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To cite this article: Vera De Cauwer, Esther Fichtler, Hans Beeckman, F Patrick Graz, Jan Mertens, Sam Van Holsbeeck & Bart Muys (2017): Predicting site productivity of the timber tree *Pterocarpus angolensis*, Southern Forests: a Journal of Forest Science, DOI: [10.2989/20702620.2016.1256042](https://doi.org/10.2989/20702620.2016.1256042)

To link to this article: <http://dx.doi.org/10.2989/20702620.2016.1256042>



Published online: 15 Mar 2017.



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Predicting site productivity of the timber tree *Pterocarpus angolensis*[§]

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Pterocarpus angolensis is an important timber tree of the miombo woodlands of sub-Saharan Africa. The species only grows in natural mixed forests and little is known about its productivity potential. This study aimed at investigating productivity of *P. angolensis* on a local scale in Namibia and Angola and on a regional scale in southern Africa. The most commonly accepted productivity indicator is stem diameter increment and this was used to study productivity at a regional scale. Indicators of productivity used at the local scale were basal area, proportional basal area and site form, which were derived from 217 forest inventory plots in Namibia and Angola. The productivity measures were modelled with abiotic site factors; biotic factors were added for the local scale. Results indicated that the most consistent site factors at local and regional scale were not related to climate but to forest cover, with the species having a competitive advantage in more open forests. Mean annual diameter increment in the open forests of Namibia was 0.51 cm after 50 years. Boosted regression tree models at a local scale showed that species presence can be modelled more successfully than species basal area, proportional basal area (correlation of 0.72 vs 0.56 and 0.45, respectively) and site form. The sites with the highest productivity of *P. angolensis* at the local scale had a temperature seasonality below 34.5 °C, a slope of less than 1.5°, tree cover less than 20% and stand basal area higher than 9 m² ha⁻¹. The results can assist in establishing a site-dependent growth model for the species and direct forest and fire management towards the most productive areas.

Keywords: basal area, boosted regression trees, diameter growth, miombo, site form

Introduction

Pterocarpus angolensis DC. is among the most important indigenous timber species in southern Africa (Vermeulen 1990; Takawira-Nyanya et al. 2010). Its wood is known under many local names, such as *umbila*, *muninga*, *mukwa*, *kiaat* and *girassonde*. It is sought after for carving, furniture and flooring because of its grain, colour, durability and stability, and is the most widely exploited wood in southern Africa (von Breitenbach 1973; Vermeulen 1990; Shackleton 2002). The species can be found where a dry season contrasts with a single wet season, and with mean annual rainfall varying between 400 and 1 250 mm (von Breitenbach 1973; Curtis and Mannheimer 2005). Its distribution coincides roughly with the revised Miombo Ecoregion, which includes the typical miombo woodlands, as well as *Baikiaea* and *Burkea* woodlands at its southern edges (Olson et al. 2001; Therrell et al. 2006; Timberlake and Chidumayo 2011) (Figure 1). The tree is threatened by land-use changes, overharvesting and/or frequent intense fires in many

countries (Shackleton 2002; Caro et al. 2005; Leadley et al. 2010; Pröpper and Vollan 2013; Stellmes et al. 2013a). In addition, climate change is expected to decrease the distribution range, especially where climate projections predict a decrease in summer rainfall (De Cauwer et al. 2014). These threats affect the species' wood availability as the tree grows only in natural mixed forests. Earlier attempts to establish plantations have been largely unsuccessful (Vermeulen 1990; Caro et al. 2005). In contrast to the importance of its timber wood, the information on *P. angolensis* is not sufficient to support forest management, especially data on population dynamics and productivity (Vermeulen 1990; Shackleton 2002; Graz 2004; Burke 2006). More knowledge on the productivity of *P. angolensis* would allow improved forecasts of its growth, mortality, recruitment and timber yield and possibly assist in establishment of plantations.

Site productivity is a quantitative estimate of the potential of a site to produce plant biomass. Assessing

[§] This article is based on a paper presented at the Symposium on Silviculture and Management of Dryland Forests, Stellenbosch University, South Africa, 16–19 March 2015, jointly organised by IUFRO unit 1.02.05 and the Department of Forest and Wood Science, Stellenbosch University

site productivity of forests remains a difficult task, even in even-aged stands (Pokharel and Froese 2009; Skovsgaard and Vanclay 2013; Bontemps and Bouriaud 2014). A site productivity indicator such as site index is difficult to establish for natural forests, especially in the tropics (Vanclay 1992; Pokharel and Froese 2009). The most commonly accepted alternative is the use of diameter increment data (Vanclay 1992; Bontemps and Bouriaud 2014). Another site productivity measure is site form; the tree height at a chosen reference diameter (Vanclay 1992). Angombe (2004) managed to use site form to classify the Namibian woodlands according to site productivity for all species. Typical forest stand measures such as biomass and basal area are other measures of productivity (Vanclay 1992; Erskine et al. 2006; Bontemps and Bouriaud 2014).

Site or stand productivity can also be approached from a different angle and be considered as a function of site factors, especially geoclimatic variables (Pokharel and Froese 2009; Bontemps and Bouriaud 2014). It allows upscaling of productivity, to map and predict it on a larger scale. This study therefore explored the relationship between productivity measures of *P. angolensis* and site factors. The amount of diameter increment data available was limited and only allowed to explore the relationship at a regional scale. Other productivity measures that could be derived from forest inventory data were modelled at a local scale.

Specifically, this study aimed at predicting the productivity of *P. angolensis* (1) on a regional scale for southern Africa based on diameter increment, and (2) on a local scale in Namibia and Angola based on other productivity measures.

Materials and methods

Study area

The regional study focused on locations within southern Africa for which relevant growth data could be found (Figure 1). The local study focused on the south-western edge of the species' distribution range, where unmitigated climate change may cause the species to disappear (De Cauwer et al. 2014). Forest inventory plots of the local study were situated in the Kavango regions of northern Namibia and the Cuando-Cubango province of southern Angola (Figure 1). It included the central catchment area of the Okavango River, locally known as the Kavango or Cubango. Detailed environmental characteristics of both local and regional study areas are described in Table 1.

The soils in the local study area are mainly nutrient-poor, deep Kalahari sand (Gröngroft et al. 2013). The vegetation outside the Okavango river valley is open forest with a canopy coverage of 10–30% and canopy heights of 10–15 m. It is characterised by few tree species, mainly *P. angolensis*, *Baikiaea plurijuga*, *Burkea africana* and *Schinziophyton rautanenii*. In Namibia, it is referred to as Northern Kalahari dry forests and woodlands (Giess 1998) and in Angola as *B. plurijuga* woodland savanna with stands of *S. rautanenii* (Diniz 1973). The human population in the Namibian part of the study area increased rapidly in recent decades, fuelled by immigration from Angola, and settlement expanded from the Okavango river valley to the woodlands, especially along roads and dry fossil

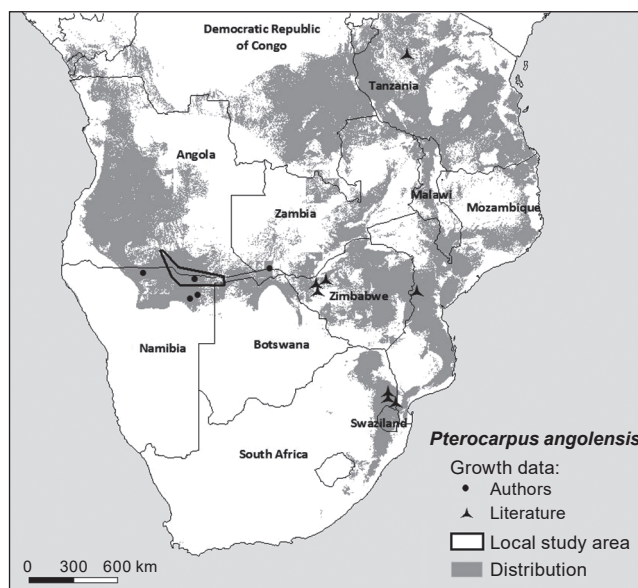


Figure 1: Location of regional diameter growth data and local study area with indication of the distribution of *Pterocarpus angolensis* according to De Cauwer et al. (2014). Sources of growth data from literature are listed in Table 3

river. Woodlands are cleared for agriculture resulting in an annual deforestation rate of 3.9% in the period 1943–1996 in the Kavango regions (Mendelsohn and el Obeid 2003). On the Angolan side, people are returning since the end of the war in 2001 and have started to clear more forest (Schneibel et al. 2013). The local population harvests small quantities of wood in all size classes and within a radius of about 5 km from their agricultural fields, mainly as firewood and for construction. Commercial logging focuses on large individuals of a few species, mainly *P. angolensis* and to a lesser extent *B. plurijuga*. Legal harvesting in Namibia is currently restricted to community forests, which form part of Namibia's Community Based Natural Resource Management programme, but illegal logging does take place (Kabajani 2013; Pröpper and Vollan 2013). Harvesting of timber in Angola is on the increase as more Angolan wood is being transported through Namibia (K Nott, IRDNC, pers. comm., 2015). Fires burn every year at the end of the dry season with about 20% of the area affected on a yearly basis (Stellmes et al. 2013a). The majority of the fires have an anthropogenic origin (Stellmes et al. 2013a).

Data

Diameter increment data

Diameter growth rate in Namibia was estimated through measurements in permanent sample plots and on tree growth rings (Table 2). The permanent sample plots were measured over a period of eight years (De Cauwer 2006; Van Holsbeeck 2015). Stem increment cores and stem discs were collected from five different locations in Namibia (Figure 1). The tree-ring data from the Zambezi and Oshana regions were already described in a dendro-chronological study (Fichtler et al. 2004). The annual nature

Table 1: Environmental characteristics in the study area (based on WorldClim; Hijmans et al. 2005)

Characteristic	Local scale: Namibia		Regional scale: Southern Africa	
	Minimum	Maximum	Minimum	Maximum
Altitude (m)	1 047	1 207	324	1 224
Annual precipitation (mm)	539	712	478	1 085
Maximum temperature warmest month (°C)	34.0	34.6	28.8	34.9
Minimum temperature coldest month (°C)	5.8	7.5	4.2	14.1
Temperature seasonality (°C) ^a	30.2	35.6	11.8	37.8

^a Temperature seasonality = standard deviation of the monthly temperature averages (O'Donnell and Ignizio 2012)

Table 2: Material used for measuring diameter increment of *Pterocarpus angolensis* in Namibia

Source of material	Region	Method	Number of trees
Fichtler et al. (2004)	Oshikoto/Ohangwena	Growth rings on stem discs + LINTAB	8
Fichtler et al. (2004)	Zambezi	Growth rings on stem discs + LINTAB	3
Own collection	Kavango West	Diameter measurements in permanent plots	12
Own collection	Kavango West	Growth rings on cores + LINTAB and Coorecorder	5
Own collection	Kavango West	Growth rings on stemdiscs + magnifying glass/ruler	3
Own collection	Otjozondjupa	Growth rings on cores + LINTAB and Coorecorder	4
Moses Moses (2013)	Kavango East	Growth rings on stem discs + loupe/ruler	2



Figure 2: Example of a cambial marking installed in August 2010 (dry season) with collection of the wood sample in May 2012 (end of wet season)

of the growth rings of *P. angolensis* has been proven (van Daalen et al. 1992; Stahle et al. 1999; Fichtler et al. 2004; Therrell et al. 2006; Worbes n.d.) and was also confirmed by cambial markings on several trees in Kavango West (Figure 2). Increment cores of *P. angolensis* are difficult to use for dendrochronological analysis because of less visible or wedging rings, but they do provide enough information to estimate age–diameter relationships based on ring counts (Stahle et al. 1999; Therrell et al. 2006). Counting and measuring of growth rings was done with the assistance of LINTAB equipment with TSAP-Win software (RINNTech), Coorecorder 7.8 software (Cybis Elektronik and Data AB) or a magnifying glass and ruler for the stem discs. Two to three samples (radii or cores) were measured per tree.

Local diameter growth rate was compared with growth data available in literature for southern Africa (Groome et al. 1957; van Daalen et al. 1992; Stahle et al. 1999; Therrell

et al. 2007). Growth rates were compared for a reference age of 50 years because annual diameter increment (ADI), diameter at 1.3 m breast height (DBH) and age are all strongly related. The reference age does not take into account the age of seedlings before reaching stump or breast height. The seedling phase of the species is characterised by a so-called suffrutex stage, during which it dies back in the dry season and resprouts in the wet season, a normal phenomenon in miombo woody species (von Breitenbach 1973; Ryan and Williams 2011). Our approach thus focuses on the age of the bole but we will continue to refer to tree age. For the permanent sample plots, trees with a DBH between 21 and 34 cm were selected as this is the approximate diameter range that the species may reach after 50 years considering the tree-ring growth information available for Namibia.

Forest inventory data

Forest inventory data of 217 sample plots in northern Namibia and southern Angola were used to analyse the local productivity measures of *P. angolensis*. Plots followed a circular nested design with maximum radius of 30 m and were measured using Namibian forest inventory methods (Burke et al. 2001). The forest inventory data include all woody plants with minimum diameter at DBH of 5 cm.

Site variables

For the local study, site factors were collected in the field and from existing or compiled geodatabases. The data collected comprised abiotic and biotic site variables, as well as stand variables. Abiotic site factors included climate variables derived from WorldClim (Hijmans et al. 2005), soil variables from the Harmonised World Soil Database (FAO/IIASA/ISRIC/ISSAS/JRC 2009) and altitude from the Shuttle Radar Topography Mission (SRTM) database of NASA. The SRTM data were used to derive aspect, slope and landscape curvature. Biotic site variables were mainly indicators of anthropogenic disturbance. Direct and indirect

measures of anthropogenic impact were used, for example cattle density (GIS data from Mendelsohn and el Obeid 2004) and severity of fire damage on the woody vegetation, or distance to villages, respectively. Fire frequency for the period 1991–2004 was available in GIS format for the Namibian plots (NRSC and Verlinden 2004). Burned area for the period 2000–2012 was derived from MODIS images by the University of Trier (Stellmes et al. 2013a). Stand variables were used to reflect stand competition at plot level: stand basal area (BA; Coomes and Allen 2007), coverage of grass, herbs, shrubs and trees in the plot as determined in the field, the enhanced vegetation index (EVI), and H/H_{\max} . The EVI was derived from MODIS images for the period 2007–2012 (Stellmes et al. 2013b). H/H_{\max} was calculated as the tree height of *P. angolensis* divided by the maximum tree height in the plot (Eid and Tuhus 2001; Namaalwa et al. 2007).

For the analysis on a regional scale, abiotic site factors were explored (FAO 2007; FAO/IIASA/ISRIC/ISSAS/JRC 2009; Hijmans et al. 2005). FAO data layers with the 'occurrence of forest, cropland, pasture and browse' were also used (FAO 2007); each pixel displayed the percentage covered by a specific land use, for example cropland. An overview of all variables and their sources can be found in De Cauwer (2016).

Data analysis

Basal area (BA), proportional BA (the proportion of the BA of *P. angolensis* in the total stand BA) and site form were selected as productivity measures for the local study. All three measures can be considered to reflect the wood production potential of the species at a site, although they are not necessarily related (McGill 2012). Proportional BA was chosen because we were particularly interested in areas where *P. angolensis* is doing better than other species, also in areas with low productivity potential.

Species presence had to be modelled first to address the skewed distribution of the productivity measures caused by the plots where the species is absent. The BA, proportional BA or site form was then modelled for the presence points (Fletcher et al. 2005). Presence was defined as occurrence of *P. angolensis* within a radius of about 60 m around the plot centre.

The reference tree diameter for site form was selected by inspecting the height–DBH relationship of the data (Figure 3). Both a reference DBH of 25 cm and 30 cm showed a fairly wide range of tree heights and appeared to have enough data for modelling; hence they were both tested as productivity measures (i.e. SF25 and SF30). SF30 was also used by Angombe (2004) in Namibia.

The relationships between presence, BA or proportional BA and site factors were modelled with boosted regression trees (BRT), a modelling method with roots in both statistical and machine learning techniques (Elith et al. 2008). BRT models combine a large number of simple tree models to optimise performance and often outperform other modelling methods (Elith et al. 2006, 2008; Araújo and New 2007; Aertsen et al. 2010). A Bernoulli distribution was used to model the presence/absence data and a Gaussian distribution for BA and proportional BA, after transformation. The BRT models were simplified by dropping variables

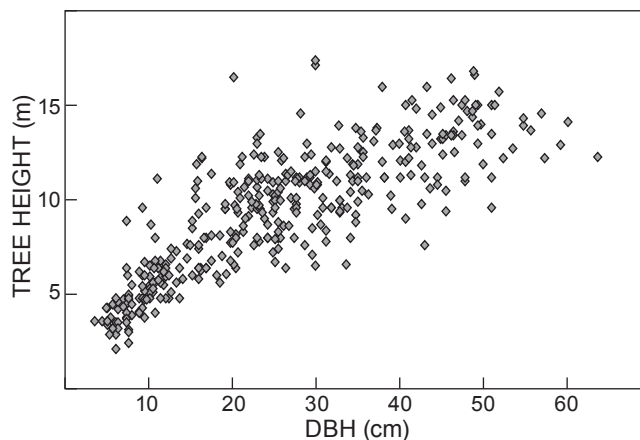


Figure 3: Relationship between diameter at breast height (DBH) and tree height for 385 *Pterocarpus angolensis* trees from forest inventory data in 217 sample plots in northern Namibia and southern Angola

that did not increase model performance. Performance of the models was evaluated by 10-fold cross-validation of deviance, a measure of lack of fit between model and test data, and correlation (Leathwick et al. 2006; Elith et al. 2008). Deviance not only measures how well calibrated the prediction values are, but also penalises errors in scaling of prediction values as they are considered probabilities of presence (Phillips and Dudík 2008). The effects of the predictors were studied through their contribution to the models and their partial dependence plots. The plots show the marginal effect of the selected variable on the model prediction (Ridgeway 2014). Modelling was performed with R version 2.15 software using the gbm package (Ridgeway 2014) and functions written by Elith et al. (2008).

BRT modelling could not be applied to site form or annual diameter growth as there were not enough data. The Spearman correlation ρ (rho) with the different site factors was explored and linear regressions were tested for the factors with the best correlations.

Results

Regional diameter growth

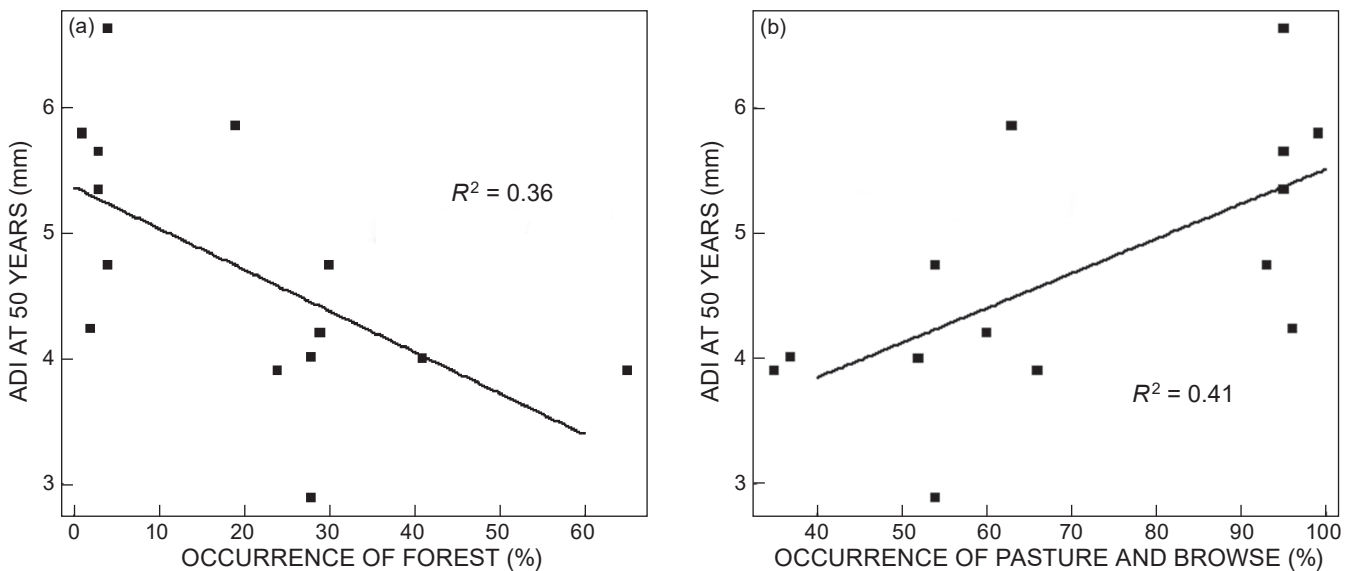
The mean ADI of *P. angolensis* after 50 years varied between 2.9 and 6.6 mm y^{-1} in southern Africa (Table 3). Namibian mean ADI was 5.1 ± 1.7 mm y^{-1} and was consistent for the different methods used. None of the climatic or soil variables showed a significant correlation ρ with ADI on a regional scale. The only variables with significant correlations ($p < 0.05$) were altitude ($\rho = 0.66$), forest occurrence ($\rho = -0.62$) and pasture occurrence ($\rho = 0.65$). Significant linear regressions could be obtained for forest and pasture occurrence (Figure 4).

Boosted regression tree models of the local study

Pterocarpus angolensis trees (DBH ≥ 5 cm) were present in 126 of 217 plots. The BA of the species varied between 0.02 and 7.9 m² ha⁻¹ in the plots where the species was present, with a mean of 1.7 ± 1.5 m² ha⁻¹, representing on

Table 3: Annual diameter increment (ADI) after 50 years with indication of number of trees sampled

Source	Country	Latitude (°S)	Longitude (°E)	ADI after 50 years (mm)	Number of trees
Stahle et al. (1999)	Zimbabwe	18.5420	26.9330	2.9	10
Therell et al. (2007)	Zimbabwe	19.0000	27.0000	3.9	18
Therell et al. (2007)	South Africa	25.0830	31.2500	3.9	13
Stahle et al. (1999)	Zimbabwe	18.3227	27.5380	4.0	14
Therell et al. (2007)	Mozambique	19.0000	33.0000	4.0	17
van Daalen et al. (1992)	South Africa	25.4650	31.2690	4.2	2
Fichtler et al. (2004) (Oshikoto/Ohangwena)	Namibia	17.8326	16.6348	4.2	7
van Daalen et al. (1992)	South Africa	25.7560	31.7040	4.7	2
Fichtler et al. (2004) (Zambezi)	Namibia	17.5607	24.2625	4.7	3
Own data (Kavango West, permanent plots)	Namibia	18.2089	19.7276	5.3	12
Own data (Kavango West)	Namibia	18.2089	19.7276	5.6	7
Own data (Otjozondjupa)	Namibia	19.3626	19.4730	5.8	4
Groome et al. (1957)	Tanzania	4.7000	32.4000	5.9	10
Own data (Kavango East)	Namibia	19.1280	19.9140	6.6	2

**Figure 4:** Relationship between annual diameter increment (ADI) of *Pterocarpus angolensis* after 50 years in sub-Saharan Africa and occurrence of forest or pasture and browse according to FAO (2007)

average 27% of the stand BA. Stand BA in all plots varied between 0.2 and 22.4 m² ha⁻¹ and had a mean value of 6.2 ± 3.9 m² ha⁻¹. The presence model for *P. angolensis* performed much better than the BA models. Table 4 shows that the deviance of the presence model did not improve much with the addition of disturbances or stand factors, while adding stand factors or disturbances explained relatively more deviance of the BA and proportional BA model. The distance to the main road was the most important disturbance-related variable.

Variables with the greatest contributions to the models differed for the presence and abundance models (Table 5). There are 16 partial dependence plots for the predictors. They illustrate straightforward relations and can easily be described, so only a few of them are shown in Figure 5. The plots showed that *P. angolensis* was mainly found in areas with EVI below 0.3 (Figure 5a), with annual temperature range below 28.3 °C, more than 1 km from fossil rivers

and with cattle density below 6 animals km⁻². Cattle density is, however, a proxy for certain abiotic variables, hence the small improvement of the model by adding this disturbance factor (Table 4). The highest BA of the species was found in areas where stand BA was higher than about 9 m² ha⁻¹ (Figure 5b), annual temperature range below 27.4 °C, more than 2 km from main roads and on plains (slope < 1°). Highest proportions of the species in stand BA were located on plains (slope < 1.5°) (Figure 5c) with tree cover below 20% (Figure 5d), far away from roads (>10 km) and with temperature seasonality below 34.5 °C. Temperature seasonality and annual temperature range both measure temperature variation over a year, but the former is based on the standard deviation of temperatures and the latter on the difference between maximum and minimum temperatures, which permits examination of the effect of extreme temperature conditions (O'Donnell and Ignizio 2012). The models for proportional BA with only abiotic or with abiotic

Table 4: Performance of boosted regression tree models for presence, basal area and proportional basal area data of *Pterocarpus angolensis* with various sets of site factors as predictors

Data	Deviance explained (%)			Correlation
	Abiotic	Abiotic and biotic	Abiotic, biotic and stand	Abiotic, biotic and stand
Presence	38	44	46	0.72
Basal area	13	17	29	0.56
Proportion of stand basal area	8	15	22	0.45

Table 5: Site factors affecting presence and productivity of *Pterocarpus angolensis* at a local scale (Namibia and Angola). (1) Contribution of predictors (%) to the boosted regression tree (BRT) model that included all site and stand factors and (2) correlation ρ with site form (SF) ($p < 0.05$). Site form is the tree height at a chosen reference diameter. BA = basal area, %BA = proportional BA, EVI = enhanced vegetation index, H = tree height, H_{max} = maximum tree height in sample plot

Site factor	(1) BRT models			(2) Site form	
	Presence	BA	%BA	SF25	SF30
Temperature annual range	36	15			
Distance to main roads		17	33		
Slope		20	26		
Total basal area stand		27			
Distance to fossil rivers	23				-0.44
EVI	23				
Tree cover			22	-0.36	
Wet season EVI		21			0.47
Temperature seasonality			20		
Cattle density	17				
Fire damage					-0.44
H/H_{max}				0.42	

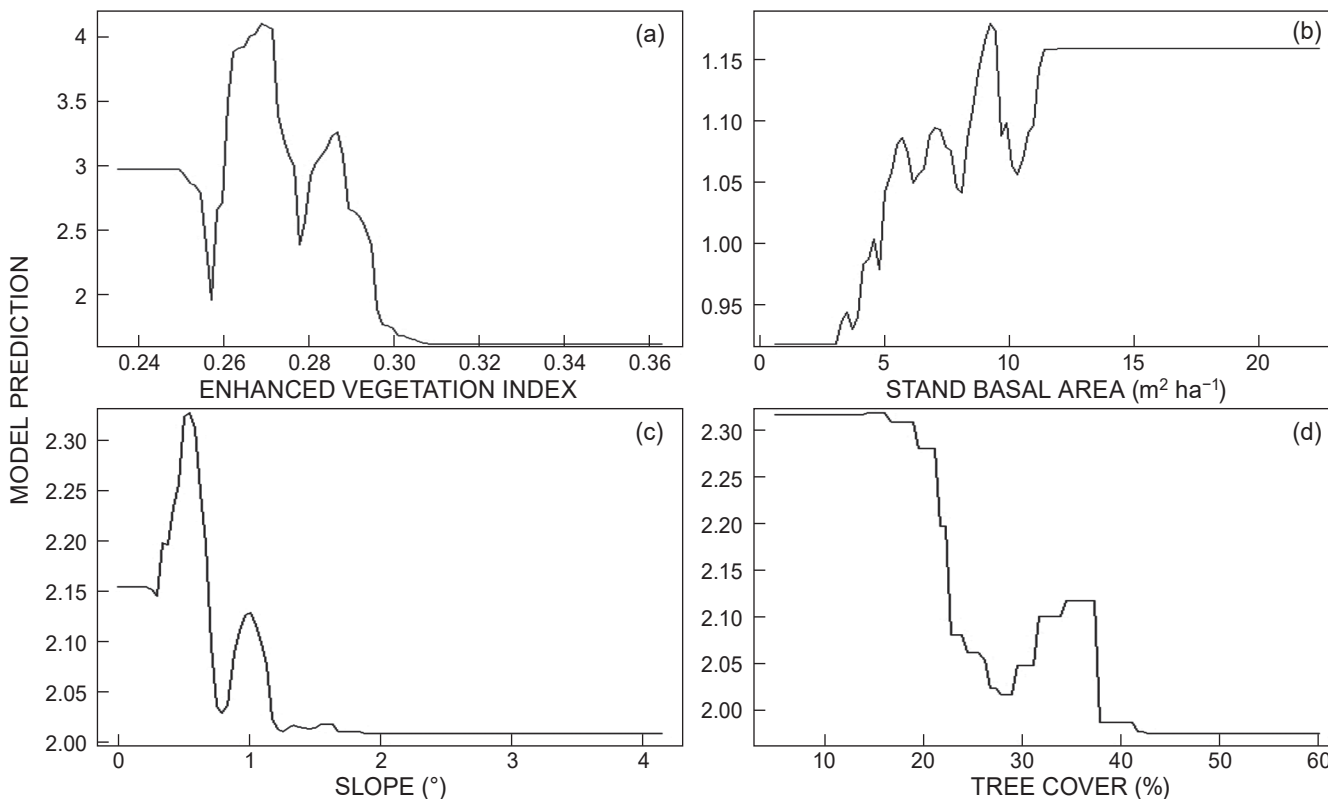


Figure 5: Partial dependence plots for predictors of the (a) presence, (b) basal area and (c) (d) proportional basal area models for *Pterocarpus angolensis* in Namibia and Angola

and biotic site factors both had aspect as an important predictor, indicating a negative effect when slopes were exposed to the east or south (50° to 200°).

Site form

There were 31 plots that contained at least one tree with DBH of 25 cm \pm 1 cm; their mean height was 9.7 m. There were 23 plots with at least one tree with DBH of 30 \pm 1 cm and with mean height of 11.1 m. There were only a few significant correlations with site factors and many of these factors were different to the main predictors of the BRT models (Table 5). The regressions for both SF25 and SF30 were not significant.

Discussion

Diameter increment data for a tree of 50 years could be derived for 14 locations in southern Africa (Table 3). These locations represented a wide range of climatic factors (Table 1), but there was limited availability of other site information that could have contributed to our understanding of the differences in growth rates. The most remarkable conclusion is that there was no relationship between diameter growth rate and rainfall at a regional scale. Namibia, which is at the south-western edge and has the lowest rainfall of the species' distribution range, shows a higher mean ADI (5.1 mm y⁻¹) compared to various studies in the region (van Daalen et al. 1992; Stahle et al. 1999; Shackleton 2002; Therrell et al. 2007). Other authors found relatively high growth rates for Namibia of 5.4 mm y⁻¹ in northern Namibia (Lückhoff 1969, unpublished report cited in van Daalen et al. 1992) and 7.1 \pm 3.8 mm y⁻¹ for Kavango West (Van Holsbeeck et al. 2016).

Growth rate correlated negatively with forest occurrence on a regional scale and showed the highest ADI for areas with less than 5% of forest. However, the forest occurrence data set (FAO 2007) underestimates the occurrence of open forests. In the study area in Namibia and Angola, most pixels are classified as having more than 90% of pasture land and less than 6% of forest. In reality, the larger part of the study area is made up of open forests (>10% canopy coverage), which are difficult to detect by remote sensing (Ganzin et al. 2005; Verlinden and Laamanen 2006; De Cauwer 2015). It can therefore be concluded that the correlations of ADI with forest and pasture occurrence indicate a better growth rate of *P. angolensis* in open forests. This is supported by the strong negative relationships found between proportional BA and tree cover, and between SF25 and tree cover at a local scale. It confirms the theory that *P. angolensis* is a light-demanding species (Vermeulen 1990). The species may have a lower competitive ability, doing well in areas where other species struggle due to less favorable environmental conditions and hence conform to the inclusive niche theory (McGill 2012). De Cauwer et al. (2014) did show that the probability to find *P. angolensis* in most of its distribution range was similar to that of potential competing species, such as *Brachystegia boehmii* and *Julbernardia paniculata*. However, in the areas where the other species had an occurrence probability lower than 60%, the occurrence probability of *P. angolensis* increased.

This study could not find any relation between presence or productivity and fire frequency, but this could be because of the short period of fire data compared to the longevity of *P. angolensis* and the limited variability in the data. The results did show a negative correlation between fire damage and tree height at a reference DBH of 30 cm (Table 5).

There was large variation in diameter increment at the stand level in Namibia, as also found in other studies (Geldenhuys 1977; Therrell et al. 2007; Van Holsbeeck 2015). It takes on average 50 years to reach a DBH of 27 cm but this has the potential to increase to 34 cm, considering the standard deviation. The large variation of local growth rates and the negative effect of high crown cover on growth rate show that interventions at stand level, such as opening up the canopy through thinning, may increase growth. Future studies on diameter increment should aim to collect stand-level information and be spread over more locations with similar geoclimatic variables to provide more insights.

The correlations of site form with site factors showed that SF30 reflects the differences in site characteristics more than SF25 because of lower interference with stand factors, affirming the selection of a reference DBH of 30 cm for site form in the Namibian open forests by Angombe (2004). At a DBH of 25 cm, the tree has not reached its full height (9.7 m) and competition may be fiercer than when the species has a DBH of 30 cm and has almost reached full height (11.1 m). Relating site form to diameter increment and thus productivity for *P. angolensis* would be advisable as Wang (1998) showed that site form is not always linked to site quality.

Temperature range and seasonality are the only climatic variables that appear to have an effect on presence and abundance of the species within the study area. The models showed that the highest proportional BA can be found in the western parts of the study area where temperature seasonality is lower. It demonstrates that the species performs best in less extreme temperature conditions. This explains its poorer performance in areas with an eastern, the major wind direction, or southern, the coldest side, exposure. *Burkea africana* can handle such extreme climate conditions better (De Cauwer et al. 2016). Temperature seasonality is a climatic variable in common with the predictors of an occurrence model at the regional scale (De Cauwer et al. 2014) that indicated that the distribution of the species is mainly influenced by summer rainfall, minimum temperature in winter and by temperature seasonality. The upper limit for temperature seasonality of the regional occurrence model is the same as the upper limit for a relatively higher proportional basal area in our local study (about 34.5 °C).

The fact that *P. angolensis* is rarely found within a distance of 1 km of fossil rivers can be explained by the fact that the soils are heavier there, supporting a different vegetation type with more *Acacia* species and *Terminalia sericea* (Strohbach and Petersen 2007). Another reason is that residents prefer to cultivate crops in the dry riverbeds and that vegetation is removed. The fact that the highest proportion of *P. angolensis* can be found in areas more than 10 km from main roads shows the impact and location of past harvesting.

The results can assist in the establishment of a tree growth model by the indication of relevant site variables. Currently, only a few simple growth models exist and they are based on a limited amount of growth measurements (Desmet et al. 1996; Schwartz et al. 2002), with exception of the age-diameter model of Therrell et al. (2007) for south-eastern Africa. The model of Schwartz et al. (2002) has a fixed time step of 50 years and the use of a diameter increment of 0.5 mm, about one-tenth of other values in literature (Table 3). The optimal site factors as indicated by this study allow production of regional site and forest attribute maps based on data derived from forest inventories, and satellite and environmental data, which is an increasingly common practice (Moisen et al. 2006). Forest managers who aim to maximise wood production of *P. angolensis* should focus their interventions, including fire management (e.g. as discussed by Ryan and Williams 2011), on stands with the highest abundance and performance of *P. angolensis*.

Conclusions

At a regional scale, no positive relationship between rainfall and diameter growth rate of *P. angolensis* could be determined. The study area in Namibia showed a higher mean annual diameter increment (ADI) of 5.1 mm y⁻¹ than many other areas in the species' distribution range with higher average rainfall. This can be explained by the fact that the species grows best in open, dry forest where there is less tree competition as long as there are no other limiting factors, such as high temperature seasonality. The high variability of ADI at stand level and within the region illustrate the potential impact of stand factors and open up possibilities for forest management to improve growth of the species.

At a local scale, the study identified site factors that can be used to predict and map the presence and the productivity of the species. The study used site form, the height of a tree with a given reference DBH, as a measure of productivity of a species at a site. Site form for a reference DBH of 25 cm reflected mainly stand characteristics, whereas site form for a reference DBH of 30 cm (SF30) was more related to site characteristics and is hence a better measure of site productivity. Future studies should confirm this by relating SF30 to diameter increment of *P. angolensis*. Species presence can be better explained by site factors than BA and proportional BA. *Pterocarpus angolensis* can be mainly found in areas with an annual temperature range below 28.3 °C, more than 1 km from dry fossil rivers, with cattle density below 6 animals km⁻² and with an enhanced vegetation index below 0.3. However, forest managers and planners will be most interested in the areas with the highest abundance and best performance of *P. angolensis*. They are mainly found in the west of the study area, more than 10 km away from main roads, with tree cover <20%, and with BA higher than 9 m² ha⁻¹. These areas have a minimal slope (<1.5°), and a western or northern aspect. This information can feed into growth models and forest attribute maps.

Acknowledgements — This study was possible through support of the Namibian Directorate of Forestry and The Future Okavango (TFO) project. The TFO project is funded by the German Federal

Ministry of Education and Research under promotion number 01 LL 0912 A. Moses Moses kindly provided stem discs and Dr Marion Stellmes provided the MODIS-derived parameters. Many people contributed to the fieldwork; we would especially like to thank Miya Kabajani and Ninda Baptista, colleagues of the University of Hamburg and the team of the Universities of Göttingen and Stellenbosch lead by Prof. Christoph Kleinn, Cori Ham, Dr César Pérez and Dr Paul Magdon. We thank two anonymous reviewers and Dr Ben Du Toit for their valuable comments on the manuscript. BM acknowledges support from the KLIMOS ACROPOLIS research platform of VLIR/ARES, financed by the Belgian Development Cooperation.

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