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Improving the knowledge base for tropical dry forest management in southern Africa: Regional volume models for *Pterocarpus angolensis*

Vera De Cauwer[1,,2,], Hans Beeckman[3], Christoph Kleinn[4,6], Moses Moses[5,6], Amber Nott[1], Thomas Seifert[6,7], & Bart Muys[2]*

[1] Namibia University of Science and Technology, Faculty of Natural Resources & Spatial Sciences, Private Bag 13388, Windhoek, Namibia. vdecauwer@nust.na

[2] KU Leuven, Division Forest, Nature and Landscape, Celestijnenlaan 200E-2411, 3001 Leuven, Belgium. Bart.Muys@ees.kuleuven.be

[3] Royal Museum for Central Africa, Service of Wood Biology, Leuvensesteenweg 13, 3080 Tervuren, Belgium. hans.beeckman@africamuseum.be

[4] University of Göttingen, Forest Inventory and Remote Sensing, Faculty of Forest Sciences and Forest Ecology, Büsgenweg 5, 37077 Göttingen, Germany. ckleinn@gwdg.de

[5]Directorate of Forestry, PO Box 13088, Eenhana, Namibia. akiant1214@gmail.com

[6] Stellenbosch University, Department of Forest and Wood Science, Private Bag X1, Matieland 7602, South Africa.

[7]Albert-Ludwigs-University Freiburg, Chair of Forest Growth and Dendroecology, Tennenbacher-Str. 4, 89106 Freiburg, Germany. Thomas.seifert@iww.uni-freiburg.de

* Corresponding author

Abstract

The development of accurate site-specific allometric models for tree species of natural tropical forests is hampered by limited resources while there is little quality control of the models developed. In this study, we developed and tested regional volume functions with diameter at breast height (*DBH*) and tree height for *Pterocarpus angolensis*, the most widely exploited timber tree of southern Africa. These new models were established for the total and merchantable wood volume of *P. angolensis* with a dataset of 415 trees collected by destructive and non-destructive methods at 14 different sites in the *Baikiaea – Pterocarpus* woodlands of Namibia and southern Angola. Sources of data heterogeneity, such as site, collector and method, were investigated using mixed models and climate variables as model predictors. The study compared the ability of the new models with ten other site and species-specific volume models and nine generic volume and biomass models to estimate wood volume at tree and stand level. Stand data of 129 sample plots in the *Baikiaea – Pterocarpus* woodlands, representing a rainfall gradient from 480 mm to 750 mm, were used. Results showed that the three best performing models with *DBH* as single predictor (error 28% - 30%), including our new model, were developed for Namibia and Zambia. Adding tree height as predictor to our model removed the heterogeneity caused by site and reduced the error to 22%. One regional generic and onepantropical generic model, both with tree height, performed as well and outperformed other *Pterocarpus* specific models. Our models showed that the mean portions of merchantable wood and heartwood were 35% of the total wood, and 58% of the merchantable wood volume respectively. Although addition of climate variables improved our models, they did not perform well at stand level. Estimated total and merchantable volume of *P. angolensis* at stand level varied from 4.7 to 8.6 m^3 ha^{-1}, and 1.9 to 2.7 m^3 ha^{-1} respectively, depending on our and other models employed. Total growing stock is estimated between 36 to 52 m^3 ha^{-1} in our study area, depending on the model, with the contribution of *P. angolensis* between approximately 13%. Our results suggest that site-specificity of models is needed as long as they only include *DBH*. The use of pantropical and regional *DBH*-height based models that are adapted to site conditions through the collection of accurate height and wood density data for biomass conversion factors, is advised rather than developing site-specific *DBH* based volume models.

Keywords: tree volume model, generic model, specific model, allometric relationship, *Baikiaea – Pterocarpus* woodlands, Kiaat, Umbila, Muninga

Introduction

Accurate models are required to provide reliable estimates of growing stock and carbon sequestration at both local and national level. Model choice can lead to large differences in such estimates (Henry et al., 2015). Several studies (Basuki et al., 2009; Goussanou et al., 2016; Henry et al., 2011; Mensah et al., 2016) recommend the development of site and species-specific models to accurately model wood volume and biomass, as they compensate for the variability in tree shape and wood density based on species or site. However, in natural tropical forests, with a large variety of species of which few are used commercially, this is an immense task for which the resources are rarely available, especially when destructive methods are used. Moreover, there is little quality control of the models that have been developed, often by national forest agencies or by Master and PhD students with a limited amount of sample trees for relatively small study areas. Henry et al. (2011) showed that at least 22% of the allometric equations reported for Sub-Saharan African forests resulted in inaccurate estimations of biomass or volume.

Generic models are typically allometric equations developed for a group of species, also referred to as multi-species models. In the tropics, they are developed at different scales from (a) local: one or a few sites within a small area with the same climate (Basuki et al., 2009; Chidumayo, 2014; Colgan et al., 2014; Goussanou et al., 2016; Henry et al., 2010; Mensah et al., 2016; Mugasha et al., 2013; Ryan et al., 2011), (b) regional: areas and regions that are large enough to cover significant rainfall and temperature gradients (Kachamba et al., 2016; Mauya et al., 2014; Ngoma et al., 2018; Nott, 2018; Verlinden and Laamanen, 2006; Vieilledent et al., 2012), and (c) pantropical: global zones (Brown, 1997; Chave et al., 2014). As we did not find definitions for local, regional and global allometric models in literature that referred to the size of the study area, we opted to link the terms to climate as it is the key driver of differences in height - diameter relationships at regional and pantropical level (Chave et al., 2014; Feldpausch et al., 2011), while climate boundaries are used in the global ecological zones for forest reporting (FAO, 2012). We cited mainly biomass models but modelling issues are very similar for volume models.

Table 1 gives an overview of generic allometric models that can be applied in southern Africa. Most generic models are calibrated with a larger amount of sample trees compared to specific models, which improves model quality (Brown, 2002; Picard et al., 2012). The pantropical generic models of Chave et al. (2014, 2005) can produce results that are almost as accurate as those obtained with local or regional generic models (Fayolle et al., 2013) or even outperform them (Mensah et al., 2016; Rutishauser et al., 2013; Vieilledent et al., 2012). The applicability of generic models to a specific region or species should however first be evaluated (Alvarez et al., 2012; Pérez-Cruzado et al., 2015).

Specific volume models are especially useful for commercially important timber species. In the tropics, they are developed at local level, while the applicability of regional volume models or use of generic biomass models to estimate volume is rarely tested. This is also the case for *Pterocarpus angolensis,* the most widely exploited timber tree of southern Africa (IRDNC, 2015; Louppe et al., 2008; Von Breitenbach, 1973). The wood of *P. angolensis* is traded as Kiaat, Mukwa, Muninga, Umbila, or Dolf, and is known for its aesthetic qualities, high durability, and high-value uses (ITTO, 2015; Takawira-Nyenya et al., 2010; Vermeulen, 1990). It has a medium basic density of 0.56 g cm^{-3} (ITTO, 2015) making it easy to work with by local communities who use manual harvesting methods with simple tools. The local timber value of *P. angolensis* is estimated to be four times as large as the carbon (CO_2) value (Moses, 2013). Centralised data on the amount of timber traded are not available, but the *P. angolensis* wood volume processed within the region is much higher than the volume exported (Lukumbuzya and Sianga, 2017). Mozambique reported the use of 47,000 m^3 for carpentry in 2012 (FAEF, 2013). Annual export is at least 5,000 m^3 for Zambia (Louppe et al., 2008), while Angola exported an average of 2,800 m^3 per year through Namibia to South-Africa in the period 2010 – 2016 (IRDNC, 2015). The wood is mainly exported in the form of planks, and round or trimmed logs.

Table 1 – Generic models for total volume (*Vtot*) and above ground biomass (*AGB*) that can be applied in the tropical dry and moist forests of southern Africa. Model characteristics include the global ecological zone (FAO, 2012), inclusion of height (*H*) as predictor, branch top diameter (*TD*), diameter at breast height (*DBH*) range, and sample size (*n*). Measures of model performance include the coefficient of determination (R^2), the residual standard error (*RSE*), relative RSE (RSE_{rel}), and bias with indication if RSE_{rel} and bias were calculated during calibration (CAL) or validation (VAL).

Source	Country	Ecological Zone	Site specificity	Vtot	AGB	With H	TD (cm)	DBH range	n	R^2 (%)	RSE	RSErel (%)	RSErel VAL	BIAS (%)	Bias VAL
1	Pantropical	NA	pantropical		X	X	0	5 - 212	4004	/	0.357 ln kg	57	X	5.3	X
1	Pantropical	NA	pantropical		X		0	5 - 212	4004	/	0.413 ln kg	72	X	9.7	X
2	Zambia	TDF	local		X		0	2 - 39	101	98	0.08 ln kg	/		4.1	
3	South Africa	TDF	local		X	X	0	2 - 79	707	82	98 kg	53		/	
4	Malawi	TMF/TMS	regional	X			2.5	5 - 111	74	92	0.937 m^3	52	X	-1.1	X
4	Malawi	TMF/TMS	regional	X		X	2.5	5 - 111	74	95	0.697 m^3	39	X	-0.4	X
5	Malawi (Phuyu)	TDF	local	X			2	5 - 40	51	95	0.003 log_{10} m^3	/		2.3	X
6	Tanzania	TDF	local	X		X	0	8 - 43	17	95	0.31 ln m^3	/		/	
7	Mozambique	TDF	local		X		0	5 - 73	29	93	0.52 log kg C	/		/	
8	Zambia	TDF/TMF	regional		X		0	5 - 70	104	/	165 kg	/		−19.9	
9	Tanzania	TDF/TMF/TS	regional	X			2.5	1 - 95	158	87	/	48	X	-0.5	X
9	Tanzania	TDF/TMF/TS	regional	X		X	2.5	1 - 95	158	88	/	48	X	-0.6	X

Global Ecological Zones: TDF = tropical dry forest, TMF = tropical moist forest, TMS = tropical mountain system, TS = tropical shrubland. Sources: 1. Chave et al. (2014), 2. Chidumayo (2014), 3. Colgan et al. (2014), 4. Kachamba et al. (2016), 5. Abbot et al. (1997), 6. Malimbwi et al. (1994), 7. Ryan et al. (2011), 8. Ngoma et al. (2018) with RSE VAL = SQRT(LOOCV) = 187 kg, 9. Mauya et al. (2014).

P. angolensis occurs sparsely in natural, virtually unmanaged forests and reaches its southern limit in the tropical dry forests of Namibia, Botswana, and South Africa at the southern edge of the Miombo Ecoregion (De Cauwer et al., 2014; FAO, 2012; Olson et al., 2001; Timberlake and Chidumayo, 2011). Timber harvest rates of *P. angolensis* are often reported as unsustainable (Caro et al., 2005; Ministry of Agriculture, Water and Forestry, 2011), while the species is underrepresented in woodland regeneration (Caro et al., 2005; De Cauwer, 2016; Dirninger, 2004; von Malitz and Rathogwa, 1999). The growing stock and allowable cut of *P. angolensis* in Namibia and Angola are however unknown. The main reason is the lack of complete and updated national forest inventory data (De Cauwer, 2015; Zweede et al., 2006). Another reason is the uncertainty of the volume models applied. There is no information on the accuracy of the available volume models for *P. angolensis* summarised in Table 2, except for the models of Abbot et al. (1997) and Mate et al. (2015). Only two of the listed models were included in the review of Sub-Saharan allometric equations of Henry et al. (2011), unfortunately with several errors included. All except one model (Mate et al., 2015) have *DBH* as a single predictor because accurate tree height measurements are often lacking. The sample area is not known for two of the models (Malimbwi and Temu, 1986 cited Hofstad, 2005, Temu, 1981 cited Hofstad, 2005), but all other are situated in tropical dry forest.

Table 2 – Tree volume models for *Pterocarpus angolensis* with diameter at breast height (*DBH*) in cm. The models of Mate et al. (2015) and Banks and Burrows (1966) estimate merchantable wood volume, all other models estimate total wood volume, as defined by the indicated top diameter.

Source	Country, Location	Overbark wood volume (V)	unit V	Top diameter (cm)	DBH range	n	R^2 (%)
1	Botswana, Chobe National Park	$V = 0.0000686 \cdot DBH^{2.678}$	m^3	5	5 - 70	50	95
2	Malawi, Phuyu	$\log_{10}V = -4.20+2.69 \cdot \log_{10}DBH$	m^3	2	5 - 30	30	94
3	Mozambique, Mavume & Inhaminga	$V = 0.016 + 0.000347 \cdot DBH^2 \cdot H$	m^3	NA	14 - 47	19	92
4	Namibia, Otjozondjupa Region	$V = (0.667061 - 0.008408 \cdot DBH + 0.0002143 \cdot DBH^2) \cdot DBH^2$	dm^3	0	5 - 75	41	?
5	Namibia, Karukuvisa District	$V = 0.0936 \cdot DBH – 2.7522$	m^3	0	31 - 64	40	62
6	Namibia	$\ln V = 2.7760988+0.1426546 \cdot DBH-0.000868738 \cdot DBH^2$	dm^3	0	5 - 75	41	?
7	Tanzania, Tabora (west)	$V = 0.092 \cdot DBH^{2.59}$	dm^3	5	?	?	97
8	Tanzania, central	$V = -170 + 35.8721 \cdot DBH-2.1968 \cdot DBH^2+0.0801 \cdot DBH^3-0.0006 \cdot DBH^4$	dm^3	5	7 - 65	?	?
9	Zimbabwe, Gwaai Forest Reserve	$V = -0.335+0.00074 \cdot DBH^2$	m^3	15	17 - 55	91	91
9	Zimbabwe, Gwaai Forest Reserve	$V = -0.3688+0.001037 \cdot DBH^2$	m^3	7.5	17 - 55	91	91

Sources: 1. Norwegian Forest Society (1992 cited Hofstad 2005), 2. Abbot et al. (1997), 3. Mate et al. (2015), 4. Korhonen et al. (1997a, 1997b), 5. Moses (2013), 6. Verlinden and Laamanen (2006), 7. Malimbwi and Temu (1986 cited Hofstad 2005), 8. Temu (1981 cited Hofstad 2005), 9. Banks and Burrows (1966)

The models in Table 2 are site-specific for the location mentioned in the table. Pantropical volume models for *P. angolensis* do not exist. Although Miombo tree species have a widely varying tree shape between sites, the tree shape of *P. angolensis* is less variable than that of many other Miombo species (Abbot et al., 1997). It therefore seems justified to verify to what extent site-specific models improve volume, and hence biomass, estimations of *P. angolensis*.

The only models available for merchantable stem volume of *P. angolensis* are those of Mate et al. (2015), and Banks and Burrows (1966). Few estimates are available for the share of the total wood volume that is merchantable (Groome et al., 1957; Moses, 2013), although the bole is often the only part of this important timber tree that is used, especially when harvested for export (Fath, 2002; Moses, 2013). The remaining wood is underutilised although it has multiple local uses including for construction, firewood, crafts, and medicines (Moses, 2013; Takawira-Nyenya et al., 2010).

Reliable data on growing stock, growth, regeneration, and potential yield are needed to support sustainable forest management and land use planning decisions. They can provide input in cost-benefit evaluations of different land uses, which gain importance considering global trends to support carbon sinks and bio-economies (Haddad et al., 2019), and regional trends of population increase with resulting deforestation for agriculture. There is also a global shift to new timber species because of depletion and stricter regulations on preferred timber species (Hofstad, 2005; Winfield et al., 2016) causing an increasing timber trade in Sub-Saharan Africa (Lukumbuzya and Anstey, 2016; Oy, 2016). The changing timber demand caused an unprecedented harvest rate of tropical hardwood in north-eastern Namibia in 2018, of which the majority still has to be exported via harbours, after the transport ban of 2019 was lifted.

This study aims at developing individual tree models to determine the volume of *P. angolensis* from a "compilation of datasets collected at different locations by independent teams" (Picard et al., 2012) for tropical dry forest in southern Africa, and to compare their performance with other species-specific volume models (Table 2) and generic volume and biomass models. Specifically, the study will (1) establish regional allometric equations for total wood volume in the study area, (2) evaluate if tree height (*H*) and climate information can improve the models, especially as this may compensate for regional differences, (3) compare the performance of the new regional models with other models at tree level for the study area: specific volume models (Table 2) and local, regional, and pantropical generic models (Chave et al., 2014; Colgan et al., 2014; Kachamba et al., 2016; Mauya et al., 2014; Ngoma et al., 2018; Ryan et al., 2011), (4) estimate and predict the share of total wood volume that is merchantable, and (5) compare volume estimations with the new and other allometric equations for all trees and *P. angolensis* at stand level for the study area. The overall aim is to contribute to putting sustainable management of important timber trees in the region on a sounder scientific base and support forest agencies in valuing timber resources.

Methods

2.1 Study area

Data were collected in the *Baikiaea - Pterocarpus* woodlands of northern Namibia and southern Angola (Figure 1) where mean annual rainfall varies between 480 and 700 mm. The study area consists of dry, open forest (FAO, 2014), with a canopy cover of 10% to 30% and canopy heights of 10 to 15 m. It is characterised by few tree species, mainly *P. angolensis*, *Baikiaea plurijuga*, *Burkea africana,* and *Schinziophyton rautanenii* (De Cauwer et al., 2016). The area is geologically homogenous, belonging to the Kalahari and Namib Sands Group (Mendelsohn et al., 2002). *P. angolensis* occurs on the deep Kalahari sands outside the river valleys (De Cauwer et al., 2016), eolian sediments that form nutrient-poor haplic to rubric arenosols (Gröngröft et al., 2013). The species reaches an average height of 11 m in this area, and most individuals have a straight, non-hollow stem unlike other species of the canopy layer.

2.2 Volume data

Our study defined wood volume as follows:

- Total wood volume (*Vtot*): the total over bark wood volume of the tree, starting from ground level and including all branches and, twigs (up to a minimum diameter of 0 cm) and the stump;
- Merchantable wood volume (*Vmer*), also referred to as timber volume: over bark wood volume of the bole that can be used as saw wood, excluding the stump. The bole is the stem up to the first branch. No minimum top diameter was defined as this is dependent on the size of the tree (Appendix A, Figure A.1). For smaller trees, it concerns the part of the stem that can be used as a straight pole or that has the potential to become saw wood. Trees for which no part of the stem had saw wood quality were removed from the data

The models combine all *Vtot* and *Vmer* data available for Namibia with some data for southern Angola. The resulting five datasets represent 14 sites: (1) data of the Namibia Finland Forestry programme (NFFP) collected between 1996 and 2000 in four administrative regions (Angombe, 2004; Chakanga et al., 1996) that were also used to develop the model of Verlinden and Laamanen (2006), (2) data of Moses (2013) collected in Kavango East, (3) data collected by Nott (2018) in three regions of Namibia, (4) data collected by De Ruytter (2015) in both Kavango regions, and (5) data collected by the first author in southern Angola and Kavango West (Figure 1; Table 3).

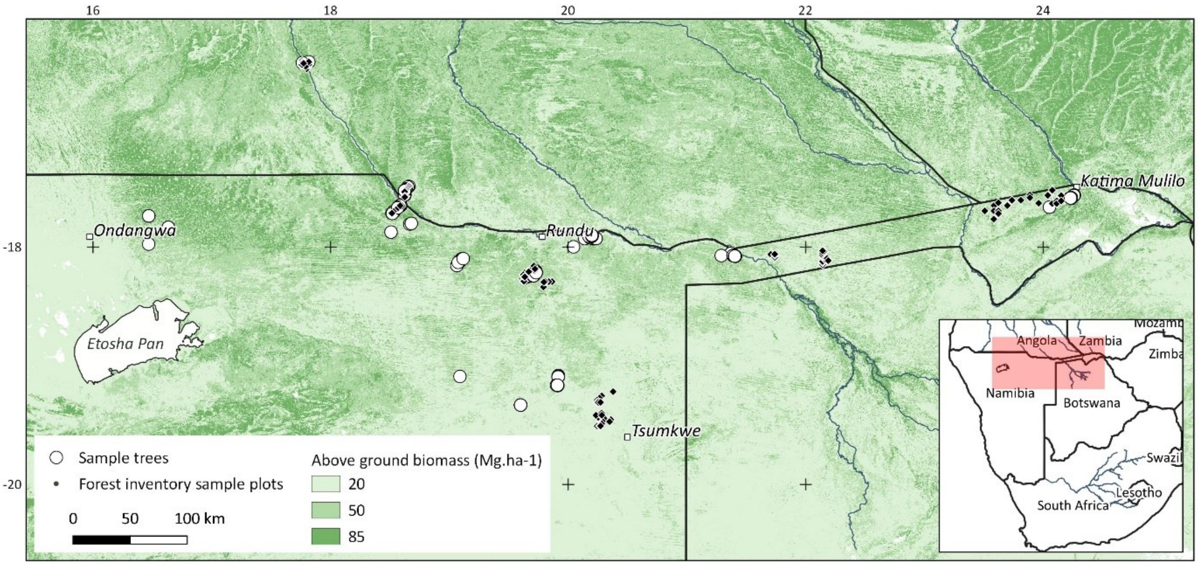

Figure 1 – Location of the study area (inset), sample trees and forest inventories in Namibia and Angola. Data of sample trees were used to determine volume models and forest inventory data to demonstrate growing stock. The above-ground biomass data is from Bouvet et al. (2018).

Table 3 – Sample trees in Namibia and Angola to determine merchantable wood volume (*Vmer*) and total wood volume (*Vtot*) with *n* the number of individual trees when both *Vmer* and *Vtot* were measured. *MAP* is the mean annual precipitation (mm), *DBH* is diameter at breast height (cm) and *SD* the standard deviation. Data were collected by Amber Nott (AN), Jolien De Ruytter (JDR), Moses Moses (MM), the Namibia Finland Forestry Programme (NFFP), and Vera De Cauwer (VDC).

Region	MAP	Data collector	Method	Number of trees			DBH			
				Vmer	Vtot	n	Mean	Min	Max	SD
Otjozondjupa	480	NFFP	Destructive	18	18	**18**	45	9	73	19
Oshikoto	522	NFFP	Destructive	8	8	**8**	42	16	58	14
Ohangwena	526	NFFP	Destructive	5	5	**5**	30	14	70	23
Kavango East	538	MM, AN	Destructive	40	40	**80**	34	5	64	15
Kavango East	584	JDR, AN	Non Destructive	76		**76**	32	5	65	17
Kavango West	566	JDR, AN, VDC	Non Destructive	161		**161**	31	5	70	15
Cuando Cubango (Angola)	623	VDC	Non Destructive	18		**18**	42	21	76	13
Zambezi	671	NFFP	Destructive	9	9	**9**	31	11	47	13
Zambezi	673	AN	Non Destructive	40		**40**	31	5	92	20
TOTAL				**375**	**80**	**415**				

The NFFP trees were selected subjectively on reasonably accessible sites to represent a *DBH* distribution between 5 and 70 cm (Angombe, 2004; Chakanga et al., 1996). It is unknown if the trees were situated in forest stands or were individuals standing along roads and agricultural fields. The results were not reported in detail, making interpretation of the volume data (Laamanen, 2002) difficult. The trees of Moses (2013) were selected subjectively in an open forest stand by an experienced logger based on their timber quality and harvestable stem size (*DBH* ≥ 39 cm). Nott (2018) selected trees at one-kilometre intervals in forest stands and equally distributed over five *DBH* classes from 5 cm to > 45 cm. The trees of the last two datasets were selected in open forest stands at regular intervals along transects perpendicular to main roads and representing the *DBH* distribution between 5 cm and 70 cm.

Volume datasets (1) to (3) were collected through destructive sampling. Total volumes of stump, stem and large branches were calculated with the Smalian formula after measuring diameters and lengths of tree and branch sections with bark. For datasets (1) and (3), the Smalian formula was applied on one-meter sections of the bole, which gives an accuracy that is similar to the application of Huber or Newton's equations on 2 m sections (de León and Uranga-Valencia, 2013). The bole data of dataset (2) were not split up in sections.

To determine total volume, branches with diameter less than 10 cm were weighed in the field and converted to volume as follows:

$$V = \frac{FM * MC}{BD} \quad \text{with} \quad BD = \frac{DM_S}{V_S} \quad \text{and} \quad MC = \frac{DM_S}{FM_S}$$

where

FM = total fresh mass of branches,

MC = conversion factor to convert from fresh mass to oven-dry mass,

BD = bulk density, determined for a sample,

DM_s = oven-dry mass of a sample,

V_s = green volume of a sample, and

FM_s = fresh mass of a sample.

A minimum of four discs of 2 cm to 10 cm thick were sampled from stems and branches of each tree, and oven-dried at 105 °C, except for the NFFP samples (Dataset 1) which were air-dried for two days (Chakanga et al., 1996). The moisture content of green *P. angolensis* wood usually varies between 70% to 80% (Vermeulen, 1990), although the data of Nott (2018) showed a mean moisture content of 65% for branches and twigs. Considering that *P. angolensis* wood takes months to reach a moisture content of 12% (Vermeulen, 1990), a correction factor of 0.63 corresponding to a moisture content of 60% (Simpson and TenWolde, 1999) was applied to the branches' volume of Dataset 1. Green volume of the samples was determined by the water displacement method. Leaf biomass was not measured as the data were collected in leaf-off season. Bark thickness was measured on stem discs.

Datasets (4) and (5) were collected through non-destructive sampling to determine the merchantable wood volume *Vmer*. Tree diameters were determined at several heights along the part of the bole that can be used as saw wood; at 0.3 and 1.3 m by measuring circumference and at 2.3 m and every consecutive 1 m up the bole with a laser dendrometer. *Vmer* was calculated with the Smalian formula for one-meter log sections. Bark thickness was measured with a metal skewer, a simplified version of a bark gauge.

Volumes were recalculated if the raw datasets were available (De Ruytter, 2015; Moses, 2013; Nott, 2018). A quality check of the total volume data was performed to verify if they are consistent with current ecological knowledge (Birigazzi et al., 2015). The total tree form factor *F*, also named cylindrical form factor, was used; this is the ratio of *Vtot* to the volume of a cylinder with a circular basal area at breast height and a length that corresponds to total tree height (Husch et al., 2002). *F* depends on tree shape and shows little variation across sites and continents, normally varying between 0.5 and 1 with a mean of 0.65 for tropical broadleaved species (Chave et al., 2005; Colgan et al., 2014). *F* very rarely exceeds 1, for example in the case of tapped *Hevea* rubber trees with 81% branches resulting in *F* equalling 1.2 (Cannell, 1984). The retained data for this study were those with $F < 1.3$. The use of *F* as a quality check is similar to the use of the interval of possibility by Henry et al. (2011), which equalled *F* values of 0 to 1 in their study.

2.3 Modelling volume

This study established models for *Vtot* and *Vmer*. The relationship between *DBH* and tree volume exhibits strong heteroscedasticity and hence were ln transformed (see e.g. Seifert and Seifert, 2014). Linear models were established for the ln transformed data, resulting in a common relation for wood volume:

$$\ln V = \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n + \varepsilon$$

with ln*V* being the natural logarithm of *Vtot* or *Vmer* in m^3, *X* the (partly ln-transformed) predictor variables with *DBH* (cm) and tree height *H* (m) as main predictors, α and β_i the intercept and slope coefficients estimated by the regression, and ε the residuals. Several standard combinations of *DBH* and *H* in the model regressions were tested (Picard et al., 2012; Verlinden and Laamanen, 2006; Vidal et al., 2016). Other predictors tested for the models were bioclimatic variables from WorldClim 2 (Fick and Hijmans, 2017) and the maximum climatic water deficit (CWD) as defined by Chave et al. (2014), as climate factors that drive water stress are important in predicting tree shape at regional and pantropical level (Chave et al., 2014; Feldpausch et al., 2011). The bioclimatic variables included long-term averages (1970-2000) for temperature seasonality, precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation of the warmest quarter. Soil and geology variables were not tested as they are fairly uniform in the areas where *P. angolensis* grows (see 2.1), while available data are not very accurate. Predictors for the models were selected based on their significance in the models.

Mixed effects modelling was also tested as it can account for sources of heterogeneity in the dataset, especially the different sampling methods used and the lack of independence between measurements per site (Chave et al., 2004; Seifert and Seifert, 2014; Zuur et al., 2009). The mixed effects models added a random component $b_i * Z_i$ (Zuur et al., 2009) reflecting differences caused by sample location, data collector, or data collection method (destructive versus non-destructive). Two formats were tested for the random component: intercept (Z_i equals 1) and both intercept and slope. Residuals of the best models were tested for differences between random sources with ANOVA (if conditions of normality and homogeneity of variances were fulfilled) or Kruskal-Wallis.

Volume estimates as predicted by the models were obtained after applying the bias correction for the back transformation of ln*Y* to *Y* as outlined by Baskerville (1972) and used by many authors, including Chave et al. (2014):

$$V = e^{\left(\alpha + \beta X + \frac{\sigma^2}{2}\right)}$$

with σ equal to the standard deviation of the residuals in log units.

Unless otherwise stated in the results, ± indicates the standard deviation (*SD*).

2.4 Model evaluation

Models were selected for evaluation when all coefficients were significant ($P < 0.05$). Model comparison and selection was done based on Akaike's information criterion (*AIC*) and the Bayesian Information Criterion (*BIC*). Both *AIC* and *BIC* measure the fit of the model and the complexity of the model, ensuring parsimonious models (Zuur et al., 2009), with a lower *AIC* and lower *BIC* for the best performing models.

The adjusted coefficient of determination R^2 was added to illustrate the performance of linear models. The residual standard error (*RSE*) was used as a measure of absolute error (Colgan et al., 2014). *RSE* was derived from the model residuals:

$$RSE = \sqrt{\frac{\sum_{i=1}^{n}\left(V_{mo,i} - V_{me,i}\right)^2}{k}}$$

with n = sample size, V_{mo} = the modelled volume, V_{me} = the measured volume for tree i, k = the degrees of freedom (n minus the number of coefficients, including intercepts).

The relative error (RSE_{rel}) was used to compare errors for different variables and areas as it is not expressed in measurement units and relative to the estimated variable (Chave et al., 2014; Colgan et al., 2014):

$$RSE_{rel} = \frac{RSE}{\frac{\sum_{i=1}^{n} V_{me,i}}{n}}$$

RSE was calculated on all data (calibration) and through 10-fold cross-validation, as described by other authors (e.g. Aertsen et al., 2010).

2.5 Bark thickness

A relationship between bark thickness and *DBH* was established to allow estimates of bark volume and timber volume without bark. A linear relationship was established between bark thickness and *DBH* for all trees for which bark thickness was measured.

2.6 Comparison of new with other models at tree level

Performance of all models was compared by applying them on the sample trees described in 2.2 and using the error measures described in 2.4. The models compared included the generic models of Table 1 that have a similar *DBH* range as our dataset and all species-specific models of Table 2. The former are the generic total volume models developed for Malawi (Kachamba et al., 2016) and Tanzania (Mauya et al., 2014), and total volume derived from four generic biomass models; both pantropical models from Chave et al. (2014), a regional model for Zambia from Ngoma et al. (2018), a local model for South-African savanna trees from Colgan et al. (2014), and a local model for Miombo trees in Mozambique from Ryan et al. (2011).

Biomass-derived from the generic models was converted to total volume by dividing by the basic wood density, the ratio of dry mass over green volume (Vieilledent et al., 2018), which serves as a proxy for the biomass conversion factor (Henry et al., 2011; Picard et al., 2012). A mean value for the basic wood density of 0.56 $g.cm^{-3}$ (ITTO, 2015) was used. This value is similar to the 0.53 $g.cm^{-3}$ and 0.60 $g.cm^{-3}$ measured for larger (*DBH* > 30 cm) and smaller trees respectively in Namibia (Korhonen et al., 1997), and represent composite densities for both stem and branches up to 5 cm diameter (Chakanga et al., 1996). No data are available on the basic wood density of *P. angolensis* twigs, which represent about 15% of the biomass (Moses, 2013; Nott, 2018). The models of Chave et al. (2014) and Colgan et al. (2014) included a correction factor for the back transformation of the natural logarithm of biomass. No correction factors were available for the back transformation of ln *V* or log *V* for the other models.

The performance of the *Vmer* models was compared with the models of Mate et al. (2015) and the model with a top diameter of 15 cm of Banks and Burrows (1966) (Table 2), as well as with the volume equation of a cylinder with saw log length.

2.7 Comparison of models at stand level

Forest inventory data from six study sites representing different rainfall zones were selected (Table 4). Own inventory data were used, as well as data collected by the Namibian Directorate of Forestry (Chakanga et al., 1998; Chakanga and Selanniemi, 1998). Each site was represented by 20 to 24 plots; if the plots were part of a larger inventory, they were randomly selected in QGIS. All plots had a minimum tree cover of 10% and consisted of two to three nested sub-plots whereby all trees with minimum *DBH* of 5 cm were measured in the smallest sub-plot with as radius 10 m, trees with *DBH* larger than 20 cm in a sub-plot with radius 20 m, and trees with *DBH* larger than 45 cm in the optional largest sub-plot with radius 30 m (Burke et al., 2001).

Table 4 – Study sites for which forest inventory data were available, representing different classes of mean annual precipitation (*MAP*). Mean basal area (*BA*) is in m^2 per ha. The basal area of *Pterocarpus angolensis* (PteAng) is expressed as a portion of the mean *BA*.

Study site	Region (Country)	MAP class (mm)	# Plots	# Trees	Mean BA	BA % PteAng
Nyae Nyae North	Otjozondjupa (Namibia)	450 - 500	20	119	2.8	3.5
Bwabwata National Park	Zambezi (Namibia)	500 - 550	20	98	2.4	3.1
Kavango East	Kavango East (Namibia)	500 - 550	24	252	5.2	11.6
Nkurenkuru - Cuangar	Kavango West (Namibia) / Cuando Cubango (Angola)	600 - 650	21	524	7.2	28.8
Caprivi State Forest	Zambezi (Namibia)	600 - 650	20	141	4.4	4.0
Caiundo	Cuando Cubango (Angola)	700 - 750	24	326	7.4	9.6
TOTAL			**129**	**1460**	**4.9**	**10.1**

The new volume models were applied to the *P. angolensis* trees of the forest inventories to estimate growing stock at stand level. The pantropical and the best regional generic models, as well as the specific NFFP models were applied to (1) *P. angolensis,* and (2) all species, to compare the differences in total volume obtained at stand level. The NFFP models include the model for *P. angolensis* and six other models covering the majority of species in the inventory data (Verlinden and Laamanen, 2006). Basic wood density was used as biomass conversion factor for the generic models and derived from global databases and literature (ICRAF, 2020; ITTO, 2015; Meier, 2020; Nygård and Elfving, 2000; PROTA, 2015) for most species. For the 7% of the trees for which no basic wood density was available, the mean basic wood density of 0.63 $g.cm^{-3}$ was assigned. Wood density obtained from the World Agroforestry database (ICRAF 2020) measured at 12% moisture was multiplied by 0.828 to obtain basic wood density (Vieilledent et al., 2018). Comparisons between model results were done with the Wilcoxon signed-rank test.

3. Results

3.1 New total wood volume (*Vtot*) models for *P. angolensis*

Models for *Vtot* were established with the data of 69 trees with mean *DBH* of 44 ± 13 cm, after 11 trees were removed with $F < 1.3$. *F* was on average 0.71 ± 0.16 for the remaining trees. Fifty-one trees had reached the minimum harvestable diameter of 40 cm (Ministry of Agriculture, Water and Forestry, 2015), and had a mean total volume of 2.2 ± 0.9 m^3. The best model with *DBH* as single predictor explained 94% of the variance and had an error of 28% (Model 1, Table 5). Addition of climate-related predictors did cause significant improvement ($P = 0.014$) and reduced the error to 25% (Model 2, Table 5).

Adding *H* as a predictor to Model 1 improved model performance even more ($P < 0.001$) resulting in the lowest error of all models (Model 3). Adding quadratic components, the interaction between *DBH* and *H* or climate variables to Model 3 did not improve performance.

Residuals of models 2 and 3 did not significantly vary with location nor collector and thus mixed effects models did not result in a better performance. The residuals of Model 1 did vary significantly with location and collector ($P < 0.001$). A mixed model with location as random intercept was significantly better than Model 1 ($P < 0.001$), however, the fixed part of the model showed a higher error during validation than Model 1.

Table 5 – Total wood volume (*Vtot* in m^3) models with intercept *a* including the Baskerville correction factor. *MinT* is the minimum temperature of the coldest month (°C), *MAP* is the mean annual precipitation (mm) and *PWQ* is precipitation of the warmest quarter (mm) of WorldClim (Fick and Hijmans, 2017), *H* is tree height (m), *RSE* is the standard error and RSE_{rel} the relative error. Data of 69 trees were used with diameter at breast height (*DBH*) in the range of 9 to 73 cm. Significance of regression coefficients is indicated as $P < 0.001$ (***) and $P < 0.01$ (**).

Model No	Model	*a*	b_1	b_2	b_3	b_4	Adjusted R^2	RSE m^3	RSErel (%)	RSE m^3	RSErel (%)
								Calibration		Validation	
1	$V_{tot} = exp(a + b_1 * lnDBH)$						0.94	0.49	28	0.49	28
		-8.796 ***	2.441 ***								
2	$V_{tot} = exp(a + b_1 * lnDBH + b_2 * MinT + b_3 * MAP + b_4 * PWQ)$						0.95	0.40	23	0.44	25
		-7.765 ***	2.392 ***	-0.758 **	0.014 **	-0.0210 **					
3	$V_{tot} = exp(a + b_1 * lnDBH + b_2 * H)$						0.96	0.36	21	0.38	22
		-8.626 ***	2.232 ***	0.041 ***							

3.2 Comparison of total wood volume (*Vtot)* models at tree level

Table 6 illustrates the performance of the other models as tested with our sample trees. The four best performing models, of which one is a biomass model, included both *DBH* and *H* as predictors. The generic models of Chave et al. (2014) and Mauya et al. (2014) performed better than all species-specific models of table 2, except our Model 3. The five best models with *DBH* as the single predictor, including our Model 1 and one biomass model, showed a similar error (28% - 30%) and were developed for Zimbabwe, Namibia, Zambia, and Tanzania. However, two of those models were applied outside their *DBH* calibration range and did not include branches with diameter smaller than 5 and 7.5 cm respectively (Table 6). The similarity of Model 1 with the models of Ngoma et al. (2018) and Mauya et al. (2014) is shown in Figure 2. The pantropical model of Chave et al. (2014) without *H* results in an underestimation (Figure 2). The local model of Moses (2013), at the southern limit of the distribution range of *P. angolensis* in Namibia, did not perform as well as the regional model developed by the NFFP (Verlinden and Laamanen, 2006). However, the model of Verlinden and Laamanen cannot be used for trees with a *DBH* slightly larger than 75 cm (Figure 2), as defined by its calibration range (Table 2).

Table 6 – Performance of specific and generic models for estimating the total wood volume of *Pterocarpus angolensis* (*Pteang*) in the *Baikiaea – Pterocarpus* woodlands. Models with diameter at breast height (*DBH*) as single predictor are indicated. *RSE* is the standard error and RSE_{rel} the relative error. Models indicated with (*) are applied outside their *DBH* range, with (**) outside their ecological zone.

Source	Country	Site specificity	*Pteang*	Only DBH	AGB	RSE m^3	RSErel (%)	n
Mauya et al. (2014)	Tanzania	regional				0.38	22	158
De Cauwer et al. : model 3 of this study	Namibia	regional	x			0.38	22	69
Chave et al. (2014): with tree height	pantropical	pantropical			x	0.39	23	4004
De Cauwer et al. : model 2 of this study	Namibia	regional	x			0.44	25	69
Banks and Burrows (1966): top diameter 7.5 cm (*)	Zimbabwe	local	x	x		0.49	28	91
De Cauwer et al. : model 1 of this study	Namibia	regional	x	x		0.49	28	69
Ngoma et al. (2018)	Zambia	regional		x	x	0.50	29	104
Verlinden and Laamanen (2006)	Namibia	regional	x	x		0.52	30	41
Temu (1981 cited Hofstad 2005) (*)	Tanzania	local	x	x		0.52	30	?
Korhonen et al. (1997)	Namibia	local	x	x		0.59	34	41
Malimbwi and Temu (1986 cited Hofstad 2005)	Tanzania	local	x	x		0.59	34	?
Mauya et al. (2014)	Tanzania	regional		x		0.64	36	158
Abbot et al. (1997) (*)	Malawi	local	x	x		0.64	36	30
Norwegian Forest Society (1992 cited Hofstad 2005)	Botswana	local	x	x		0.69	39	50
Chave et al. (2014): without tree height	pantropical	pantropical		x	x	0.69	40	4004
Moses (2013)	Namibia	local	x	x		0.70	40	40
Colgan et al. (2014)	South Africa	local			x	0.77	44	707
Kachamba et al. (2016) (**)	Malawi	regional				0.79	45	74
Ryan et al. (2011)	Mozambique	local		x	x	0.82	47	29
Kachamba et al. (2016): without tree height (**)	Malawi	regional		x		0.89	51	74

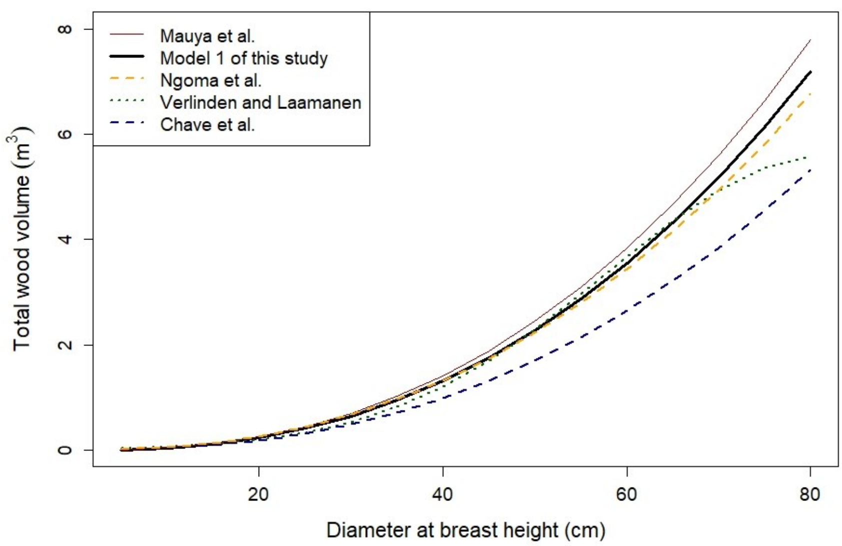

Figure 2 – Comparison of total tree volume models with diameter at breast height as a single predictor: three generic models (Chave et al., 2014; Mauya et al., 2014; Ngoma et al., 2018) and two models for *Pterocarpus angolensis*. The environmental stress variable *E* of Chave et al.'s model without height was set to the mean of our dataset (*E* = 0.892).

3.3 Bark thickness

Mean bark thickness was 22 mm ± 9 mm. A linear relation between bark thickness (mm) and *DBH* (cm) explained 26% of the variability (n = 367):

$$Bark\ thickness\ (mm) = 12.5768 + 0.2754\ DBH\ (P < 0.001)$$

3.4 Merchantable volume models at tree level

The portion of merchantable wood was on average 35 ± 13% of *Vtot*. About one third of the trees (126) had reached a *DBH* of 40 cm or more, with a mean sawlog length of 4.2 ± 1.5 m and a mean *Vmer* of 0.71 m^3 or 34 ± 13% of *Vtot*. Trees with the minimum harvest *DBH* of 40 cm had a mean *Vmerc* of 0.41 ± 0.11 m^3 and mean sawlog length of 4.0 ± 1.2 m.

A model with *DBH* as single predictor resulted in an error of 50% (Model 4, Table 7). Model residuals varied significantly (P < 0.001) with location and collector, but not with method (P = 0.083). A mixed model with the addition of a random factor per collector improved the model significantly (P < 0.001) and more than a mixed model with a random factor per location. The intercept for the collector varied from -0.248 for Amber to 0.138 for Jolien. Random factors for Moses (0.071) and Vera (0.039) were small. However, the fixed part of the model showed a higher error during validation than Model 4.

Table 7 - Merchantable volume (*Vmer* in m^3) models with intercept a including the Baskerville correction factor. All regression coefficients are significant with P < 0.001 (***), P < 0.01 (**), and P = 0.010 (*). Model error is measured with the standard error *RSE* and the relative error RSE_{rel}. Predictors include diameter at breast height *DBH* (cm), tree height *H* (m), the sawlog length *SL* (m), the mean annual precipitation *MAP* (mm), the mean precipitation in the warmest quarter *PWQ* (mm) and the temperature seasonality *TS* as the standard deviation * 100 (°C). Data of 340 trees were used for Model 6 and 356 trees for all other models. *DBH* range is between 5 and 92 cm.

Model No	Model	a	b_1	b_2	b_3	b_4	b_5	Adjusted R^2	RSE (m^3)	RSErel (%)	RSE (m^3)	RSErel (%)
									Calibration		Validation	
4	$Vmer = \exp(a + b_1*(\ln DBH)^2 + b_2*(\ln DBH)^3$							0.92	0.18	49	0.18	50
		-7.533 ***	0.896 ***	-0.110 ***								
5	$Vmer = \exp(a + b_1*(\ln DBH)^2 + b_2*(\ln DBH)^3 + b_3*PWQ + b_4*MAP + b_5*TS)$							0.94	0.16	45	0.17	46
		-13.477 ***	0.891 ***	-0.108 ***	-0.021 ***	0.010 **	0.011 *					
6	$Vmer = \exp(a + b_1*(\ln DBH)^2 + b_2*(\ln DBH)^3 + b_3*\ln H)$							0.95	0.17	46	0.17	47
		-7.821 ***	0.599 ***	-0.064 ***	0.800 ***							
7	$Vmer = \exp(a + b_1*\ln DBH + b_2*(\ln DBH)^2 + b_3*\ln(SL) + b_4*\ln(SL)*(\ln DBH)^2$							0.99	0.07	20	0.07	21
		-9.913 ***	2.556 ***	-0.120 ***	0.504 ***	0.030 ***						

Adding climate related predictors was a significant improvement (P < 0.001) (Model 5), although residuals still varied significantly with location (P = 0.008), collector (P < 0.001), and method (p<0.001). Adding height to Model 4 also increased model performance (P < 0.001) (Model 6), with residuals showing significant differences per method (P = 0.009) and per collector (P < 0.001), but not location (P = 0.066). Addition of climate variables to Model 6 did not improve model performance (P = 0.024). The best mixed model structure for Models 5 and 6 had a random intercept for collector and performed better than their linear counterparts (P < 0.001), although the fixed parts did not lower the validation error.

The best prediction that can be made for *Vmer* is when the bole length is known (Model 7). The model performed better than the volume equation for a cylinder, which overestimates *Vmer* (Table 8). The volume models of Banks and Burrows (1966) and Mate et al. (2015) were applied outside their calibration range and resulted in large errors.

Table 8 – Performance of merchantable wood volume models for *Pterocarpus angolensis* in south-western Africa. Model predictors include diameter at breast height (*DBH*), tree height (*H*), and sawlog length. *RSE* is the standard error and RSE_{rel} the relative error. Models indicated with (*) are applied outside their *DBH* range.

Source	Country	*Pterocarpus angolensis*	DBH	H	Saw-log	RSE m^3	RSErel (%)
De Cauwer et al. : model 7 of this study	Namibia	x	x		x	0.07	21
Volume equation of a cylinder	NA		x		x	0.14	38
De Cauwer et al. : model 5 of this study	Namibia	x	x			0.17	46
De Cauwer et al. : model 6 of this study	Namibia	x	x	x		0.17	47
De Cauwer et al. : model 4 of this study	Namibia	x	x			0.18	50
Banks and Burrows (1966): top diameter 15 cm (*)	Zimbabwe	x	x			0.68	187
Mate et al. (2015) (*)	Mozambique	x	x	x		8.26	2288

3.5 Comparison of models at stand level

The mean *Vtot* of *P. angolensis* was estimated with our models, as well as five other models for all inventory plots (Figure 3). There was a large variation in number of trees (15.0 ± 28.7 ha^{-1}) and basal area (0.63 ± 1.1 $m^2.ha^{-1}$) between plots, with 57% of the 129 forest inventory plots not containing *P. angolensis* trees, resulting in high standard deviations (> 9 m^3). The two Chave et al. (2014) models gave significantly lower volume estimates than our best Model 3 ($P < 0.001$), while all others gave significantly higher estimates. Model 1 overestimates total volume with 8% compared to Model 3, which includes H as a predictor. The mean for our Model 2 was affected by one unrealistically high outlier (126 $m^3.ha^{-1}$) caused by an abrupt decrease of about 120 mm in precipitation of the warmest quarter in the northern area of the Caprivi State Forest.

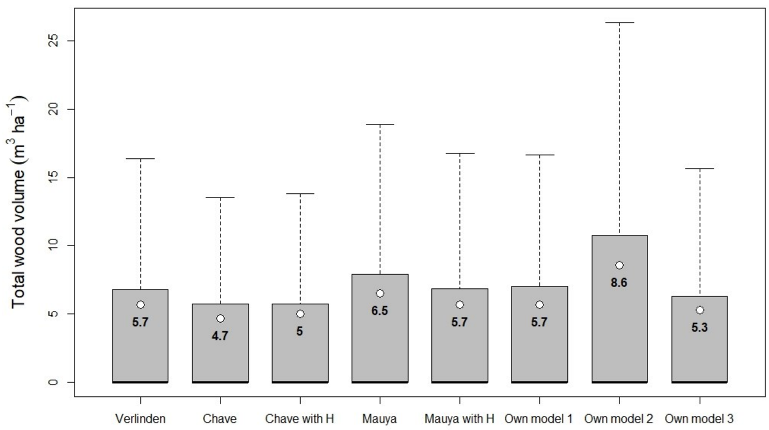

Figure 3 – Total wood volume of *Pterocarpus angolensis* for the inventory data (129 plots) of the *Baikiaea – Pterocarpus* woodlands as estimated with pantropical generic models (Chave et al., 2014), the best regional generic model (Mauya et al., 2014) with and without tree height (H), regional specific models of this study and Verlinden and Laamanen (2006). Mean values are added to the boxplot, with the grey boxes representing the data between median and third quartile.

Figure 4 illustrates the differences in merchantable wood volume of *P. angolensis* obtained with our models and the cylinder equation for the inventory data. There were no significant differences between the estimates of Models 4, 6, and 7, while the volume equation of a cylinder and Model 5 gave significantly higher results than our best Model 7 ($P < 0.001$).

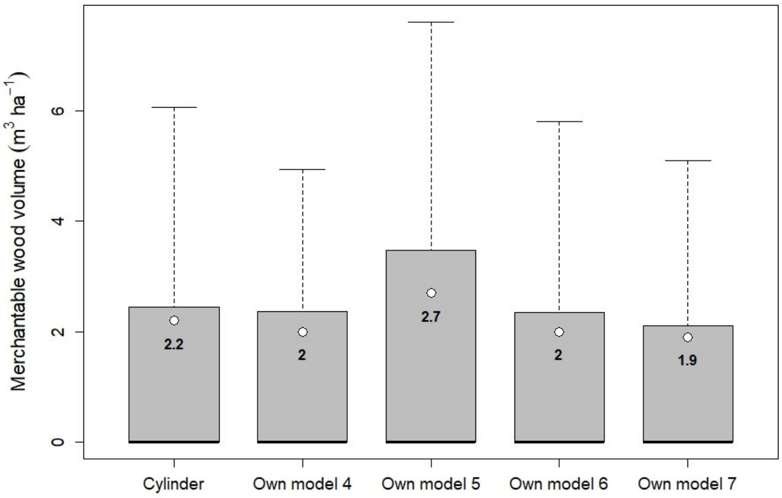

Figure 4 – Merchantable wood volume of *Pterocarpus angolensis* for the inventory data of the *Baikiaea – Pterocarpus* woodlands with the models of this study compared with the application of the volume of a cylinder. Mean values are added to the boxplot.

Application of other models on all tree species showed volume estimates between 35.7 m^3 and 52.3 m^3 (Figure 5). The estimate of 44.3 ± 32.5 $m^3.ha^{-1}$ with the species-specific models of Verlinden and Laamanen (2006) was the closest to the estimate of 42.0 ± 31.3 $m^3.ha^{-1}$ by the generic model of Mauya et al. (2014) that included *H*.

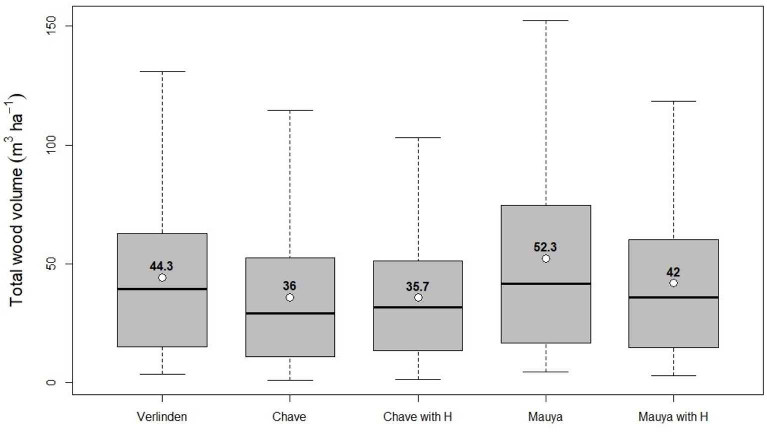

Figure 5 – Estimated total wood volume of all species from inventory data of the *Baikiaea – Pterocarpus* woodlands with regional specific volume models (Verlinden and Laamanen, 2006), and pantropical (Chave et al., 2014) and regional (Chidumayo, 2013; Mauya et al., 2014) generic biomass models. Mean values of total wood volume are added to the boxplot.

4. Discussion

4.1 New total wood volume (*Vtot*) models for *P. angolensis*

Three individual tree models were derived to estimate *Vtot* for *P. angolensis* on a regional level. The model with *DBH* as a single predictor (Model 1) had the same format as one of the generic biomass models of Brown (1997) for tropical dry forest. The error of 28 % was better than reported for the regional models of Mauya et al. (2014) and Kachamba et al. (2016) (Table 1). The model gives a bias per location which was removed by adding climatic predictors, indicating that tree shape does vary slightly within Namibia and southern Angola.

Use of the form factor *F* proved a good measure for determining data quality. Mean *F* of the 11 removed trees was 2.1, unrealistically high and probably caused by measurement or calculation errors, and/or the fact that the wood was less dry than the estimated 60%. A test was performed by removing only trees with *F* < 1.8 because Henry et al. (2010) report a form factor up to 1.66 in a tropical rainforest in Ghana. However, this increased model error with about 20% with a high heterogeneity for the model residuals that could not be removed with climate factors or *H* (Figure B.1). Mean *F* of the 69 trees used for our models (0.71) was very similar to those estimated by other studies (Chave et al., 2005; Colgan et al., 2014).

4.2 Tree height (*H*) as predictor

Adding *H* as a predictor to Model 1 increased the adjusted R^2 with 2% and reduced our model error with 6% (Model 3), more than many studies in Miombo woodlands indicate (Abbot et al., 1997; Hofstad, 2005; Mugasha et al., 2013) although Malimbwi *et al*. (1994) and Kachamba et al. (2016) show an even a larger increase in model performance. Model 3 also resolved the heterogeneity in the data caused by location, hence becoming site independent, as also indicated in other studies (e.g. Köhl et al., 2006). Moreover, two of the generic models with *DBH* and *H* as predictors (Chave et al., 2014; Mauya et al., 2014) performed as good as the new Model 3 and outperformed all other specific models. However, the model of Mauya et al. does not account for twigs with diameter smaller than 2.5 cm. If accurate *H* data are available, no local or even specific volume model is required for *P. angolensis*, rather a robust model that includes *DBH* and *H*. A problem is that accurate *H* measurements are often lacking in the study area, and that good site-specific *H:DBH* relations need to be developed (Chave et al., 2014; Mensah et al., 2018). Development of local and accurate *H:DBH* relations that feed into volume or biomass models with *H* as predictor is a more efficient and less expensive method than the development of site-specific volume or biomass models.

4.3 Comparison of total wood volume (*Vtot)* models at tree level

Comparison with other volume models showed that an error of 28% to 30% is the best model accuracy that can be obtained for a regional model in our study area when using *DBH* as a single predictor. Other studies that developed regional models with *DBH* as single predictor showed errors of 48% and higher (Table 1). Unfortunately, few models are summarised in literature with characteristics that allow an objective comparison, such as the use of RSE_{rel}, which does not include a measurement unit, or indication if error was calculated during calibration or validation. The other models that performed as well as our Model 1 with *DBH* as single predictor, and that were applied within the *DBH* range of calibration, were the regional volume model for Namibia (Verlinden and Laamanen, 2006) and a regional generic biomass model for Zambia (Ngoma et al., 2018). From all models in Table 1, the study area of Ngoma et al. (2018) was the closest to ours. No regional generic models were found for the tropical dry forest of south-west Africa. The pantropical model of Chave et al. (2014) with *DBH* as a single predictor is not advised for Namibia as it underestimates the tree volume of *P. angolensis* with an error of 40% (Figure 2). The model is based on trees that are on average much taller and with a smaller crown than the trees in our study because of an underrepresentation of very dry tropical forest sites in the database of Chave et al. (2014); 22 of the 58 forest sites are dry forest sites of which only three sites have a mean annual rainfall below 800 mm and an environmental stress variable *E* higher than 0.8, as in our study area.

The performance of generic models was not affected by the use of a biomass model with basic wood density as biomass conversion factor, but rather by the site specificity of the model. Pantropical and regional models performed much better than local models. The only exception is the model of Kachamba et al. (2016), but this model was applied outside its ecological zone. The model of Mauya et al. (2014) did cover three ecological zones, but included tropical dry forest (Table 1).

4.4 Merchantable wood volume (*Vmer)* of *P. angolensis*

The *Vmer* of all sample trees with *DBH* > 40 cm was on average 0.71 m^3, however large trees were oversampled to represent an equal *DBH* distribution while in reality, there are very few trees with *DBH* larger than 55 cm in the *Baikiaea-Pterocarpus* woodlands (De Cauwer, 2016). The *Vmerc* of a *P. angolensis* tree with minimum harvest *DBH* of 40 cm is only 0.41 m^3, and about 8% is bark (using our bark thickness relation) and 34 % sapwood (using the heartwood relation in De Cauwer, 2016), resulting in only 58% or 0.25 m^3 of heartwood. Bark thickness increases with *DBH*, although this explains only 26% of the variability, relatively low compared with the R^2 values of the Bark:*DBH* relation found by Nygård and Elfving (2000) for a range of species (21 - 54 %).

Vmerc represents on average only 35% of *Vtot*, which is the same as the portion found by Groome et al. (1957) for *P. angolensis*. The remaining portion of *Vtot* is rarely utilised in the study area, except for firewood or by wood carpenters, as the sawlog is considered the only part with enough heartwood for furniture and planks, the main market demand (Moses, 2013). Another reason for the limited use of branch wood may be that transport from the harvest site to towns is not always cost efficient.

Our results show that *Vmer* cannot be accurately modelled, yielding errors of almost 50% if no information on the length of the sawlog is available. The length of the sawlog is difficult to predict in a natural forest because it is not only depending on the size of the tree, but on many other factors including the site, former competition by other vegetation, genetic factors, which influence length and straightness of stem, and damage or resprouting caused by fire or insects (Figure A.1). The mixed models demonstrated that the estimation of *Vmer* is subjective, as it requires determining the length of the sawlog. Hence, *Vmer* measurements varied with the collector with some collectors giving systematically higher estimates, although the use of a destructive versus a non-destructive method had no effect.

The *Vmer* model of Mate et al. (2015), which does not use information on sawlog length, performed very badly for our dataset. The model was developed with a limited dataset of 19 trees within the *DBH* range 14 – 47 cm. Reducing our dataset to the same *DBH* range still gave an error of 1892%, but the *H* range of our dataset (3.9 – 20.7 m for *DBH* range 14 – 47 cm) was much larger than that of Mate et al. (2015) in Mozambique (6.5 – 14.8 m). It further highlights the need to use a large amount of trees for model development (Picard et al., 2012) and to develop site-specific *H:DBH* models.

If the sawlog length is measured with non-destructive methods in the field, *Vmer* can be estimated with an error of about 21% (Model 7). In Namibia, *Vmer* is often estimated with the volume of a cylinder for forest inventories. However, our study shows that this practice results in overestimations with an error of about 40%.

4.5 Comparison at stand level for *P. angolensis* and climate as predictor

The similarity of calibration and validation errors of the three new total volume models showed they are robust and can be used for determining the growing stock of *P. angolensis* in the study area. Although adding climate variables improved model performance, the models did not perform well at stand level, indicating overfitting of the models to the dataset of Table 2. Hence, climate information of WorldClim cannot compensate as well for regional differences as *H* does. WorldClim data may not be of sufficient quality for our purposes as they are based on extrapolations of data collected by few weather stations in our study area (Hijmans et al., 2005), while there is a high spatial and temporal variability in rainfall. Use of climate variables derived from satellite data may provide better predictors.

The number of plots included in this study was not high enough to capture the high variability in total tree volume in the large study area. This is especially the case for volume estimates of *P. angolensis*, for which the standard deviation was higher than the volume estimates. Despite the high error caused by the limited sample size, the differences between the model estimates do indicate the effect of model errors. Resource managers should however invest in regional and national forest inventories to capture the high variability in the dry tropical forest of southwestern Africa, especially of a valuable timber tree such as *P. angolensis*. The relative proportion of *P. angolensis* in the study area (10% of the basal area, Table 4) is higher than in most sub-Saharan forests and woodlands with better water availability, where it represents about 1% to 4% of the basal area (Banda et al., 2008; De Cauwer et al., 2018; Kalaba et al., 2013; Malimbwi et al., 1994; Mudekwe, 2007; Syampungani, 2009). The few other sites with a similar proportion of *P. angolensis* include the Bushbuckridge Nature Reserve in South Africa where it represents 18% of the basal area (Shackleton and Scholes, 2011) and southern Mozambique where it represents 4.7% of the basal area for wet Miombo and 17.5% for dry Miombo (Mate et al., 2014).

4.6 Comparison at stand level for all tree species

The mean growing stock of all species in the inventory plots was estimated at 35.7 m^3 ha^{-1} with the model of Chave et al. (2014), considerably less than the 44.3 m^3 ha^{-1} estimated with the regional models (Mauya et al., 2014; Verlinden and Laamanen, 2006). Although the study has shown how well the pantropical model of Chave et al. (2014) with height performs for *P. angolensis*, the model will have to be validated further for a wider range of species in the *Baikiaea* – *Pterocarpus* woodlands. More studies on basic wood density, such as done by Nygård and Elfving (2000), may suffice as wood density was not available for all species.

Conclusions

Three regional allometric equations for the total tree volume of *P. angolensis* were developed with data from 69 Namibian trees of sites representing tropical dry forest and a rainfall gradient (480 – 670 mm). The best performing model was a log model with *DBH* and tree height (*H*) as predictors (RSE_{rel} 22%). If accurate *H* data are available, no site-specific volume models are required for *P. angolensis.* Volume estimations can be done with our regional specific model, the regional generic model of Mauya et al. (2014), or the pantropical generic model of Chave et al. (2014), all with *DBH* and *H* as predictors (RSE_{rel} 22 - 23%). The performance of generic models was not affected by the use of a biomass model to estimate total volume. Although local and specific models may appear more relevant, many specific and local generic models have a restricted number of sample trees and *DBH* range. Model choice should be based on objective model characteristics such as the relative model error, the ecological zone, and the number and *DBH* range of the sample trees. Pooling data of the same global ecological zone increases the number of samples, the *DBH* range and the accuracy of the models, and should be given higher priority than collecting new data.

Without *H* or climate data as predictors, models became site dependent and the error increased to 28% - 30% for the best models, which included our model as well as a generic specific model of Verlinden and Laamanen (2006) for Namibia, and a biomass model of Ngoma et al. (2018) for Zambia. The second pantropical model of Chave et al. (2014) that does not include *H* should not be used as it underestimates total volume with an error of 40%.

Merchantable wood volume can only be accurately modelled (*n* = 356, 21%) when sawlog length is available,although mixed models proved sawlog length to be a subjective measurement. *Vmerc* of a *P. angolensis* tree with minimum harvest *DBH* of 40 cm is 0.41 m^3, of which only 58% is heartwood, the main market demand.

The mean growing stock of *P. angolensis* varies between 4.7 and 8.6 m^3 ha^{-1} based on the model used, with the contribution to the total growing stock between 13% and 14%. The differences in growing stock affect sustainable yield estimates and illustrate the need for accurate allometric equations.

Our results show that allometric studies in the tropics should be directed towards the collection of accurate basic wood density data, preferably for all tree components (twigs, branches, stem), and the collection of enough *H* and *DBH* data to develop accurate site-specific *H:DBH* models, rather than developing site-specific volume or biomass models with a limited amount of sample trees. This will improve the performance of the best volume and biomass models, including the pantropical model of Chave et al. (2014), and is a more efficient and less expensive method.

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References

Abbot, P., Lowore, J., Werren, M., 1997. Models for the estimation of single tree volume in four Miombo woodland types. Forest Ecology and Management 97, 25–37.

Aertsen, W., Kint, V., Van Orshoven, J., Özkan, K., Muys, B., 2010. Comparison and ranking of different modelling techniques for prediction of site index in Mediterranean mountain forests. Ecological Modelling 221, 1119–1130.

Alvarez, E., Duque, A., Saldarriaga, J., Cabrera, K., de Las Salas, G., del Valle, I., Lema, A., Moreno, F., Orrego, S., Rodríguez, L., 2012. Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. Forest Ecology and Management 267, 297–308.

Angombe, S., 2004. Site form and improving volume estimation of uneven-aged forest stands in northern Namibia (Master in Environmental Science). Australian National University, Canberra.

Banda, T., Mwangulango, N., Meyer, B., Schwartz, M.W., Mbago, F., Sungula, M., Caro, T., 2008. The woodland vegetation of the Katavi-Rukwa ecosystem in western Tanzania. Forest Ecology and Management 255, 3382–3395.

Banks, P.F., Burrows, P.M., 1966. Preliminary local volume tables for Baikiaea plurijuga, Guibourtia coleosperma and Pterocarpus angolensis in Rhodesia. Commonwealth Forestry Review 45, 256–264.

Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2, 49–53.

Basuki, T., Van Laake, P., Skidmore, A., Hussin, Y., 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. Forest Ecology and Management 257, 1684–1694.

Birigazzi, L., Gamarra, J.G., Sola, G., Giaccio, S., Donegan, E., Murillo, J., Henry, M., Picard, N., 2015. Toward a transparent and consistent quality control procedure for tree biomass allometric equations. Presented at the Xiv World Forestry Congress, Durban, South Africa.

Bouvet, A., Mermoz, S., Le Toan, T., Villard, L., Mathieu, R., Naidoo, L., Asner, G.P., 2018. An above-ground biomass map of African savannahs and woodlands at 25m resolution derived from ALOS PALSAR. Remote Sensing of Environment 206, 156–173. https://doi.org/10.1016/j.rse.2017.12.030

Brown, S., 2002. Measuring carbon in forests: current status and future challenges. Environmental Pollution 116, 363–372.

Brown, S., 1997. Estimating biomass and biomass change of tropical forests: a primer. Food & Agriculture Org.

Burke, A., Juola, V., Korhonen, K., Selaniemmi, T., Chakanga, M., 2001. Field instructions for the NFI.

Cannell, M.G.R., 1984. Woody biomass of forest stands. Forest Ecology and Management 8, 299–312.

Caro, T.M., Sungula, M., Schwartz, M.W., Bella, E.M., 2005. Recruitment of Pterocarpus angolensis in the wild. Forest Ecology and Management 219, 169–175. https://doi.org/10.1016/j.foreco.2005.07.004

Chakanga, M., Juola, V., Korhonen, K., 1996. Field instructions: collection of sample tree data for volume and biomass tables, National Forest Inventory Project. Directorate of Forestry, Windhoek.

Chakanga, M., Korhonen, K., Selaniemmi, T., 1998. Forest inventory report of Caprivi region. National Forestry Inventory sub-component. [WWW Document].

Chakanga, M., Selanniemi, T., 1998. Forest Inventory report of Nkurenkuru concession area. Namibia Finland Forestry Programme, Windhoek.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. Philosophical Transactions of the Royal Society of London: Biological Sciences 359, 409–420.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20, 3177–3190.

Chidumayo, E.N., 2014. Estimating tree biomass and changes in root biomass following clear-cutting of Brachystegia-Julbernardia (miombo) woodland in central Zambia. Environmental Conservation 41, 54–63.

Chidumayo, E.N., 2013. Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots. Forest Ecology and Management 291, 154–161.

Colgan, M.S., Swemmer, T., Asner, G.P., 2014. Structural relationships between form factor, wood density, and biomass in African savanna woodlands. Trees 28, 91–102.

De Cauwer, 2015. Towards estimation of growing stock for the timber tree Pterocarpus angolensis in Namibia, in: Bridging the Gap between Forest Information Needs and Forest Inventory Capacity. Presented at the DAAD World Forestry Congress Workshop, University of Göttingen, Pietermaritzburg, South Africa.

De Cauwer, V., 2016. Autecological aspects of the African timber tree Pterocarpus angolensis in support of its sustainable management (PhD). KU Leuven, Leuven, Belgium & Windhoek, Namibia.

De Cauwer, V., Geldenhuys, C.J., Aerts, R., Kabajani, M., Muys, B., 2016. Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa. Forest Ecosystems 3, 23. https://doi.org/10.1186/s40663-016-0080-9

De Cauwer, V., Knox, N., Kobue-Lekalake, R., Lepetu, J.P., Ompelege, M., Naidoo, S., Nott, A., Parduhn, D., Sichone, P., Tshwenyane, S., Elizabeth, Y., Revermann, R., 2018. Woodland resources and management in southern Africa, in: Climate Change and Adaptive Land Management in Southern Africa – Assessments, Changes, Challenges, and Solutions, Biodiversity & Ecology. pp. 296–308.

De Cauwer, V., Muys, B., Revermann, R., Trabucco, A., 2014. Potential, realised, future distribution and environmental suitability for Pterocarpus angolensis DC in southern Africa. Forest Ecology and Management 315, 211–226. https://doi.org/10.1016/j.foreco.2013.12.032

de León, G.C., Uranga-Valencia, L.P., 2013. Theoretical evaluation of Huber and Smalian methods applied to tree stem classical geometries. Bosque 34, 311–317.

De Ruytter, J., 2015. The growing stock of Pterocarpus angolensis in Namibia (M.Sc.). University of Ghent, Gent, Belgium.

Dirninger, P., 2004. Natural regeneration and management implications of the miombo forests in Tanzania. Working Paper No.25.

FAEF, 2013. Assessment of harvested volume and illegal logging in Mozambican natural forest. Faculty of Agronomy and forestry engineering, Eduardo Mondlane University, Maputo.

FAO, 2014. Global Forest Resources Assessment 2015. Country report. Namibia, FRA. Food and Agricultural Organization of the United Nations, Rome.

FAO, 2012. Global Ecological Zones for FAO forest reporting: 2010 update (No. 179), Forest Resources Assessment Working Paper. Food and Agricultural Organization of the United Nations, Rome.

Fath, H., 2002. Commercial timber harvesting in the natural forests of Mozambique. Food and Agriculture Organization of the United Nations.

Fayolle, A., Doucet, J.-L., Gillet, J.-F., Bourland, N., Lejeune, P., 2013. Tree allometry in Central Africa: testing the validity of pantropical multi-species allometric equations for estimating biomass and carbon stocks. Forest Ecology and Management 305, 29–37.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J., Berry, N.J., Bird, M., 2011. Height-diameter allometry of tropical forest trees. Biogeosciences.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315.

Goussanou, C.A., Guendehou, S., Assogbadjo, A.E., Kaire, M., Sinsin, B., Cuni-Sanchez, A., 2016. Specific and generic stem biomass and volume models of tree species in a West African tropical semi-deciduous forest. Silva Fennica 50, 1474.

Gröngröft, A., Luther-Mosebach, J., Landschreiber, L., Eschenbach, A., 2013. Mashare - Soils. Biodiversity and Ecology 5, 105. https://doi.org/10.7809/b-e.00259

Groome, J.S., Lees, H.M.N., Wigg, L.T., 1957. A summary of information on Pterocarpus angolensis. Forestry Abstracts 18, 1–8.

Haddad, S., Britz, W., Börner, J., 2019. Economic Impacts and Land Use Change from Increasing Demand for Forest Products in the European Bioeconomy: A General Equilibrium Based Sensitivity Analysis. Forests 10, 52.

Henry, M., Besnard, A., Asante, W.A., Eshun, J., Adu-Bredu, S., Valentini, R., Bernoux, M., Saint-André, L., 2010. Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. Forest Ecology and Management 260, 1375–1388.

Henry, M., Jara, M.C., Réjou-Méchain, M., Piotto, D., Fuentes, J.M.M., Wayson, C., Guier, F.A., Lombis, H.C., López, E.C., Lara, R.C., 2015. Recommendations for the use of tree models to estimate national forest biomass and assess their uncertainty. Annals of Forest Science 72, 769–777.

Henry, M., Picard, N., Trotta, C., Manlay, R., Valentini, R., Bernoux, M., Saint André, L., 2011. Estimating tree biomass of sub-Saharan African forests: a review of available allometric equations. Silva Fennica 45, 477–569.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.

Hofstad, O., 2005. Review of biomass and volume functions for individual trees and shrubs in southeast Africa. Journal of Tropical Forest Science 17, 151–162.

ICRAF, 2020. Tree Functional Attributes and Ecological Database.

IRDNC, 2015. Collaboration on Forest Management and Timber Trade. Presented at the Angola - Namibia - Zambia Joint Workshop (4-8 Aug 2015)., TRAFFIC, SASSCAL & IRDNC, Windhoek, Namibia.

ITTO, 2015. International Tropical Timber Organization: lesser used species [WWW Document]. URL http://www.tropicaltimber.info

Kachamba, D.J., Eid, T., Gobakken, T., 2016. Above-and belowground biomass models for trees in the miombo woodlands of Malawi. Forests 7, 38.

Kalaba, F.K., Quinn, C.H., Dougill, A.J., Vinya, R., 2013. Floristic composition, species diversity and carbon storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia. Forest Ecology and Management 304, 99–109.

Köhl, M., Magnussen, S., Marchetti, M., 2006. Sampling Methods, Remote Sensing and GIS Multiresource Forest Inventory, Tropical forestry. Springer.

Korhonen, K., Juola, V., Chakanga, M., 1997. Woody resources of East and South Tsumkwe, Otjinene and Okakarara Districts (Forest Inventory Report). Windhoek.

Laamanen, R., 2002. List of variables in the felled tree data file.

Louppe, D., Oteng-Amoaka, A., Brink, M., 2008. Plant resources of tropical Africa. Timbers 1. PROTA Foundation. Leiden: Blackhuys Publishers 7, 562–3.

Lukumbuzya, K., Anstey, S., 2016. Notes from the woodlands. An overview of key findings from TRAFFIC and WWF timber trade studies in East and southern Africa between 2013 and 2016 (Bulletin No. 28 (2)). TRAFFIC.

Lukumbuzya, K., Sianga, C., 2017. Overview of the timber trade in East and Southern Africa. TRAFFIC, Cambridge, UK.
Malimbwi, R., Solberg, B., Luoga, E., 1994. Estimation of biomass and volume in miombo woodland at Kitulangalo Forest Reserve, Tanzania. Journal of Tropical Forest Science 230–242.
Mate, R., Johansson, T., Sitoe, A., 2015. Stem volume equations for valuable timber species in Mozambique. Journal of Sustainable Forestry 34, 787–806.
Mate, R., Johansson, T., Sitoe, A., 2014. Biomass equations for tropical forest tree species in Mozambique. Forests 5, 535–556.
Mauya, E.W., Mugasha, W.A., Zahabu, E., Bollandsås, O.M., Eid, T., 2014. Models for estimation of tree volume in the miombo woodlands of Tanzania. Southern Forests: a Journal of Forest Science 76, 209–219.
Meier, E., 2020. The wood database. URL www.wood-database.com
Mendelsohn, J., Jarvis, A., Roberts, C., Robertson, T., 2002. Atlas of Namibia. A portrait of the land and its people. David Philip, Cape Town.
Mensah, S., Pienaar, O.L., Kunneke, A., du Toit, B., Seydack, A., Uhl, E., Pretzsch, H., Seifert, T., 2018. Height–Diameter allometry in South Africa's indigenous high forests: Assessing generic models performance and function forms. Forest Ecology and Management 410, 1–11.
Mensah, S., Veldtman, R., Seifert, T., 2016. Allometric models for height and aboveground biomass of dominant tree species in South African Mistbelt forests. Southern Forests: a Journal of Forest Science 1–12. https://doi.org/10.2989/20702620.2016.1225187
Ministry of Agriculture, Water and Forestry, 2015. Forest Regulations: Forest Act.
Ministry of Agriculture, Water and Forestry, 2011. A Forest Research Strategy for Namibia (2011–2015). Ministry of Agriculture, Water and Forestry, Windhoek, Namibia.
Moses, M., 2013. Assessment of trade-offs between timber and carbon values of Pterocarpus angolensis (Kiaat) in the Kavango Region of Namibia - a comparison of current and potential values (M.Sc. Thesis). University of Stellenbosch.
Mudekwe, J., 2007. The impact of subsistence use of forest products and the dynamics of harvested woody species populations in a protected forest reserve in western Zimbabwe.
Mugasha, W.A., Eid, T., Bollandsås, O.M., Malimbwi, R.E., Chamshama, S.A.O., Zahabu, E., Katani, J.Z., 2013. Allometric models for prediction of above-and belowground biomass of trees in the miombo woodlands of Tanzania. Forest Ecology and Management 310, 87–101.
Ngoma, J., Moors, E., Kruijt, B., Speer, J.H., Vinya, R., Chidumayo, E.N., Leemans, R., 2018. Below and above-ground carbon distribution along a rainfall gradient. A case of the Zambezi teak forests, Zambia. Acta Oecologica 87, 45–57.
Nott, A.J., 2018. Impact of a rainfall gradient on carbon storage in the dry woodland ecosystem of Kavango and Zambezi regions of Namibia (Master). Namibia University of Science and Technology, Windhoek.
Nygård, R., Elfving, B., 2000. Stem basic density and bark proportion of 45 woody species in young savanna coppice forests in Burkina Faso. Annals of Forest Science 57, 143–153.
Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. BioScience 51, 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2
Oy, A., 2016. Intra-African trade in tropical timber and timber products and options for trade facilitation. ITTO.
Pérez-Cruzado, C., Fehrmann, L., Magdon, P., Cañellas, I., Sixto, H., Kleinn, C., 2015. On the site-level suitability of biomass models. Environmental Modelling & Software 73, 14–26. https://doi.org/10.1016/j.envsoft.2015.07.019

Picard, N., Saint-André, L., Henry, M., 2012. Manual for building tree volume and biomass allometric equations: from field measurement to prediction. Manual for building tree volume and biomass allometric equations: from field measurement to prediction, FAO; Food and Agricultural Organization of the United Nations (2012).

PROTA, 2015. PlantUse English. Acacia nigrescens. URL uses.plantnet-project.org

Rutishauser, E., Noor'an, F., Laumonier, Y., Halperin, J., Hergoualc'h, K., Verchot, L., 2013. Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia. Forest Ecology and Management 307, 219–225.

Ryan, C.M., Williams, M., Grace, J., 2011. Above-and belowground carbon stocks in a miombo woodland landscape of Mozambique. Biotropica 43, 423–432.

Seifert, T., Seifert, S., 2014. Modelling and simulation of tree biomass, in: Bioenergy from Wood. Springer, pp. 43–65.

Shackleton, C.M., Scholes, R.J., 2011. Above ground woody community attributes, biomass and carbon stocks along a rainfall gradient in the savannas of the central lowveld, South Africa. South African Journal of Botany 77, 184–192.

Simpson, W., TenWolde, A., 1999. Physical properties and moisture relations of wood. Chapter 3, 2–1.

Syampungani, S., 2009. Vegetation change analysis and ecological recovery of the Copperbelt miombo woodland of Zambia. Stellenbosch: University of Stellenbosch.

Takawira-Nyenya, R., Louppe, D., Oteng-Amoako, A.A., Brink, M., 2010. Pterocarpus angolensis DC. [WWW Document]. Protabase. URL database.prota.org

Timberlake, J.R., Chidumayo, E.N., 2011. Miombo Ecoregion vision report (revised). WWF - SARPO., Occasional Publications in Biodiversity. Biodiversity Foundation for Africa, Bulawayo, Zimbabwe.

Verlinden, A., Laamanen, R., 2006. Modeling woody vegetation resources using Landsat TM imagery in northern Namibia. The Southern African Forestry Journal 207, 27–39. https://doi.org/10.2989/10295920609505250

Vermeulen, W.J., 1990. A monograph on Pterocarpus angolensis.

Vidal, E., West, T.A., Putz, F.E., 2016. Recovery of biomass and merchantable timber volumes twenty years after conventional and reduced-impact logging in Amazonian Brazil. Forest Ecology and Management 376, 1–8.

Vieilledent, G., Fischer, F.J., Chave, J., Guibal, D., Langbour, P., Gérard, J., 2018. New formula and conversion factor to compute basic wood density of tree species using a global wood technology database. American Journal of Botany 105, 1653–1661.

Vieilledent, G., Vaudry, R., Andriamanohisoa, S.F., Rakotonarivo, O.S., Randrianasolo, H.Z., Razafindrabe, H.N., Rakotoarivony, C.B., Ebeling, J., Rasamoelina, M., 2012. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. Ecological Applications 22, 572–583.

Von Breitenbach, F., 1973. Pterocarpus angolensis. A monograph. Trees in South Africa. Journal of the Tree Society of South Africa XXV.

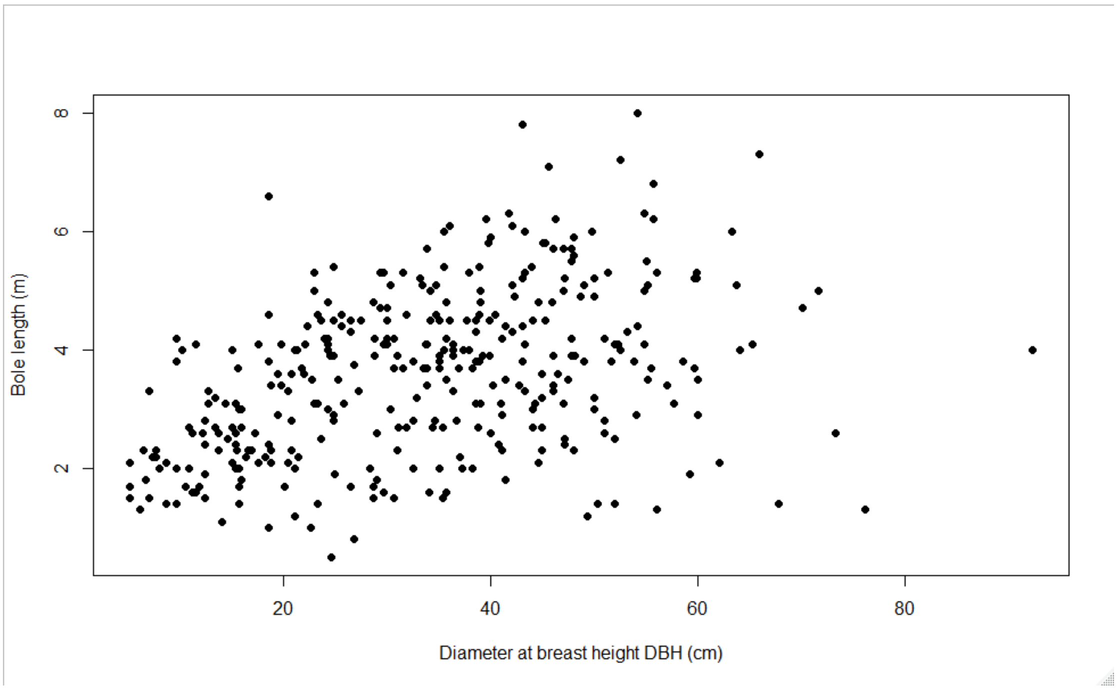
von Malitz, G.P., Rathogwa, H.R., 1999. Dynamics of Pterocarpus angolensis (Kiaat) in South Africa, in: Natural Forests and Savanna Woodlands Symposium II. Knysna, South Africa.

Winfield, K., Scott, M., Grayson, C., 2016. Global status of Dalbergia and Pterocarpus rosewood producing species in trade. Presented at the 17th Conference of the Parties, CITES, pp. 1–30.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Zweede, M., Safford, H., Juergens, G., 2006. Forest Resource Assessment Trip. Kuando Kubango Province, Angola. USDA Forest Service.

Appendix A



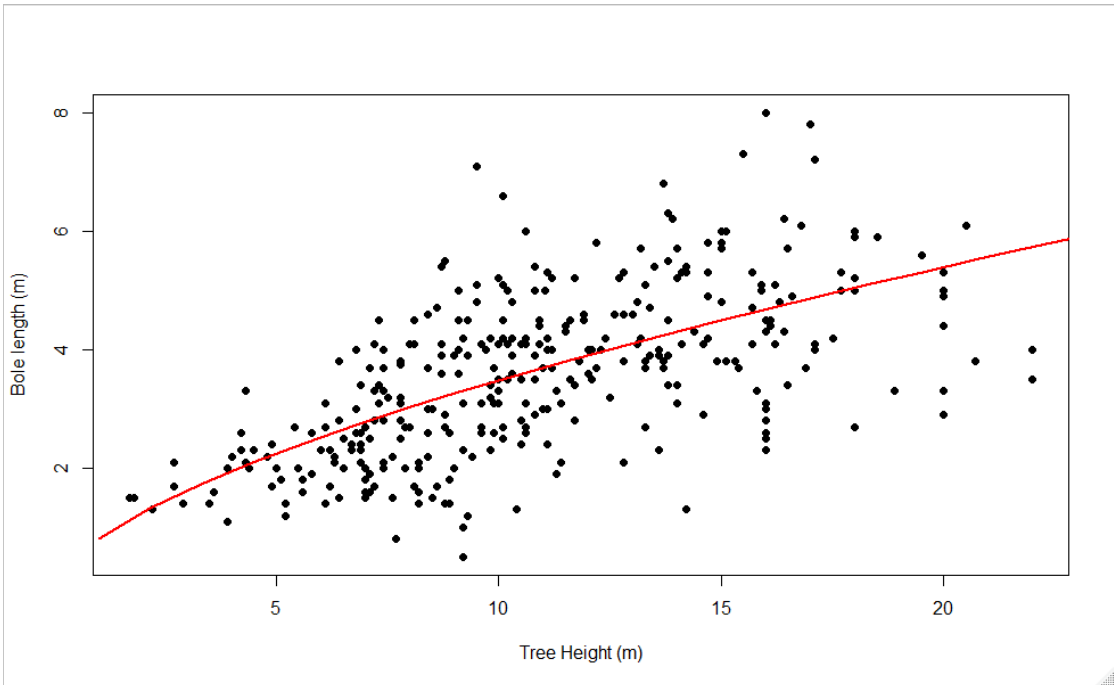


*Figure A.1 – Bole length in function of diameter at breast height DBH (top) and tree height (bottom). Data of 353 trees were used with DBH range of 5 to 92 cm and tree height range of 1.7 to 22 m. An exponential function was fitted to the bottom graph: bole length = e^(-0.2101906 +0.63285*log(tree height)) (adjusted R square = 0.38).*

Appendix B

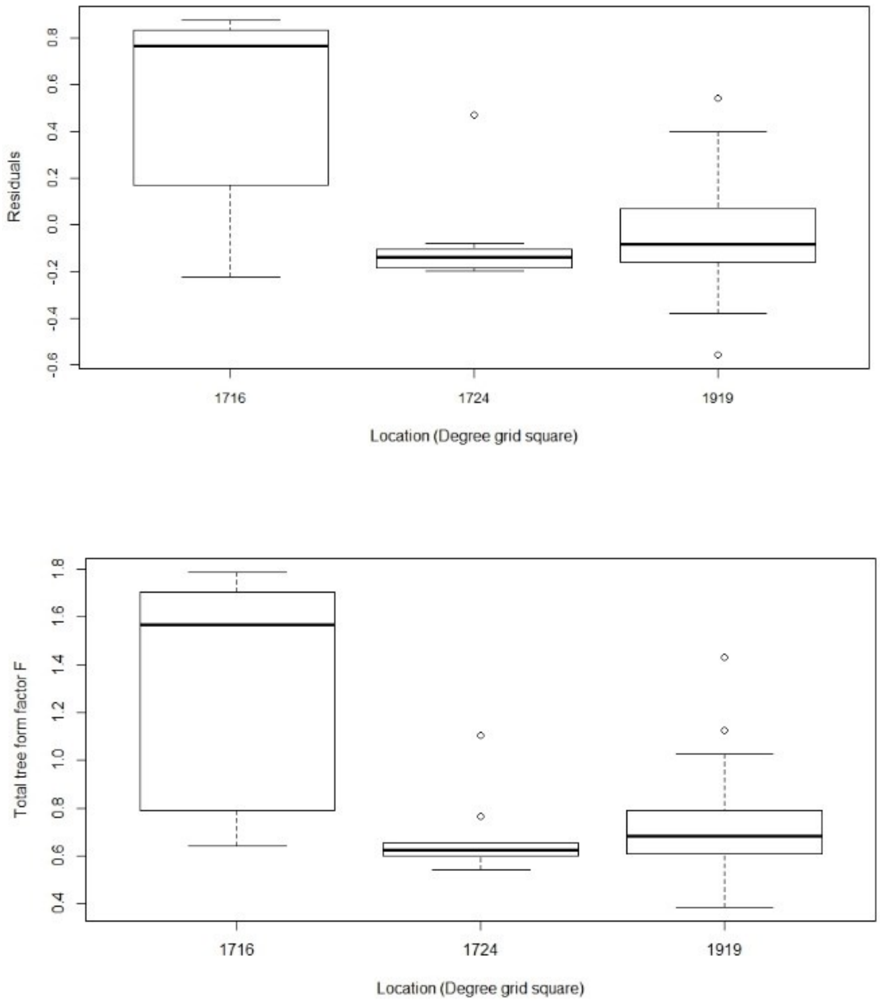


Figure B.1 – Residuals for a total volume model with diameter at breast height and tree height as predictors for a dataset with form factor F < 1.8 (top) and Total tree form factor per location (bottom).