angolan part of the study area than in the Zambian one (see also De Cauwer et al., 2018).

Fire can have a major impact on species composition and regeneration of woodlands. Generally, a rule of thumb indicates that fire return periods shorter than five years hinder trees from reaching mature stages that are more resistant to fire (Bond & Keeley, 2005). Thus, it is astonishing that the GLM indicated a weak but positive relationship between the number of fires and AGB. Maps of spatial and temporal patterns of fire in southern Africa (Röder et al., 2018) reveal that fire frequency does not follow a continuous gradient that can be explained purely by environmental factors. Instead, fire is controlled by human management or the lack thereof. As such, there is a clear difference in fire frequency among the *Baikiaea* woodlands. This woodland type occurs both in south-eastern Angola and in northern Namibia. In northern Namibia fire frequency is low compared to the areas to the north across the Okavango River in Cuando Cubango Province in Angola, where fire frequencies were among the highest in southern Africa (Röder et al., 2018).

Because of increased canopy closure, miombo woodlands exhibit a higher fire resistance. Fire is used for multiple purposes by humans, however, such as for the preparation of fields in shifting agriculture. Furthermore, many grasslands of the miombo region burn annually (Stellmes et al., 2013). Thus, vegetation plots in the miombo region situated close to the woodland edge can be erroneously identified as having a high fire frequency as a result of a mixed pixel problem. In conclusion, high fire frequency and fire season are not suitable variables to explain AGB on a regional scale. As other studies have shown, frequent fires can convert woodlands to long-term stable grasslands or shrublands.

This underlines that AGB patterns on this regional scale cannot be explained by environmental predictors alone. Instead, anthropogenic factors (e.g., the use of woodlands for shifting cultivation, charcoal production, or timber extraction) have a long-lasting impact on the species composition and structure of the woodland, and as such on AGB. The index

used for human impact in this study did not turn out to be an important predictor variable, however, and did not remain in the final model after variable selection.

This might also explain the high variability of AGB on the local scale: the estimates of AGB per vegetation type showed a high MAD, which was almost as high as the median. This high spatial variability at the local scale makes generalization about drivers of the AGB difficult and is responsible for the low model performance of the GLM.

Still, it also needs to be pointed out that the environmental data used in the modelling exercise were derived from global datasets and were not measured at the site scale by in situ measurements. The soil data, regionalized using predictive modelling approaches and various environmental data layers as explanatory variables, are particularly prone to errors.

Conclusion

This study provides a contribution to the estimates of the above-ground biomass of the woodlands in the Zambezi Phytoregion, where studies based on in situ data on a regional scale are very scarce. The most powerful variable explaining the spatial pattern of AGB was mean annual precipitation. However, models using environmental variables failed to fully explain the pattern observed in woodlands of the region. The reasons are most likely twofold. First, there is high local variability as a result of environmental heterogeneity that is not captured by the regional or global data layers used. Second, the woodlands are strongly affected and shaped by anthropogenic activities such as shifting cultivation, charcoal production, and the (unintended) use of fire.

To come to a better understanding of spatial patterns of AGB in southern African woodlands, we reiterate the importance of improving ground-based monitoring networks that will feed into the calibration and validation of remotely sensed data. Robust, standardised networks of field monitoring sites to complement global satellite observations are still insufficient. Long-term in situ monitoring is needed to investigate growth

rates to establish sustainable harvesting schemes for timber. Furthermore, they give insights into the regeneration capacity of the woodlands after clearing for agriculture or charcoal production.

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