

Autecological aspects of the African timber tree *Pterocarpus angolensis* in support of its sustainable management



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Dissertation presented in partial
fulfilment of the requirements for the
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Aan mijn drie Namibiërs

Preface

Several institutions and people have contributed to this dissertation and I refer to most of them at the end of chapters 2 to 5. Here I want to thank the institutions and persons without whom my PhD studies would not have been possible or that have safeguarded my sanity over the last six years.

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Contents

Preface.....	I
Contents	III
Abbreviations and Symbols.....	VII
Summary	IX
Samenvatting.....	XI
Chapter 1 - Introduction.....	1
1.1 <i>Pterocarpus angolensis</i>	2
1.2 The <i>Baikiaea</i> - <i>Pterocarpus</i> forests.....	5
1.3 Autecological methods to support sustainable forest management.....	7
1.4 Research objectives and outline of the study	9
1.5 Research approach	10
Chapter 2 - Potential, realised, future distribution and environmental suitability of <i>Pterocarpus angolensis</i> in southern Africa	13
2.1 Introduction.....	14
2.2 Methods.....	16
2.2.1 Ecology of <i>P. angolensis</i>	16
2.2.2 Model algorithm	17
2.2.3 Occurrences	17
2.2.4 Environmental data.....	18
2.2.5 Realised distribution	19
2.2.6 Model validation	21
2.2.7 Estimating future distribution.....	23
2.3. Results.....	23
2.3.1 Potential distribution	23
2.3.2 Realised distribution	26
2.3.3 Future model.....	27
2.4 Discussion	28
2.5 Conclusions.....	33
Chapter 3 - Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa	35
3.1 Background.....	36
3.2 Methods.....	38
3.2.1 Study area	38

3.2.2 Forest inventory data.....	40
3.2.3 Site variables	41
3.2.4 Data analysis	41
3.3 Results.....	44
3.3.1 Tree communities	44
3.3.2 Historical trends in tree community composition	47
3.3.3 Population structure of <i>P. angolensis</i>	48
3.4 Discussion	50
3.4.1 Species and structural composition in the study area.....	50
3.4.2 Impact of abiotic variables on forest composition	51
3.4.3 Impact of disturbances on forest composition.....	52
3.4.4 Trends in forest composition over the last 40 years	53
3.5 Conclusions.....	53
Chapter 4 - Predicting site productivity of the timber tree <i>Pterocarpus angolensis</i>	55
4.1 Introduction	55
4.2 Material and methods	57
4.2.1 Study area	57
4.2.2 Data	58
4.2.3 Data analysis	61
4.3 Results.....	63
4.3.1 Growth data	63
4.3.2 Boosted regression tree models	64
4.3.3 Site form.....	66
4.4 Discussion	66
4.5 Conclusions.....	69
Chapter 5 – Individual tree growth and yield models for the African timber tree <i>Pterocarpus angolensis</i>	71
5.1 Introduction.....	71
5.2 Methods.....	73
5.2.1 Study area	73
5.2.2 Wood volume and biomass data	74
5.2.3 Diameter growth data.....	76
5.2.4 Volume and biomass modelling.....	77
5.2.5 Model for the proportion of heartwood	78
5.2.6 Radial growth models	78

5.2.7 Model evaluation	79
5.2.8 Model predictors.....	79
5.3 Results.....	80
5.3.1 Wood volume and biomass models.....	80
5.3.2 Proportion of heartwood	82
5.3.3 Age – diameter relationship	82
5.3.4 Explanatory BAI models	83
5.3.5 Predictive BAI model.....	83
5.3.6 Simulation of yield prediction.....	85
5.4 Discussion	86
5.4.1 Wood volume and Biomass	86
5.4.2 Heartwood portion	86
5.4.3 Growth	87
5.5 Conclusions.....	89
Chapter 6 - Conclusions.....	91
6.1 Environmentally suitable area for <i>Pterocarpus angolensis</i> : where does the species occur?	91
6.2 Forest composition and population structure	92
6.3 Site productivity of <i>Pterocarpus angolensis</i>	92
6.4 Biotic factors influencing the occurrence and abundance <i>Pterocarpus angolensis</i>	95
6.5 Impacts of climate change and rising atmospheric CO ₂	96
6.6 Implications for sustainable management of southern African dry forests	97
6.7 Prospects for future research.....	100
References.....	103
Annex A – Glossary.....	123
Annex B – Sources of occurrences for <i>Pterocarpus angolensis</i>	125
Annex C – Absences of <i>Pterocarpus angolensis</i> used in the presence-absence validation..	126
Annex D – Response curves of environmental variables created by Maxent during the potential distribution modelling of <i>Pterocarpus angolensis</i>	127
Annex E – Sample design of forest inventories.....	129
Annex F – Tree species in the <i>Baikiaea – Pterocarpus</i> forests.....	131
Annex G – Performance of boosted regression tree models for the five tree communities of the <i>Baikiaea – Pterocarpus</i> forests	132
Annex H - Kruskal-Wallis tests of site variables for the tree communities.....	133
Annex I – Description of the tree communities in the <i>Baikiaea – Pterocarpus</i> forests.....	134
Annex J – Predictor variables used for the productivity models	136

Abbreviations and Symbols

AIC	Akaike information criterion
AUC	Area under the receiving operating characteristic (ROC) curve
BA	Basal area
BAI	Basal area increment
BAL	Basal area of larger trees
BRT	Boosted regression tree
Btot	Total above ground wood biomass
CI	Competition index (for trees)
CRUTS	Climatic Research Unit time-series
CWD	Climatic water deficit
DBH	Diameter at breast height (1.3 m)
DRC	Democratic Republic of Congo
EVI	Enhanced Vegetation Index
GAM	Generalised additive model
GIS	Geographic Information System
GLS	Generalised least squares
ha	Hectare
Hmax	Maximum tree height (in a forest stand)
HWSD	Harmonised World Soil Database
MAP	Mean annual precipitation
ME	Mixed effects
MRPP	Multi-response permutation procedures
n	number of observations
NAD	Namibian dollar
PA	Presence/absence
PDSI	Palmer Drought Severity Index
PO	Presence only
PSP	Permanent sample plot
R ²	Coefficient of determination
RCPs	Representative Concentration Pathways
RSE	Residual standard error
RSErel	Relative residual standard error
SD	Standard deviation
SDM	Species distribution model
SRTM	Shuttle Radar Topography Mission
V10	Wood volume of stem and branches
VDC	Vera De Cauwer
Vtim	Timber volume
Vtot	Total wood volume

A glossary is added in Annex A.

Summary

Tropical dry forests cover less than 13% of the tropics with the majority situated in Africa and South America. In southern Africa, they form part of the Miombo ecoregion or the Zambesian Centre of Endemism. The Miombo forests are under pressure of an increasing population and are one of the world's most threatened regions with regard to biodiversity loss, even though they are considered one of the five wilderness areas that should be given priority for global conservation. The most widely harvested timber species within the Miombo ecoregion is *Pterocarpus angolensis*, also known as Kiaat, Muninga, Mukwa or African Teak. There are many reports of unsustainable harvesting and lack of natural regeneration of the species, resulting in an IUCN Red List status of near threatened. Forest management has the potential to improve the sustainable wood production of this important forest resource in the remaining forests, but so far management interventions such as assisted regeneration, thinning, pruning, and selection of the best genetic material rarely take place in the region. Information about *P. angolensis* is also not sufficient to support sustainable forest management, in contrast to the importance of its timber wood.

The overall aim of the study is to contribute to the sustainable management of *Pterocarpus angolensis* through an autecological study of the species using state-of-the-art ecological methods and modelling techniques. The dissertation focuses on the environmental conditions that influence the occurrence and productivity of *P. angolensis*. Some parts of the study encompass the southern African region while others focus on a large study area in the *Baikiaea - Pterocarpus* forests of northern Namibia and southern Angola. Both historical and recent data sources are used covering 40 years and an area of approximately 21,000 km². Recently developed modelling techniques were applied such as species distribution, boosted regression trees and mixed effects modelling to allow insight in the ecological requirements of the species and to assess the impact of scenarios of change.

The species distribution models (SDM) show that *P. angolensis* has occupied most of its potentially suitable habitats in southern Africa and that it has a smaller range (60%) than previously published, mainly because our map omits a large area in eastern Angola, western Zambia, and the southern Democratic Republic of Congo. The environmental requirements of *P. angolensis* at a regional level are described with more quantitative and objective measures than available in literature. Occurrence is to a large extent determined by the rainfall amount (e.g. mean annual rainfall > 430 mm, February rainfall 50 – 250 mm) and seasonality (> 55% standard deviation). *P. angolensis* is exposed to much more extreme environmental conditions, especially frost and drought, in the Kalahari basin than in the wetter eastern part of southern Africa. The SDMs show that unmitigated climate change can decrease the species' distribution area with 20% to 50% by 2080. The species is most sensitive to climate change in Namibia, Angola, and Botswana because of a predicted decrease of early wet season rainfall. A northward shift of *P. angolensis*' distribution in south-western Africa is a realistic scenario by the end of the 21st century and hence, climate adaptation strategies are needed to deal with the potential impact on this important timber species.

In the *Baikiaea - Pterocarpus* forests of the study area, *P. angolensis* is one of the most common and characteristic trees. The study shows that it was the second most common tree with 8 stems ha⁻¹, contributed to 16% of the basal area of all trees (minimum stem diameter at breast height (DBH) of 10 cm), and hence is more common than in wetter Miombo

forests. It was an indicator species for the most common tree community, the *Pterocarpus angolensis* – *Dialium englerianum* community, which is mainly situated on the sandy plateaux in the study area. The community showed a significantly higher annual fire frequency (24% or on average a fire every 4 years) than the other tree communities, and the least resilience towards climate change. The latter is demonstrated by the mortality rate and decreasing basal area of *D. englerianum*. We found no evidence of a negative effect of the high fire frequency on the occurrence of the species, but there are indications that the fire frequency negatively affects both small and larger trees. There is less natural regeneration (DBH < 10 cm) compared to other woody species in the *Baikiaea* – *Pterocarpus* forests. Few trees make it to the senescence phase, which is reached at a DBH of approximately 60 cm or an age of approximately 100 years. Human presence, measured as the distance to human infrastructure such as agricultural fields (< 7 km), roads (< 10 km), and villages (< 9 km), has a negative effect on the abundance of *P. angolensis*. However, the available data could not indicate a decline in the basal area of *P. angolensis* over the last 40 years.

The study presents the first comprehensive overview of drivers of productivity for *P. angolensis*. Most are different from the drivers of occurrence; abiotic variables are not sufficient to explain productivity and information on anthropogenic disturbances and forest structure is needed. This can be explained by the lower competitive ability of the species in optimal environments. The species grows best in areas with less extreme temperature conditions and stands with less tree competition. It does not handle light and root competition well until it has almost reached canopy height (60 % of maximum tree height in stand). The low competitive ability explains why the mean diameter increment of the species in the open *Baikiaea* – *Pterocarpus* forests (5.5 mm per year), the driest area in the species' distribution, is at the higher end of the increment range found by other studies in southern Africa (2.9 to 6.6 mm per year). Diameter growth is atypical and hardly varies with DBH. The longevity, constant growth rate, limited regeneration, and medium wood density (620 kg per m³ in Namibia) are not typical for an early succession species, as some authors describe it, but rather place in the late succession stages.

Basal area increment in the study area is mainly explained by stem diameter (76%) and to a small extent by mean climatic conditions at the site. There is an indication of a fertilisation effect of the increasing atmospheric CO₂ concentration in areas with higher mean summer rainfall (> 135 mm). The mean portion of heartwood in the study area was 64% of the stem diameter (for diameters of 20 to 70 cm); it increased with DBH and decreased with latitude. Variations in heartwood portion and annual diameter growth within the study area were large and to a large extent at individual tree level. It points to the large impact of forest structure and/or genetic differences, both of which can be improved with silvicultural treatments.

The dissertation showed that *P. angolensis* is a long-living, late successional species that has weak competitive abilities, especially during the juvenile phase. It therefore performs well in open, dry forests such as the *Baikiaea* – *Pterocarpus* forests of Namibia and Angola. Sustainable forest management needs to include more fire prevention measures, assisted regeneration and silvicultural treatments such as thinning to improve juvenile growth rates.

Samenvatting

Tropische droge bossen bedekken slechts 13% van de tropen met de meerderheid gesitueerd in Afrika en Zuid-Amerika. In Zuid-Afrika vormen ze een deel van de Miombo ecoregio. De Miombo bossen worden bedreigd door een toenemende bevolking en worden beschouwd als één van de meeste bedreigde gebieden ter wereld op het vlak van biodiversiteit. Ze maken tevens deel uit van één van de vijf wildernisgebieden die wereldwijd prioriteit voor natuurbescherming vereisen. De boomsoort die over het grootste gebied in de Miombo bossen gekapt wordt voor zijn hardhout is *Pterocarpus angolensis*, gekend onder lokale namen zoals Kiaat, Muninga, Mukwa en Afrikaanse Teak. Verscheidene studies rapporteerden reeds een niet duurzame houtoogst en een gebrek aan natuurlijke regeneratie wat onder meer heeft geleid tot een IUCN Rode Lijst klassering als bijna bedreigde soort. Bosbeheer heeft het potentieel om de duurzame houtproductie van deze soort te verbeteren, maar momenteel worden er geen interventies zoals dunnen, snoeien, selectie van het beste genetische materiaal, aanplantingen of maatregelen die natuurlijke verjonging bevorderen uitgevoerd. Er is ook niet voldoende informatie over *P. angolensis* beschikbaar om zulke bosbeheersmaatregelen te ondersteunen ondanks de belangrijkheid van deze houtsoort in zuidelijk Afrika.

Het doel van deze studie is om bij te dragen aan het duurzaam beheer van *P. angolensis* door een autecologische studie met behulp van de meest recente ecologische methoden en modelleringstechnieken. Het doctoraat concentreert zich op omgevingsfactoren die de aanwezigheid en de productiviteit van de soort beïnvloeden. Sommige delen van de studie omvatten zuidelijk Afrika en anderen een studiegebied in de *Baikiaea – Pterocarpus* bossen van noordelijk Namibië en zuidelijk Angola. Historische en recente veldgegevens worden gebruikt die een periode van 40 jaar en een gebied van ongeveer 21,000 km² omvatten. Modellen worden ontwikkeld om de relatie tussen aanwezigheid en productiviteit met omgevingsfactoren te analyseren en om het effect van toekomst scenario's te analyseren.

De distributiemodellen tonen aan dat *P. angolensis* aanwezig is in het merendeel van de potentiële habitats in Afrika and dat het in een kleiner (60%) gebied voorkomt dan voorheen gepubliceerd, voornamelijk omdat de bekomen distributiekartaat een groot gebied aan de grenzen van Zambië, Angola en de Democratische Republiek van Congo uitsluit. De informatie bekomen over de vereiste omgevingsfactoren is meer gedetailleerd en gekwantificeerd dan deze beschreven in de literatuur. Hieruit blijkt dat vooral de neerslag hoeveelheid (bv. > 430 mm per jaar en 50 – 250 mm in februari) en seizoentaliteit (> 55% standaardafwijking) de distributie van de soort beïnvloedt. *P. angolensis* is onderhevig aan extremere condities, voornamelijk droogte en vorst, in de Kalahari (zuidwestelijk Afrika) dan in andere delen van het verspreidingsgebied. Het distributiemodel illustreert dat klimaatsveranderingen het verspreidingsgebied van de soort 20% tot 50% kan doen inkrimpen tegen 2080. De grootste veranderingen zijn te verwachten in Namibië, Botswana en Angola omwille van de voorspelde daling van regenval in het regenseizoen. Een noordelijke verschuiving van het verspreidingsgebied is een realistisch scenario en aanpassingsstrategieën die de gevolgen van klimaatverandering op deze belangrijke boom- en houtsoort anticiperen zijn noodzakelijk.

De studie toont aan dat *P. angolensis* één van de meest algemene en karakteristieke boomsoorten is in de *Baikiaea – Pterocarpus* bossen. Het was de tweede meest algemene boomsoort met 8 stammen per hectare en droeg bij tot 16% van de basale oppervlakte van

alle bomen met een minimum stamdiameter van 10 cm, veel meer dan in de typische Miombo bossen. Het is een indicatorsoort van de meest voorkomende *Pterocarpus angolensis* – *Dialium englerianum* gemeenschap die zich vooral op de zandplateau's in het studiegebied bevindt. De brandfrequentie was er hoger (24% of gemiddeld een brand elke 4 jaar) en de weerstand voor klimaatsverandering lager dan bij de andere gemeenschappen. Het laatste wordt geïllustreerd door de sterfte en afnemende basale oppervlakte van *D. englerianum*. De studie vond geen bewijs van een negatief effect van de hoge brandfrequentie op de aanwezigheid van de soort. Er zijn echter duidelijke indicaties van een negatief effect op zowel de verjonging als op oudere bomen. Het aandeel jonge bomen van *P. angolensis* (stamdiameter < 10 cm) is veel lager dan bij andere boomsoorten in het studiegebied. Weinig bomen bereiken maturiteit of maximale productie, hetgeen bereikt wordt bij een stamdiameter van ongeveer 60 cm en een leeftijd van ongeveer 100 jaar. De studie toonde aan dat menselijke aanwezigheid, gemeten door de afstand tot wegen (< 10 km), dorpen (< 9 km) en velden (< 7 km), een negatief effect heeft op het aantal bomen van de soort.

De studie geeft het eerste uitgebreid overzicht van de factoren die de productiviteit van *P. angolensis* beïnvloeden. Het betreft voornamelijk andere factoren dan deze die de aanwezigheid van de soort verklaren aangezien abiotische factoren het aantal bomen en de groei slechts in geringe mate bleken te verklaren. De soort is minder competitief in optimale milieuomstandigheden en daardoor is er informatie over bosstructuur en antropogene invloeden nodig om de hoeveelheid en groei van de soort te kunnen voorspellen. Het verklaart waarom *P. angolensis* in de open *Baikiaea* – *Pterocarpus* bossen, die de laagste neerslaghoeveelheid binnen het verspreidingsgebied hebben, een relatief hoge groei van de stamdiameter heeft (5.5 mm per jaar) in vergelijking met deze in andere gebieden van zuidelijk Afrika (2.9 tot 6.6 mm per jaar). Jaarlijkse groei van de basale oppervlakte werd in het model voornamelijk bepaald door stamdiameter (78%) en in mindere mate door de gemiddelde klimaatsomstandigheden. In de gebieden met hogere zomer regenval (> 135 mm) blijkt er tevens een CO₂ fertilisatie effect te zijn. Groei van de stamdiameter was atypisch aangezien het bijna niet varieerde met diameter, een aanwijzing van het negatieve effect van competitie in de juveniele fase. De lange levensduur van de soort, de constante groei, de gemiddelde houtdichtheid (gemiddeld 620 kg per m³ in Namibië) en de geringe hoeveelheid verjonging wijzen erop dat de soort in de laatste successie fasen thuis hoort.

Het aandeel donkere hardhout in het studiegebied neemt toe met de stamdiameter en was gemiddeld 64% voor stamdiameters tussen 20 en 70 cm. Het aandeel hardhout blijkt af te nemen met toenemende breedtegraad in Namibië en dus met toenemende regenval. Verschillen in de portie hardhout en in diametergroei zijn vooral tussen individuele bomen en niet per streek of locatie. Dit wijst op de belangrijke rol van de bosstructuur en/of genetische factoren, welke beide door bosbeheersmaatregelen kunnen beïnvloed worden.

Deze doctoraatsstudie toont aan dat *P. angolensis* een langlevende soort is van de latere successie stadia en met geringe competitieve capaciteiten, voornamelijk in de juveniele fase. Daarom is de productie beter in de open, droge *Baikiaea* – *Pterocarpus* bossen van Namibië en Angola. Duurzaam bosbeheer in dit gebied dient zich te concentreren op brandpreventie, regeneratie en dunning om groei, vooral in de juveniele fase, te verbeteren.

Chapter 1 - Introduction

Tropical dry forests grow in tropical climates with a long dry period during winter (FAO, 2012). This ecological zone covers only 6% of earth's land surfaces and 13% of the tropical ecological zone (Hansen et al., 2013). The forests are adapted to cope with harsh climatic conditions but are susceptible to ecosystem transitions under influence of rainfall variability and anthropogenic disturbances (Hirota et al., 2011; Holmgren et al., 2001; Leadley, 2010). Virtually all are threatened by either climate change, habitat fragmentation, fire and an expanding population and should be given high conservation priority (Miles et al., 2006). Next to the provision of important ecosystem services such as local and regional climate regulation, carbon storage, timber and non-timber forest products (Foley et al., 2005; Shackleton et al., 2007; Snyder et al., 2004), they provide food security for both people and animals, which is especially important during dry years (Chidumayo and Gumbo, 2010; Mannheimer and Curtis, 2009).

The majority of tropical dry forests is situated in Africa and South America (Hansen et al., 2013). In southern Africa, they form part of the Miombo ecoregion or the Zambesian Centre of Endemism (Figure 1.1), supporting more than 4,500 endemic species of higher plants and about half of the African elephants (*Loxodonta africana*) and rhinoceros (*Diceros bicornis*, *Ceratotherium simum*) left in Africa (Byers, 2001; Skarpe et al., 2004; Timberlake and Chidumayo, 2011; White, 1983). The Miombo forests show a trend of degradation and fragmentation caused by shifting cultivation, fires, and wood collection (Cabral et al., 2011; Miles et al., 2006; Sloan and Sayer, 2015). An increasing population induces changes in fire regimes and land use practices, which are enforced by climate change (Hély et al., 2006; Leadley, 2010; Thuiller et al., 2006), and negatively affect biodiversity and carbon storage (Chidumayo, 2013; Jew et al., 2016). It makes the region one of the world's most threatened with regard to biodiversity loss (Leadley, 2010), in sharp contrast with the fact that it is considered one of the five speciose wilderness areas that should be given priority for global conservation (Mittermeier et al., 2003).

One of the most important timber trees of the Miombo ecoregion is *Pterocarpus angolensis*, a tree species that has been harvested on a large scale since the 20th century (Boaler, 1966a; Pedro et al., 1955; Von Breitenbach, 1973). The ongoing deforestation and degradation threatens the sustainable use of this important forest resource. An additional concern are the reports of limited natural regeneration (Caro et al., 2005; Dirninger, 2004; Kabajani, 2016; von Malitz and Rathogwa, 1999). Silviculture has the potential to improve the sustainable wood production of this timber tree in the remaining forests, but so far management interventions such as assisted regeneration, thinning, pruning, and selection of the best genetic material rarely take place.

Detailed understanding of the ecology, population dynamics, and potential yield of the species is required to design and support sustainable forest management practices. The information currently available is not sufficiently detailed, especially for the drier parts of the Miombo ecoregion (Baptista, 2014; Graz, 2004; Shackleton, 2002). Valuable information was gathered in the past, but often not published or data analysis was done with the software and techniques available at the time (e.g. Geldenhuys, 1992, 1977). Deriving relevant ecological information from historical and recent data as a support for the sustainable management of *P. angolensis* is the main aim of this dissertation.

The study focuses on the south-western and driest parts of the Miombo ecoregion. The area is at the border of Namibia and Angola and is characterised by open *Baikiaea – Pterocarpus* forests (Figure 1.1). Annual rainfall in the area (480 – 710 mm) is the lowest within the distribution range of *P. angolensis* (Curtis and Mannheimer, 2005; Hijmans et al., 2005), but the species still occurs as a medium sized tree reaching heights of on average 11 m and up to 18 m. The branch-free bole is often straight and 3 to 6 m tall (Figure 1.2), which makes it the most important timber tree of Namibia (Chakanga and Kojwang, 2001; Mendelsohn and el Obeid, 2005).

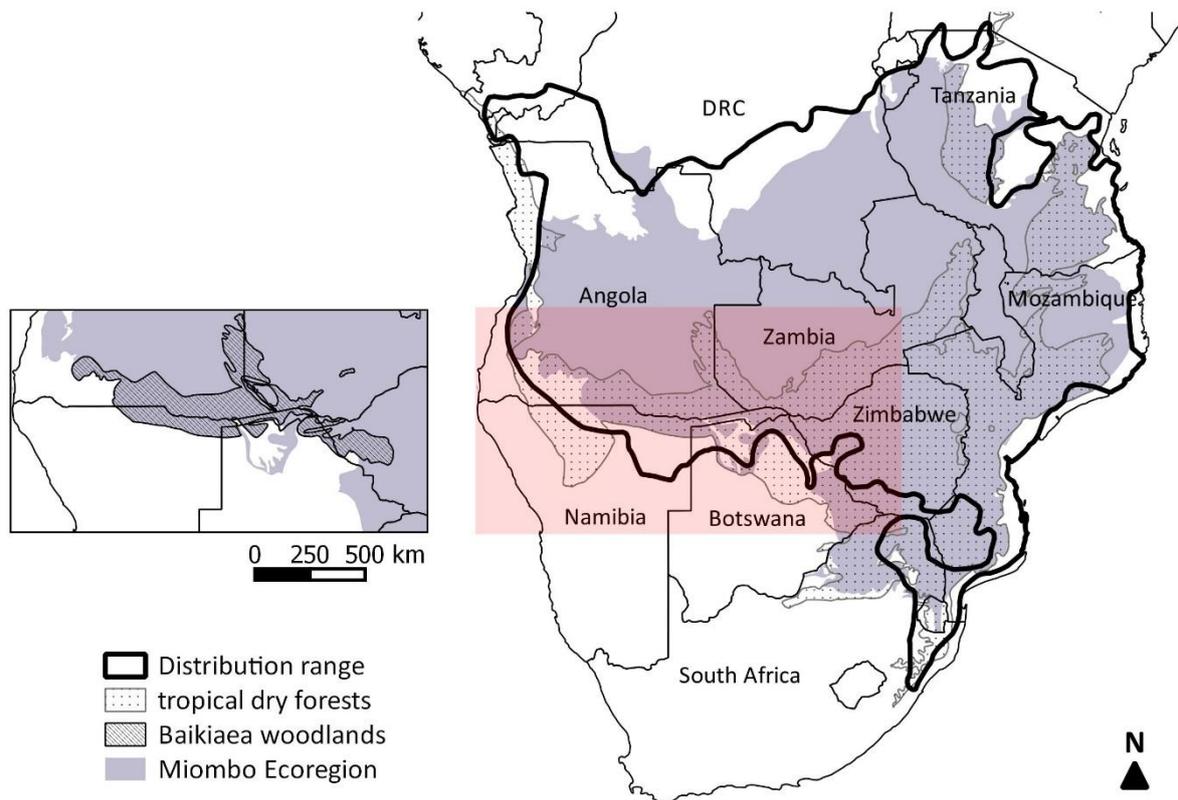


Figure 1.1 – Miombo ecoregion in southern Africa with indication of the tropical dry forest ecological zone (FAO, 2012) and the distribution range of *Pterocarpus angolensis* (De Cauwer et al., 2014). The *Baikiaea* woodlands are a vegetation type within the Miombo ecoregion (Olson et al., 2001; Timberlake and Chidumayo, 2011).

1.1 *Pterocarpus angolensis*

Pterocarpus angolensis D.C. is a dry forest tree species belonging to the family of the Fabaceae. It can be found in large parts of Sub-Saharan Africa where a dry season contrasts with a single summer wet season, and with mean annual rainfall varying between 400 and 1250 mm (Curtis and Mannheimer, 2005; Von Breitenbach, 1973). Its distribution coincides roughly with the revised Miombo ecoregion, which includes the typical, wetter Miombo forests, as well as the open, dry *Baikiaea* and *Burkea* forests at the southern edges (Olson et al., 2001; Therrell et al., 2006; Timberlake and Chidumayo, 2011) (Figure 1.1). The area with the lowest mean annual rainfall where the species can be found is in Namibia.



Figure 1.2 – Typical growth forms of *Pterocarpus angolensis* in the *Baikiaea - Pterocarpus* forests a) Kanovlei, northern Namibia, dry season 2006; b) Hamoye, northern Namibia, rainy season 2006; c-d) Mashare, northern Namibia, dry season 2011; e – h) Cuangar, southern Angola, rainy season 2013; i) Hamoye, northern Namibia, dry season 2010.

P. angolensis is a deciduous tree of about 10 - 20 m tall, sometimes reaching heights up to 30 m in Mozambique, Tanzania, and Zambia (Gillett, 1971; Palmer and Pitman, 1972; Vermeulen, 1990). However its growth form differs in certain areas of Angola where it grows as a shrub to small tree (Groome et al., 1957; Monteiro, 1957). The species only grows in natural mixed forests and is sometimes co-dominant or dominant in the canopy layer. Tree densities can reach 75 trees ha⁻¹, but most often it is scarcely distributed with densities of 3 to 20 trees ha⁻¹ (Backeus et al., 2006; Brummitt et al., 2007; Groome et al., 1957; Modest, 2006; Schwartz et al., 2002). The species can easily reach an age of 100 to 140 years (Therrell et al., 2007). It is well adapted to dynamic forest environments due to its fire tolerance and light demand (Banda et al., 2006; Geldenhuys, 1977; Von Breitenbach, 1973). More information on the ecology of the species can be found in Chapter 2 (2.2.1).

The attractive wood of *P. angolensis* is known under many local names, such as African teak, Umbila, Muninga, Mukwa, Kiaat, Dolf, and Girassonde and is sought after for carving, furniture, and flooring (Vermeulen, 1990). It has a beautiful grain and the portion and colour of the heartwood varies a lot between and even within individual tree stems (Figure 1.3). The small white spots that sometimes occur in the wood and are caused by crystalline deposits (Vermeulen, 1990) have not been observed in Namibian wood. It has a medium wood density varying between 440 and 680 kg m⁻³ with the lower densities recorded for Namibia. It is not particularly strong because of frequent changes in directions of the grain. The heartwood is moderately durable, moderately resistant to termites, and very stable with limited shrinkage when drying (Takawira-Nyenyanya et al., 2010; Vermeulen, 1990).



Figure 1.3 – Wood of *Pterocarpus angolensis* collected in the Kavango East region of Namibia by Moses (2013) (Photos: P. Nichol)

Intensive exploitation goes back to the middle of the 20th century and took place on a large scale that was unprecedented for a southern African species (Clarke, 1995; Hauman et al., 1954; Lees, 1962; Timberlake et al., 2010; Von Breitenbach, 1973). Legal and illegal harvesting continues up till today (Ball and Gregory, 2006; Dondeyne et al., 2004; Pröpper and Vollan, 2013) with cases of unsustainable harvesting reported for Tanzania among others (Caro et al., 2005; Schwartz et al., 2002). In South Africa, demand has exceeded supply and crafts people are increasingly looking for populations in other countries (Shackleton, 2005). The species received the IUCN Red List status of near threatened. It is a protected species in Namibia, Tanzania, and South Africa, although harvest is sometimes allowed (Government Gazette, 2015; Jew et al., 2016; Mehl et al., 2011).

In contrast to the importance of its timber wood, the information available for *P. angolensis* is not sufficient to support forest management (Burke, 2006; Graz, 2004; Shackleton, 2002; Vermeulen, 1990). Some examples of areas that need further research include:

- Ecological niche: the species grows in natural mixed forests of dry to moist climate zones that are characterised by disturbances such as drought, browsing and fire, making it difficult to disentangle the effects of geo-climatic factors from other drivers of forest composition and complicating autecological studies. The few autecological studies available focus on Tanzania and South Africa (Backeus et al., 2006; Caro et al., 2005; Desmet et al., 1996; Mehl et al., 2011; Schwartz et al., 2002; Shackleton, 2002; van Daalen, 1991) ;
- Resilience towards climate change: Africa is one of the most vulnerable continents to climate change (Niang et al., 2014) and forest managers need to consider the potential effects on this important timber species. The role of climate change in the widely reported die-back incidences (Mehl et al., 2011; Mmolotsi et al., 2012) has not been explored yet. This die-back is caused by a fungal infection on trees that are vulnerable, especially because of drought or physical damage (Mehl et al., 2011; Slippers and Wingfield, 2007);
- Resistance to fire: the species is known to tolerate fire well, especially “colder” fires (Backeus et al., 2006; Banda et al., 2006; Geldenhuys, 1977). However, little is known of the long-term impact of high fire frequencies on the population.
- Succession status: although *P. angolensis* is a light demanding species (Vermeulen, 1990), its position in forest succession is not obviously that of a pioneer. It often forms an important part of the canopy layer (Geldenhuys, 1992; Shackleton and Scholes, 2011) and it has no abundant regeneration, no low wood density (Chave et al., 2006), nor does it establish in single-species stands.
- Sustainable yield: diameter growth studies have been limited to a few locations within the distribution range (Table 4.3) and little is known about the species’ maximum growth potential. Growth models that were established are based 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;
- Productivity: it is not clear what affects the productivity of the species, except that it performs best in open forests due to its high light-demands, on well drained soils, and better in mixed stands than in monocultures (Vermeulen, 1990);
- Heartwood: carpenters are mainly interested in the dark heartwood and thus in wood with a high heartwood portion. Little is however known about the extent of the variability in heartwood portion of the wood and the factors influencing it (Shackleton, 2002; Vermeulen, 1990).

1.2 The *Baikiaea* - *Pterocarpus* forests

The Miombo forests were recently classified under the Miombo ecoregion, an extension of White’s Zambesian Regional Centre of Endemism (Olson et al., 2001; Timberlake and Chidumayo, 2011; White, 1983). The south-western Miombo ecoregion consist of dry open

Baikiaea - Pterocarpus forests that form part of the “*Baikiaea* woodlands” vegetation type (Olson et al., 2001; Timberlake and Chidumayo, 2011) (Figure 1.1). The *Baikiaea - Pterocarpus* forests are situated north and north-west of the famous Okavango river delta, a recently declared UNESCO world heritage site. Tree canopy coverage in the forest varies between 10% and 30% and canopy heights between 10 m and 15 m. It can be classified as open forest according to FAO (Annex A) and will be named as such in this dissertation. Unlike wetter Miombo, the *Baikiaea - Pterocarpus* forests are characterised by only few tree species, including *P. angolensis*, *Baikiaea plurijuga*, *Burkea africana*, and *Schinziophyton rautanenii*. Indicator species of wetter and typical Miombo forests, such as *Brachystegia spiciformis*, *B. boehmii*, *Cryptosepalum exfoliatum* and *Julbernardia globiflora* (Backeus et al., 2006; Baptista, 2014; Revermann et al., 2013), are not present. Mean annual rainfall (480 – 750 mm) is much lower than in most Miombo forests where it can reach up to 1400 mm. The soils are poor deep Kalahari sands (Oldeland et al., 2013; Olson et al., 2001; Timberlake and Chidumayo, 2011). It is a relatively flat landscape where the main topographic features are the Okavango River valley and its dry tributaries.

In Namibia, the vegetation is referred to as northern Kalahari dry forests and woodlands (Giess, 1998) and in Angola as *B. plurijuga* woodland savannah with stands of *S. rautanenii* (Diniz, 1973). It has also been suggested to name it the *Burkeo - Pterocarpetea*, the *Baikiaea - Burkea* or the *Baikiaea - Pterocarpus* forests (De Cauwer et al., 2016; Stellmes et al., 2013a; Strohbach and Petersen, 2007). The open forest extends northwards where they gradually change into more typical miombo forest with *J. paniculata*, *Brachystegia bakeriana*, and *B. spiciformis* (Coelho, 1967, 1964; Fanshawe, 2010; Santos, 1982). Southwards, the tree layer becomes more open, intermingled with *Acacia* species and changes into scrublands (Ben Shahr, 1998; Burke, 2002).

The *Baikiaea - Pterocarpus* forests contribute directly and indirectly to national economies. Annual revenues of commercial timber logging in Namibia, mainly of *P. angolensis* and *B. plurijuga*, were estimated at NAD/ZAR 1.3 million or USD 100,000 (2016 values with www.inflationcalc.co.za) for the period 1993 - 2000 (Chakanga and Kojwang, 2001); no more recent data are available. However, the largest wood value is its local use for amongst others construction, firewood, crafts, and medicine (Chakanga, 2000). Total wood value, excluding timber wood, was estimated at USD 140 million in 2004 (2016 values with www.inflationcalc.co.za) (Barnes et al., 2010). The values of the forests as fodder for game and livestock or of ecosystem services have not been accurately assessed (Chakanga, 2000). The importance of ecotourism in the region is underlined by the establishment of The Kavango Zambezi Trans-frontier Conservation Area (KAZA TFCA), the largest trans-frontier conservation area in existence (WWF, 2012).

Land use in the study area differs from many other Miombo areas because of the lower population density (6.9 persons per km² compared to 25.6 persons per km² in more northern parts of the distribution area of *P. angolensis* (Linard et al., 2012)), and the absence of shifting cultivation (Pröpper et al., 2010) and charcoal production. However, population is continuously increasing, e.g. from 116,830 to 222,500 (+ 90%) in the Kavango regions of Namibia during the period 1991 – 2011 (NPC, 2011), and settlement is extending deeper into the forest. The local population considers the forests as a land reserve for semi-permanent subsistence agriculture, inconsiderate of the poor sandy soils that have very low potential yields (mean potential maize yields between 250 and 600 kg per ha) (Pröpper et al., 2015). Other disturbances, especially fire and drought, but also browsing, have a large impact on

this dynamic forest ecosystem (Archibald et al., 2008; Burke, 2006; Fanshawe, 2010). Every year, about 20% of the area burns with almost all fires taking place in the months August and September, towards the end of the dry season and because of human ignition (Stellmes et al., 2013b).

Climate projections indicate increasing temperatures and decreasing summer rainfall for the *Baikiaea-Pterocarpus* forests, potentially causing a reduction of tree range and cover (Hewitson, 2006; Thuiller et al., 2006). Such changes, enforced by the altering land use practices and fire regimes of an increasing population, could potentially induce a shift from an open forest ecosystem to woodland, shrub, or grassland ecosystem (Chidumayo, 2013; Higgins and Richardson, 1999; Lavorel et al., 2007).

Forest management in the *Baikiaea - Pterocarpus* forests is limited to combatting illegal wood harvesting, firefighting, and fire prevention in Namibia and Botswana and no silvicultural treatments take place. In Namibia, timber harvesting and transporting is only allowed with permission of the Directorate of Forestry. Local communities can harvest for own use on communal land that is not classified as forest reserve or forest management area. Most classified forests are community forests, where the community can harvest wood for own use and authorise others to harvest according to a management plan (Forest Act, 2001). In 2012, the Namibian Directorate of Forestry issued a harvest ban on all commercial timber wood because of increasing illegal harvesting (Hailwa, 2012). The ban was lifted in 2015 but only for registered and gazetted community forests (Amber Nott, IRDNC, pers.com.).

1.3 Autecological methods to support sustainable forest management

Autecology is the study of the interaction of a species with its environment. Knowledge of the minimal and optimal environmental conditions of a species at different stages of its life history is necessary to allow its sustainable management. This is especially the case for tree species in natural, mixed forests that serve multiple functions. For *P. angolensis*, information is rarely sufficient to support regional claims that current harvesting of the species is unsustainable (Hailwa, 2012; Jew et al., 2016), that the species' population is threatened because of changing fire regimes, climate change, and die-back incidences (Mehl et al., 2011; Mmolotsi et al., 2012; Strohbach and Petersen, 2007) or that the yield and value of the forest compares favourably to other land-uses.

There are a range of ecological disciplines and modelling techniques that allow studying a tree species for which relatively little is known and can give insight in general ecological patterns over larger areas. One such discipline is biogeography that deals with the geographical distribution of plants and animals. **Species distribution modelling (SDM)** or ecological niche models provide an important input in this discipline; they are tools that relate species occurrences and/or absences with environmental data (Elith and Leathwick, 2009). SDM contributes to the understanding of spatial patterns, an important component of ecosystems (Legendre, 1993), and objectively predict the geographical range of a species or its environmental requirements (Peterson, 2001). The increasing availability of detailed global environmental data (Harris et al., 2013; Hijmans et al., 2005) and powerful computers has fuelled the development of new modelling methods and the use of SDM's, especially for predictions under changing climatic conditions (Araújo et al., 2005; Peterson et al., 2008).

Most SDM's used to be based on regression models that required both presence and absence data. New machine-learning methods have shown to outperform traditional regression techniques (Elith et al., 2006) and can often model with presence-only data. Considering the large quantities of presence-only data in herbaria, modelling plant distribution based on presence-only data is especially useful for large, poorly sampled areas (Phillips et al., 2006) such as the Miombo ecoregion. Despite the valuable contribution of species distribution maps to conservation planning, their development has been limited, particularly in the tropics (Cayuela et al., 2009).

Regeneration ecology covers a range of aspects, such as phenology, soil seed bank studies, seed germination, seedling establishment, and population structure. Population structure, the distribution of trees over different stem diameter classes, assists in assessing the regeneration status within a forest (Sop et al., 2011) and allows to derive potential species extinction, colonization, and recruitment (Thijs et al., 2014). Tree regeneration is not always well understood in tropical dry forests as many species develop mechanisms to survive droughts, browsing, and fires (e.g. Kayofa, 2015). To get more insight in these complex processes and in parallel to this dissertation, the PhD candidate supervised or is co-supervising students' work on seed germination and natural regeneration of *P. angolensis* and other woody species of Namibia (Chaka, in preparation; De Cauwer and Younan, 2015; Heita, in preparation; Hilukwa, in preparation; Kabajani, 2016; Mwansa, in preparation; Vander Heyden, 2014).

Dendrochronology or the scientific study of growth rings (Fritts and Swetnam, 1989) is based on the existence of annual growth rings in a species. The existence of annual growth rings in tropical species has been proven in more than 20 tropical countries and is based on inter-annual variation in precipitation, unlike the temperate zones where temperature is often the limiting factor (Worbes, 2002). Stem diameter increment estimations made by ring-width measurements can contribute to the establishment of sustainable management systems in tropical forests (Mbow et al., 2013; Therrell et al., 2007; Worbes, 2002).

Habitat or **site productivity models** analyse the biological response of a species, such as abundance or site index¹, to biotic or abiotic predictors through mathematical or logical constructs (Bontemps and Bouriaud, 2014; McCune and Mefford, 2011). Linear regression models are often not adequate for ecological data as the data rarely conforms to normality, homogeneity and independence of the variables. Therefore, non-linear, non-parametric and machine learning methods are increasingly used. Successful modelling methods used in ecology include mixed effects, generalised additive or boosted regression tree models (Aertsen et al., 2010; Elith et al., 2006; Zuur et al., 2009). Modelling a species' response in function of geo-climatic variables and possibly spectral signals, allows to upscale; to perform **predictive mapping** on a larger scale (Franklin, 1995), which is an increasingly common practice (Moisen, 2006).

Allometric functions estimate biomass or wood volume based on morphometric variables, especially stem diameter at breast height (DBH) and sometimes tree height, as main predictors (Chave et al., 2014; Seifert and Seifert, 2014; Shackleton and Scholes, 2011). Recent studies have also shown how wood density can improve biomass models (Chave et al., 2014; Henry et al., 2010). The need for accurate and user friendly biomass models has

¹ Site index is the mean height of the dominant trees at a reference age at the site (Pokharel and Froese, 2009; Skovsgaard and Vanclay, 2013).

increased with the international interest in carbon sequestration benefits and bioenergy (Seifert et al., 2014a; Shackleton and Scholes, 2011). **Yield models** incorporate allometric functions and growth models as they assess the accumulated BAI, volume or biomass at the end of a period (Pretzsch, 2009; Vanclay, 1994). They allow to compare different forest management techniques and goals, e.g. storage of carbon, production of timber wood, production of poles or a combination (Buongiorno et al., 2012).

In addition to autecological methods, a part of the study also makes use of a synecological method: community analysis. **Community ecology** seeks patterns in an ecosystem by multivariate analysis, the simultaneous analysis of multiple species in their habitat (McCune and Mefford, 2011). This is done through the distinction of communities - assemblages of species populations characterised by indicator species - and ordering them along environmental gradients. It not only allows to understand the main drivers of community composition (Laughlin and Abella, 2007), but also offers the possibility to monitor indicator species instead of an entire species' population (De Cáceres et al., 2012). Despite community analysis being a discipline with a long tradition, it keeps attracting attention in recent research, as a valuable tool for environmental monitoring studies (Aarrestad et al., 2011; Aerts et al., 2009; Gutiérrez-Granados et al., 2011) or to further improve methodology (De Cáceres et al., 2012; De Cáceres and Legendre, 2009).

1.4 Research objectives and outline of the study

The overall aim of the study is to contribute to the sustainable management of *Pterocarpus angolensis*, particularly in the *Baikiaea – Pterocarpus* forests, through an autecological study of the species. The dissertation focuses on the environmental conditions that influence occurrence and productivity of *P. angolensis*.

The specific research objectives are formulated as research questions below and reference is made to the chapters and autecological methods that address them.

1. What is the environmentally suitable area for *P. angolensis* and what are the main variables that influence the species' occurrence in southern Africa?
 - Chapter 2: Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis* in southern Africa.
 - Autecological method: SDM
2. How can climate change affect the distribution of *P. angolensis* in southern Africa?
 - Chapter 2: Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis* in southern Africa.
 - Autecological method: SDM
3. In which tree communities does *P. angolensis* occur in the *Baikiaea - Pterocarpus* forests and how abundant and dominant is it within those communities?
 - Chapter 3: Patterns of forest composition and their long-term environmental drivers in the tropical dry forest transition zone of southern Africa.
 - Autecological methods: community ecology, regeneration ecology (population structure)

4. What is the productivity of *P. angolensis* in the *Baikiaea - Pterocarpus* forests and what are the variables that influence it? Under which conditions can maximum productivity be reached?
- Chapter 4: Predicting site productivity of the timber tree *Pterocarpus angolensis*.
 - Chapter 5: Individual tree growth and yield models for the African timber tree *Pterocarpus angolensis*.
 - Autecological methods: dendrochronology, site production models including yield modelling

The knowledge gathered should allow determining under which conditions better and maximum productivity can be reached in order to support forest management and silvicultural interventions.

1.5 Research approach

Table 1.1 gives an outline of the structure of the thesis and how spatial patterns of environmental suitability, forest composition and productivity were assessed. Some parts of the study encompass the entire southern African region whereas others focus on the study area in the *Baikiaea - Pterocarpus* forests. The study makes use of both historical and recent data sources. The dataset collected for the study area was large (e.g. own forest inventory data: 217 plots, all data used for community analysis: 1230 plots) and collected over a large area (e.g. community analysis over 21,000 km²).

Site productivity is a quantitative estimate of the ability to produce plant biomass, including wood, at a site. Analysis of forest productivity is a challenging task when it is not possible to rely on the traditional forest site index¹ (Bontemps and Bouriaud, 2014; Pokharel and Froese, 2009; Skovsgaard and Vanclay, 2013). The most commonly accepted alternative to assess site productivity is the use of diameter growth (Bontemps and Bouriaud, 2014; Vanclay, 1992) and this was done in Chapters 4 and 5. Other measures of productivity were also assessed: measures of abundance (basal area and proportional basal area), relevant to measure productivity in natural mixed forests, and another measure of growth (site form). Basal area is the sum of the cross sectional areas of trees at DBH in a stand and expressed per unit ground area (i.e. 1 ha) (West, 2009). Site form is the height of a tree with a reference DBH (Vanclay, 1992).

Models were developed to understand the relationships of occurrence, abundance and diameter growth with environmental variables, including disturbances, and sometimes competition. The models provide insight in the requirements of the species and allow predicting the impact of scenarios of change. Several recently developed modelling techniques were used, such as species distribution, boosted regression trees and mixed effects modelling (see 1.3). Chapter 5 combines the information gathered in the previous chapters with the establishment of allometric and growth models.

Table 1.1 – Outline of the thesis: environmental suitability, forest composition, and productivity of *Pterocarpus angolensis* are studied by assessing occurrence, abundance, population structure, tree communities, site form, and diameter growth.

	Environmental suitability	Forest composition	Productivity
southern Africa	<p>Chapter 2 Potential, realised and future distribution and environmental suitability for <i>Pterocarpus angolensis</i> DC in southern Africa</p> <p>OCCURRENCE</p>		<p>Chapter 4 Predicting site productivity of the timber tree <i>Pterocarpus angolensis</i></p> <p>DIAMETER GROWTH</p>
Study area: <i>Baikiaea</i> - <i>Pterocarpus</i> woodlands (Namibia - Angola)	<p>Chapter 3 Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa</p> <p>ABUNDANCE</p>	<p>Chapter 3 Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa</p> <p>POPULATION STRUCTURE</p> <p>COMMUNITIES</p>	<p>Chapter 4 Predicting site productivity of the timber tree <i>Pterocarpus angolensis</i></p> <p>Chapter 5 Individual tree growth and yield models for the African timber tree <i>Pterocarpus angolensis</i></p> <p>SITE FORM</p> <p>ABUNDANCE</p> <p>DIAMETER GROWTH</p>

Chapter 2 - Potential, realised, future distribution and environmental suitability of *Pterocarpus angolensis* in southern Africa

Adapted from:

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.

VDC collected the data, performed the data analysis, and drafted the manuscript.

Abstract

The deciduous tree species *Pterocarpus angolensis* occurs in the dry forests of southern Africa and grows under a broad range of environmental conditions. It is threatened by overharvesting due to its valuable timber (Blood wood, Kiaat) and by land use changes. Information on the most suitable environmental conditions for the species is often outdated and anecdotal and data on its occurrence refer to range extent and not to distribution. Species distribution models could provide more accurate information on distribution and environmental requirements and thereby assist sustainable management of this tree species. Maxent models were developed to estimate the potential, realised, and future distribution of *P. angolensis* and to identify detailed environmental requirements. Occurrence of the species were sourced from herbaria and other published sources; environmental data from global GIS databases. Relevant environmental predictors were selected through a jack-knife test of the first model runs. The addition of information on competing species, fires and deforestation was tested to determine realised distribution. Model quality was evaluated with an independent presence-absence dataset. The model was projected with two climate change scenarios to study their effect on the distribution by 2080. Our analysis resulted in a potential distribution map with good discriminatory power of the presence of the species (AUC 0.83) and fairly good calibration (correlation coefficient 0.61). Range extent and environmental requirements are more detailed than those described in the literature. The distribution of the species is mainly influenced by the amount of summer rainfall, the minimum temperature in winter, the precipitation seasonality, the diurnal range and the temperature seasonality. Potential and realised distributions are very similar. Adding the fire history of the last 13 years or the distribution maps of potentially competing species as predictor variables did not improve the distribution model. It did illustrate that *P. angolensis* is mainly found in areas with annual fire frequency below 45% and that only a few of the tested species show signs of competition. Using a forest cover map improved the realised distribution slightly (Kappa coefficient 0.64). Climate change is projected to decrease the species range considerably, especially in the west, threatening species presence in Namibia and Botswana. On the other hand, the species' occurrence is projected to increase in Zambia under future climate change.

2.1 Introduction

Pterocarpus angolensis is a dry forest tree species belonging to the family of the Fabaceae and can be found in most of tropical southern Africa, including the Miombo forests. The tree is intensively harvested for its attractive hardwood and is considered the most important timber tree over much of its range (Boaler, 1966a; Pedro et al., 1955). Intensive exploitation goes back to the 1950s or earlier in the Democratic Republic of Congo (DRC), Tanzania, Zambia, and Mozambique (Clarke, 1995; Hauman et al., 1954; Lees, 1962; Timberlake et al., 2010). A few decades later, Von Breitenbach (1973) mentioned that no other African species south of the equator had been exploited on such a large scale. Nowadays, unsustainable harvesting is reported for many areas in the region, although only a few reports are based on research into recruitment rate, growth rate, and/or population size structure (Caro et al., 2005; Schwartz and Caro, 2003; Schwartz et al., 2002). The species has the status “Lower Risk/Near Threatened” on the IUCN Red List. As the natural regeneration of *P. angolensis* is reported to be limited in certain parts of the region (Caro et al., 2005; Chakanga, 2000; Dirninger, 2004; von Malitz and Rathogwa, 1999; van Daalen, 1991), it remains a question if the species’ conservation status can be maintained and if the species can be sustainably used as an important timber resource without forest management interventions.

Accurate information about the distribution and environmental requirements of the species is needed to allow an assessment of the species’ status and coordinate protection measures at a national and regional scale. Abundant information exists on *P. angolensis*, but it is mainly descriptive or general in nature (Vermeulen, 1990; Von Breitenbach, 1973) or focuses on only a single country (Banda et al., 2006; Shackleton, 2005; van Daalen, 1991; von Malitz and Rathogwa, 1999). The range extent or the distribution of the species is often summarised as a list of countries, herbaria sample locations or regions where the species can be found (Brummitt et al., 2007; Coates Palgrave et al., 1957; Gillett, 1971; Hauman et al., 1954; Palmer and Pitman, 1972). Existing maps refer to the species’ range or extent of occurrence (EOO), not to the area of occupancy (AOO) (Boaler, 1966b; Coates Palgrave, 1983; Van Wyk and Van Wyk, 1997; Von Breitenbach, 1973). Very little information is given on how the maps were compiled; it can be assumed that they are based on collations of existing locality records at the margins of the range, as is the case for many distribution or range maps in field guides and monographs (Gaston and Fuller, 2009). Therell et al. (2007) provide the most detailed range map but indicate that the northern limit of the range extent in the DRC is uncertain (Figure 2.1).

Information about the environmental requirements of *P. angolensis* illustrates that the species tolerates a broad range of environmental conditions, as illustrated in section 2.2.1. However, the most suitable environmental conditions within these ranges are not clearly documented. Species distribution models (SDMs) can serve as a tool to produce more precise predictions of the environmental requirements and the geographical distribution of a species than mere species observations, especially for large areas (Peterson and Kluza, 2005; Phillips et al., 2006). SDMs relate environmental data to species occurrences and sometimes species absences. They are also called ecological niche models (ENM) or species habitat models, although these terms place more emphasis on potential distribution modelling (Elith and Leathwick, 2009; Peterson et al., 2008). Only a minority of SDM or ENM studies focus on the African continent. Cayuela et al. (2009) illustrated that 8% of 123 SDM studies in the period 1995 – 2007 dealt with African species, and mainly plants from South Africa (4%).

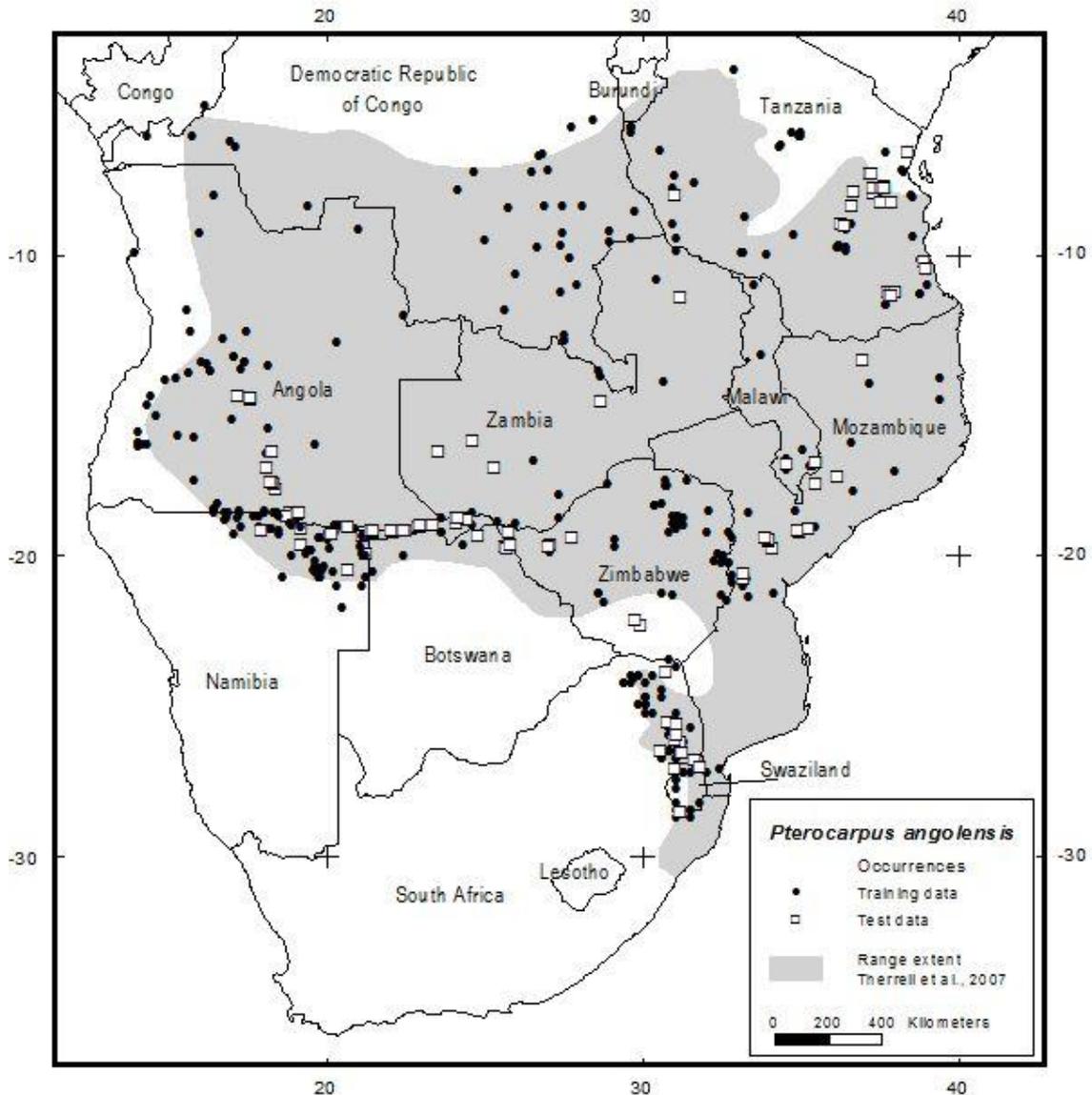


Figure 2.1 – Approximate range of *Pterocarpus angolensis* (Therrell et al. (2007) based on Boaler (1966b), von Breitenbach (1973) and Palgrave (1983)). Occurrences are presence locations collected for this study to train ($n=220$) and validate (test, $n=100$) the species distribution model. The northern limit of the current known range extent in the Democratic Republic of Congo is uncertain (Therrell et al., 2007).

In the past, most SDMs have been based on regression models. Over the last decade, machine-learning methods have been used increasingly, and have shown to outperform traditional regression techniques. Our study estimates the potential and realised distribution as well as environmental requirements of *P. angolensis* in southern Africa with the machine-learning algorithm Maxent (Phillips et al., 2006). Literature on the ecology of the species was reviewed in order to allow a proper interpretation of the results.

Africa is one of the most vulnerable continents to climate change (Niang et al., 2014) and forest managers need to consider the potential effects on this important timber species in combination with all other short-term threats to southern Africa's forests. Therefore, the SDM for *P. angolensis* was also used to derive the future distribution of the species based on two global climate change scenarios.

2.2 Methods

2.2.1 Ecology of *P. angolensis*

P. angolensis is a deciduous tree that can be found in the mixed miombo or other deciduous forests of southern Africa. It is about 10 - 20 m tall, sometimes reaching a height of 30 m (Coates Palgrave et al., 1957; Gillett, 1971; Palmer and Pitman, 1972; Pedro et al., 1955). In certain parts of Angola, it is reported to belong to the shrub stratum with heights of 2 - 8 m (Groome et al., 1957; Monteiro, 1957). The diameter at breast height (DBH) of mature trees is 40 – 70 cm (Groome et al., 1957). The species can easily reach an age of 100 to 140 years (Therrell et al., 2007).

The tree is sometimes co-dominant or dominant in the canopy layer, with tree densities up to 75 trees per ha, but most often it is distributed scarcely with densities of 4 to 20 trees per ha (Backeus et al., 2006; Brummitt et al., 2007; Groome et al., 1957; Modest, 2006). There are no records of homogenous stands of this species (Pedro et al., 1955). Tree associates vary within the distribution area and include amongst others *Uapaca* species and *Oxystigma buchholzii* in Angola, *Burkea africana* in Namibia and South Africa, and *Julbernardia* and *Brachystegia* species in Mozambique and Tanzania (Groome et al., 1957; Pedro et al., 1955; Von Breitenbach, 1973).

The forests where *P. angolensis* occurs are characterised by disturbances, especially fire and shifting cultivation and the species is well adapted to this dynamic environment due to its fire tolerance and its light demands (Banda et al., 2006; Geldenhuys, 1977; Von Breitenbach, 1973). It is deciduous with a long season of leaflessness, usually from May or June to September or October.

The juvenile (up to 11) years of tree growth are characterised by a suffrutex stage (see glossary in Annex A) during which the above-ground part dies back each dry season, a normal phenomenon in miombo woody species (Boaler, 1966b; Von Breitenbach, 1973). The species produces pods at a DHB from 11 to 19 cm onwards (Shackleton, 2002; De Cauwer, unpublished data). They can be dispersed several kilometres away from the mother tree by wind (Groome et al., 1957) and the warm updraught of fires.

The species is only commercially interesting when it reaches a DBH that is large enough to saw planks of the dark heartwood; the sapwood has no commercial value. In many countries this DBH is set at 35 to 45 cm, although illegal loggers and local users do harvest smaller sizes, mainly for construction of houses and fences. The wood is called Blood wood, Kiaat, Dolf, or African Teak in Namibia and South Africa.

P. angolensis can be found in a wide range of localities where a dry season contrasts with a single wet season (Coates Palgrave, 1983; Von Breitenbach, 1973). It can be found from sea level up to 1650 – 1800 m altitude (Takawira-Nyenyanya et al., 2010; Von Breitenbach, 1973). Average rainfall in its range varies between 400 mm (Curtis and Mannheimer, 2005) and

1250 mm (Palmer, 1997; Von Breitenbach, 1973) and average temperature between 15 and 32 °C (Takawira-Nyenyanya et al., 2010). The species is sensitive to frost, especially young trees, (Groome et al., 1957; Vermeulen, 1990) and is limited to areas with a mean minimum temperature of at least 20 °C for the warmest month and 4 °C for the coldest month (Von Breitenbach, 1973). Extreme cold events can have an effect on the flowering of *P. angolensis*, which takes place between September and December, with the northern parts of the distribution area flowering earlier (Curtis and Mannheimer, 2005; Groome et al., 1957; Shackleton, 2002).

The species occurs on a wide range of soil types from sandy to clayey, but is mainly found on deep sands with the biggest trees on well-drained soils with a sandy or loamy texture (Groome et al., 1957; Palmer and Pitman, 1972; Strohbach and Petersen, 2007; Vermeulen, 1990; World Agroforestry Centre (ICRAF), 2013). It is not adapted to black clays (Boaler, 1966b; World Agroforestry Centre (ICRAF), 2013) and can be found on plains, dunes, and sometimes hill slopes (Curtis and Mannheimer, 2005; von Malitz and Rathogwa, 1999; World Agroforestry Centre (ICRAF), 2013).

2.2.2 Model algorithm

A presence-only (PO) species distribution model Maxent (Phillips et al., 2006) was chosen for this study because species data for *P. angolensis* have not been collected in a systematic matter at regional scale. Maxent is a general-purpose machine learning method, which uses a maximum-entropy approach. Its application in SDMs is fairly recent and gives superior results compared to other methods (Elith et al., 2006; Kumar et al., 2009; Phillips et al., 2006, 2004; Poulos et al., 2012). The prediction of the model indicates the areas within the study region that satisfy the requirements of the species' ecological niche. It offers a natural probabilistic interpretation, giving a smooth gradation from marginally to most suitable conditions. The standard parameter set proposed by Maxent version 3.3.3k - with exception of the generation of the pseudo-absences or background points - was used as several test runs showed that altering them did not improve the results.

The model uses pseudo-absences or background points to represent the environmental conditions in the study area. Instead of letting the algorithm randomly select the 10,000 background points for each Maxent run, the random background dataset of one Maxent run was used for all models to allow a better comparison of validation results. Background points in Madagascar (606) were removed to create the same bias as in the occurrences (Phillips, 2008a; Phillips et al., 2009). The species does not occur in Madagascar, whereas large parts are potentially suitable according to all model runs (see 2.3.1).

2.2.3 Occurrences

A regional dataset of 570 observed presence locations was created for *P. angolensis* by consulting herbaria records, scientific articles and reports, data of tree atlas projects, e-floras, forest inventories, and own or colleagues' field observations and data (Annex B). The spatial accuracy was estimated and only data with a spatial accuracy less than 10 km and collected after 1940 were retained. A lot of the herbaria data originated from early colonial times but did not match the temporal range of the environmental data (1950-2000). Of the

remaining 480 occurrences, 38% are in Namibia and South Africa, whereas only 4% of the range extent covers those countries (Figure 2.1). This can be explained by the fact that there is an easier access to data, rather than by a higher occurrence of the species in Namibia and South Africa. To reduce this bias, the dataset was randomly reduced for the two countries, resulting in a final dataset of 320 occurrences for the region. This dataset was then split up in two independent datasets: the 220 points collected as incidental records or through unsystematic surveys, including herbaria and e-floras, were used as training data and for PO validation. The remaining 100 occurrences from systematic surveys and with accurate locations were set aside for presence/absence (PA) validation (see 2.2.6).

The amount of training points (220) is appropriate compared to other SDM studies performed on a regional scale (Anderson et al., 2003; Elith et al., 2006; Trabucco et al., 2010), but not yet the optimal sample size of at least 500 observations as advised by Hanberry et al. (2012).

The preliminary Maxent runs and the literature review on environmental requirements (2.2.1) indicated that the ecological requirements of *P. angolensis* may differ in the southwest of the distribution range compared to the rest of the study area. Therefore, the model was also run separately for two zones of the study area: the Kalahari basin and outside the basin (Figure 2.2). The Kalahari basin was determined based on a GIS dataset extracted from the South African Council of GeoSciences (Mendelsohn and el Obeid, 2004). Other divisions of the study area were tested – e.g. based on aridity and occurrence of frost – but yielded less good validation results.

2.2.4 Environmental data

The environmental data needed for a SDM must have the potential to ecologically explain the distribution of the species. After consideration of the environmental requirements of *P. angolensis* (see 2.2.1), the datasets listed in Table 2.1 were collected. The climate variables are available as averages over the time period indicated, except for (spring) frost days for which the averages were derived from the Climatic Research Unit time-series datasets (CRUTS v.3.10.01) (Harris et al., 2013). The Harmonised World Soil Database (HWSD) lists a range of soil attributes per soil unit. Only the dominant soil unit was linked to the map unit and soil attributes were averaged when there were two dominant soil units. Test runs showed that this method of establishing a one-to-one relation appeared to be the most suitable for the species.

All environmental datasets were converted to the ASCII raster file format necessary for Maxent, with a resolution of 30 arc seconds (about 920 m at the equator). The climate data accuracy will be much lower because of the low density of climate stations in southern Africa (Hijmans et al., 2005). In total, 68 predictor variables were collated. However, there are several reasons to reduce the number of variables in a model: to minimise computing time, to minimise the amount of correlated variables that can cause overfitting, to increase transferability, to increase signal to noise ratio and to better understand the causal relationships of the model (Mac Nally, 2000; Trabucco et al., 2010). After several test runs it was decided to select the twelve most relevant environmental variables to build the final model for the potential distribution of *P. angolensis*. Selection was based on two different measures of variable contributions calculated by Maxent for a model run with all

environmental data. The jack-knife test gives an indication of how important a certain variable is in the model by measuring the training gain obtained with and without each environmental variable. The permutation importance determines the contribution to the model of each variable by randomly permuting its values during training and measuring the resulting decrease in model performance (Phillips, 2008b). Important variables have a high permutation importance and a low training gain obtained without the variable.

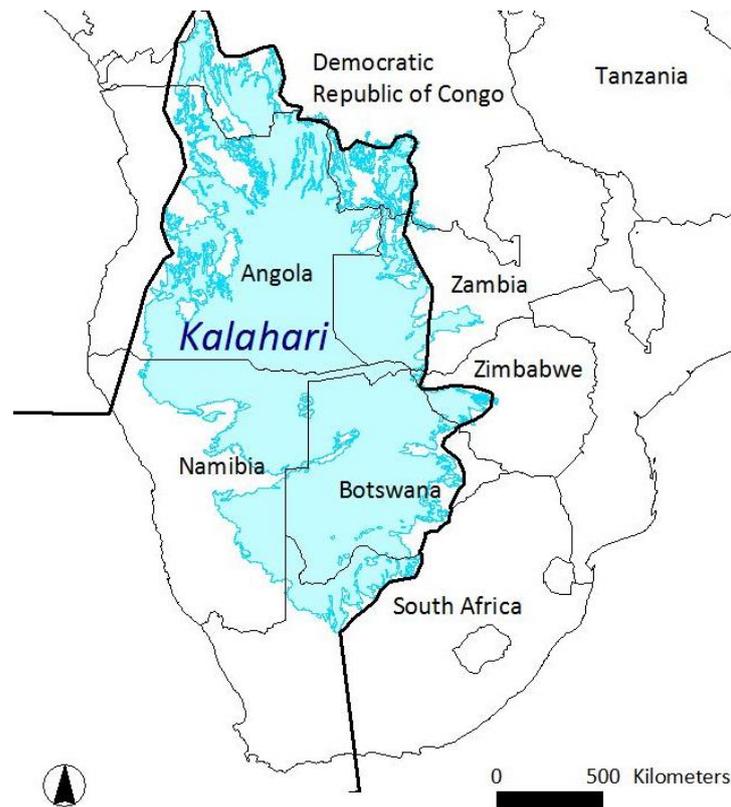


Figure 2.2 - Segmentation of the study area in two zones: the Kalahari basin in the southwest and the area outside the Kalahari basin. The position of the Kalahari Group deposits is based on data of Mendelsohn and el Obeid (2004).

2.2.5 Realised distribution

The distribution area predicted by a SDM will typically be larger than the species' realised distribution as few species occupy the entire area of the potential distribution (Phillips et al., 2006). The difference is caused by processes not controlled by the earlier mentioned environmental variables. Four factors with potential influence on the distribution of *P. angolensis* were considered: fire, competing species, geographic barriers, and deforestation. Wood harvesting will have had a limited impact on the species' distribution as *P. angolensis* can reproduce long before it becomes commercially interesting to harvest (Shackleton, 2002; De Cauwer, unpublished data). Browsers could also influence the species' distribution, but this was not considered in the study.

Table 2.1 – Environmental predictor variables included in the first runs of the modelling. All data have an interval scale. Climate variables are averages over the time period indicated. A glossary of terms is in Annex A.

Variables	Source	Period	Resolution
Annual mean temperature (temp.), mean diurnal range, Isothermality, Temp. seasonality, Max. temp. warmest month, Min. temp. coldest month, Temp. annual range, Mean temp. wettest quarter (qrt.), Mean temp. driest qrt., Mean temp. warmest qrt., Mean temp. coldest qrt., Annual precipitation (prec.), Prec. wettest month, Prec. driest month, Prec. seasonality, Prec. wettest qrt., Prec. driest qrt., Prec. warmest qrt., Prec. coldest qrt., Min. temp. of August, Sept. and Oct., Mean temp. of July, August, Sept. and Oct., Average monthly prec. of February, June, July, Sept., Oct., Nov. and Dec., Rainmonths (Monthly prec. \geq 20mm; derived in GIS)	WorldClim (Hijmans et al., 2005) http://www.worldclim.org	1950/1960 - 1990/2000 (depending on dataset)	30 arc sec (\pm 920 m at equator)
Frost days, Spring frost days (frost in Sept. & Oct.)	Climatic Research Unit time-series datasets (CRUTS v.3.10.01) (Harris et al., 2013)	1941-2002	30 arc min (\pm 55 km at equator)
Length of growing period	FAO-UN (FAO and IIASA, 2000)	1960-2002	5 arc min (\pm 9 km at equator)
Potential evapotranspiration (PET) of April, June, Sept., Oct. and Dec., Soil water content (SWC) of January, April, July, Sept., Oct. and Dec., Priestley-Taylor alpha coefficient, Aridity Index	CGIAR-CSI (Consortium for Spatial Information) (Trabucco, 2010; Zomer et al., 2007)	1950-2000	30 arc sec
Altitude, Slope and Aspect (Derived from altitude in GIS)	Shuttle Radar Topography Mission (SRTM) http://srtm.csi.cgiar.org		3 arc sec (\pm 90 m)
Drainage class, Average Water Capacity (AWC) class, pH Topsoil, Organic Carbon Topsoil, Base Saturation Topsoil, Cation Exchange Capacity (CEC) Topsoil, CaCO ₃ Topsoil, Sand/Clay/Gravel/Silt Fraction of Topsoil, Reference soil depth of soil unit	Harmonised World Soil Database (HWSD) (FAO/IIASA/ISRIC/ISSAS/JRC, 2009)		30 arc sec
Nutrient availability, Nutrient retention capacity, Rooting conditions	Harmonised World Soil Database (HWSD) (Fischer et al., 2008)		5 arc min

Burke (2006) indicated that fire tolerance of the species may provide further understanding of its distribution. Fire is both a natural and anthropogenic disturbance in southern Africa, although most fires are currently ignited by humans (Archibald et al., 2009 ; own observations). The effect of fire on the distribution of *P. angolensis* was evaluated by adding it as an explanatory variable to the model. A GIS layer was created that reflected the number of years an area had burnt in the period 2000 – 2012. It was derived from MODIS fire observations extracted from NASA’s archive (NASA, 2013). Only fire points with a confidence level over 50% were withheld.

No information was found in the literature about tree species with a specific competing behaviour towards *P. angolensis*. Potentially competing tree species were selected that have

a partially overlapping range extent with *P. angolensis*, that occur in the upper tree canopy layers, and for which at least 25 occurrence points from herbaria were available for the study area. It concerns (with indication of number of occurrence points): *Brachystegia boehmii* (61), *Brachystegia microphylla* (28), *Brachystegia spiciformis* (33), *Brachystegia utilis* (44), *Burkea africana* (158), *Dalbergia melanoxylon* (172), *Faurea saligna* (166), *Julbernardia globiflora* (75), *Julbernardia paniculata* (25), *Pericopsis angolensis* (93), and *Schinziophyton rautanenii* (36). The effect of competition of those tree species on the distribution of *P. angolensis* was evaluated by adding their distributions as explanatory variables to the model. The distribution maps of the competing species were created with Maxent using the same settings and predictor variables as for *P. angolensis*. AUC (area under the receiving operating characteristic (ROC) curve) of the SDMs varied between 0.840 (*B. spiciformis*) and 0.967 (*B. microphylla*). A number of studies (Hernandez et al., 2006; Phillips and Dudík, 2008; Stockwell and Peterson, 2002; Wisz et al., 2008) show that model performance increases with sample size of the occurrence data, but that results of satisfactory discriminatory power can be obtained when the sample size is larger than circa 25 to 30 points, especially with Maxent.

Areas where the species is known to be absent because of geographic barriers were removed. The only major geographic barrier in the study area is the ocean as there are no large mountain chains that could affect dispersal. Seeds of *P. angolensis* can be dispersed over several kilometres, as explained in section 2.2.1. Hence, only Madagascar was removed.

The SDM output of Maxent is a raster image that represents probabilities of the species' occurrences. A threshold of probability needs to be selected to classify pixels into the categories "present" and "absent" of a realised distribution map. Maxent gives the occurrence probabilities for several commonly used thresholds. No general threshold rule is applicable (Phillips et al., 2006), and there has been no comparative study that includes all those thresholds. Some studies (Bean et al., 2012; Liu et al., 2005) do however indicate that the threshold whereby sensitivity and specificity equal each other works well. This threshold, as well as the 10 percentile training presence which was not included in the studies, were used. The 10 percentile training presence threshold excludes the 10% lowest model probabilities.

Forest clearing for subsistence agriculture, cash crops or urbanisation plays an important role in the study area. Deforestation was taken into account by projecting the SDM, after applying the threshold, on a woody vegetation map. The SAFARI2000 tree cover dataset of DeFries et al. (1999) was used for this purpose. It is based on 1992-1993 AVHRR data and has a resolution of ca. 1 km. Areas with shrubs or trees canopy coverage of at least 10% were considered as woody vegetation. The data of the Global Forest Resources Assessment 2000 (FRA2000) was also tested but gave less good results, especially for open forests.

2.2.6 Model validation

Validation with PO data

Maxent allows to perform an automatic division of occurrence points and subsequent cross-validation in batch mode as explained by Elith et al. (2011). This method allows assessing how stable the performance of each algorithm is and can derive average performance measures. The Maxent models were tested with a 10-fold cross-validation procedure.

The AUC was used as a validation tool. This test statistic was introduced by Fielding and Bell (1997) and is currently the most commonly used for testing SDM's outputs (Elith et al., 2006; Phillips et al., 2006, 2004). An advantage of AUC is its independence of a fixed threshold as it evaluates all presence threshold scenarios. For PO modelling, it represents the probability that a randomly chosen presence site is ranked better than a random pseudo-absence site: a value higher than 0.5 indicates performance better than random (Phillips et al., 2006). However, AUC increases with the proportion of the study area that falls outside the presence domain of a species (Lobo et al., 2008). AUC values obtained within this study can be compared as the same study area is used for all model runs; however they can only be compared with AUC values of other studies when they have a similar relative occurrence area. Furthermore, AUC only measures the model's capacity to discriminate between presence and absence. It does not consider the values of the predictions, thus how well the model is calibrated (Elith and Graham, 2009; Lobo et al., 2008; Phillips and Elith, 2010). An additional validation with independent PA data, was performed to assess model calibration.

Validation with PA data

An independent PA validation requires a dataset not used for the training. In addition to the 100 occurrences that were set aside, 100 absences had to be collected. Obtaining absence data is less evident than presence data as their locations should reflect areas large enough compared to the model resolution (1 km²). This is especially difficult to determine in areas with insufficient inventory data (Anderson, 2003). Most of the systematic surveys used for the occurrence data could not be used to derive absences as they covered a too small area, had a too small sample size or did not publish the complete inventory data.

Fifty absence points were added based on literature (Annex C), the tree atlases of Swaziland and Namibia (Curtis and Mannheimer, 2005; Loffler and Loffler, 2005), and the Seronga study area of The Future Okavango project. Another 50 absences were created by random generation in areas where *P. angolensis* is known to be absent and that are within 500 km from the known range extent, i.e. Rwanda, Uganda, Lesotho, Kenya, Gabon, central and southern Botswana and western and central South Africa (Coates Palgrave, 1983; Germishuizen et al., 2006; Kobisi, 2005; Setshogo and Venter, 2003) (Annex C).

The point bi-serial correlation coefficient (COR) and deviance were used as validation statistics. Both parameters measure discrimination and calibration of the model, with deviance more emphasising calibration (Elith and Graham, 2009; Phillips and Elith, 2010). COR is a measure for the correlation between the predicted probabilities and the actual absences (0) or presences (1). The better the correlation, the closer COR is to 1. Deviance is a measure of lack of fit between the model and the test data; the larger the deviance, the poorer the model. It is calculated as explained by Phillips and Dudík (2008) and averaged for all test points.

The realised distribution can be validated by calculating the omission error (false-negative prediction), the commission error (false-positive prediction), as well as the Kappa coefficient (Cohen, 1960), as a threshold has been applied. A Kappa coefficient of 1 indicates perfect agreement between realised distribution and training points and a coefficient between 0.61 and 0.8 good agreement beyond chance (Banerjee et al., 1999; Landis and Koch, 1977).

Wrongly classified occurrence points are mapped to understand distribution of model errors and look for any residual geographic pattern (Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Lobo et al., 2008).

2.2.7 Estimating future distribution

The effect of a changing global climate on the future distribution of *P. angolensis* was estimated in Maxent. Land use changes or the potential effect of climate change on fire occurrence were not taken into account. Projections of the 12 most relevant climate layers in the 2080's, based on the HADCM3 model with A2a and B1 SRES emission scenarios, were extracted from the WorldClim dataset. Global and regional climate change models vary a lot in their projections for the African continent (Hewitson, 2006) and by using these two scenarios a medium high emission (A2a) and a low emission (B1) scenario are presented and their central tendency can be explored (Araújo et al., 2005). The A2a emission scenario predicts a global temperature rise of 2 to 5.4 °C by the end of the 21st century compared to the period 1980-1999, while the B1 scenario – with global population and carbon emissions projections that are much lower – predicts a temperature rise of 1.1 to 2.9 °C (IPCC, 2007).

Future projections of the amount of frost days are not available and instead a Maxent model was used whereby the amount of frost days was replaced by the environmental variable with the next highest contribution to the model.

2.3. Results

2.3.1 Potential distribution

The AUC values of the Maxent model runs with different sets of environmental layers (Table 2.2) all indicated a good discrimination of occurrences, much better than random. The PA validation results resembled those of the PO validation with the point bi-serial correlation coefficient (COR) giving a similar ranking of the models compared to AUC, whereas deviance indicated another model (A) as that with the lowest quality. The model that used all input data (A) showed a discontinuity at the Namibian borders. This is caused by the soil dataset, which is a compilation of existing regional and national soil databases causing abrupt changes at country borders. A model without soil data (W) did not show this effect and had a better deviance. No soil data were therefore added to model R with the 12 most relevant environmental data layers (Figure 2.3). This was also the model that performs best for discrimination and calibration and was used to derive the realised distribution.

Table 2.3 indicates the contribution of each environmental variable to model R by listing the results of permutation importance and jack-knife test. The contributions are not a direct indicator of the ecological importance of each environmental variable on the distribution of *P. angolensis*, as they represent the best statistical solution for the whole region. When dividing the study area in two zones, the Kalahari basin and the area outside the basin (Figure 2.2), the models created for each of these zones showed a very different ranking of the environmental factors (Table 2.3). Rainfall in October and February are more important predictors for the Kalahari model than for the non-Kalahari model.

Table 2.2 – Maxent model results with differing sets of predictor layers (# layers). AUC gives the outcome of the presence-only validation, the point bi-serial correlation coefficient (COR, $p < 0.001$) and deviance (DEV) are measures of the presence-absence validation. The most relevant environmental data are listed in Table 2.3.

Model	Predictor dataset	# layers	AUC	COR	Dev
Potential distribution					
A	All environmental data	68	0.810	0.576	1.206
W	All environmental data without soil	56	0.807	0.568	1.184
R	Most relevant environmental data	12	0.828	0.609	1.068
Realised distribution					
C	Most relevant environmental data + competing trees	23	0.844	0.540	1.215
F	Most relevant environmental data + fire history	13	0.834	0.573	1.128

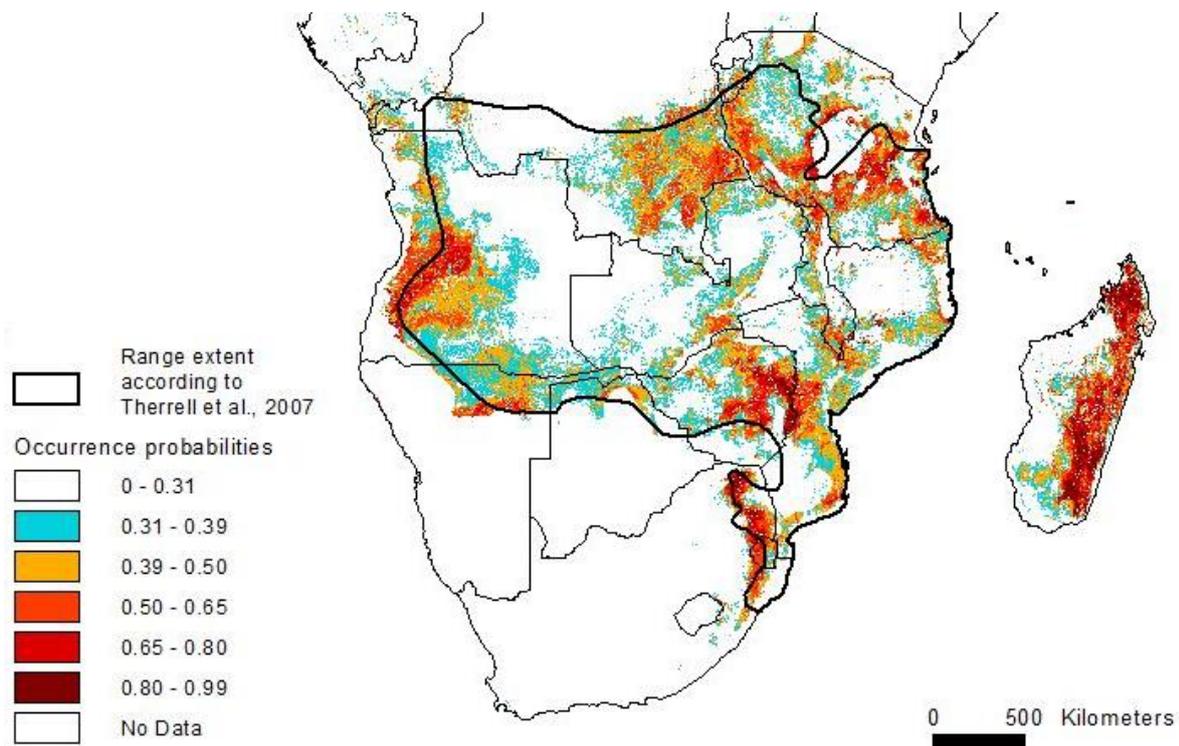


Figure 2.3 – Potential distribution for *Pterocarpus angolensis* with indication of the range extent from Therrell et al. (2007). The model (R) was run in Maxent with the 12 most relevant data layers (listed in Table 2.3); output is the logistic format of Maxent. Thresholds applied were 10 percentile training presence, equalling 0.31, and training sensitivity equal to specificity, equalling 0.39.

Table 2.3 – Contribution of environmental variables to model R for the total study area (ALL), the Kalahari basin, and the area outside the Kalahari basin, ranked according to training gain without the variable. Important variables have a high permutation importance and a low training gain obtained without the variable. A glossary of terms is in Annex A.

Variable	Training gain without variable	Permutation importance		
	ALL	ALL	Kalahari	non-Kalahari
Slope	0.834	4.2	0.5	4.0
Seasonality precipitation	0.846	24.7	15.4	3.1
Rainfall November	0.849	11.7	0.0	11.6
Rainfall February	0.852	12.3	20.3	7.9
Diurnal range	0.860	7.2	3.3	26.6
Minimum temperature coldest month	0.877	6.8	0.0	2.7
Rainfall October	0.886	9.5	26.6	4.4
Rainfall driest month	0.888	7.9	19.0	7.0
Altitude	0.889	1.6	9.7	1.6
Frost days	0.896	6.3	3.8	9.0
Rainfall coldest quarter	0.899	1.5	1.4	5.2
Seasonality temperature	0.900	6.3	0.0	17.0

Response curves for each variable allow analysing the effect on the probability of occurrence for *P. angolensis* (Figure 2.4). They indicate the optimal range for each of the variables, for example the highest probability to find *P. angolensis* is when rainfall seasonality is between 55 and 110%, rainfall in November is between 45 and 210 mm and the minimum temperature of the coldest month is between 4 and 18 °C. The response curves in Figure 2.4 show the average for the total study area, whereas the response curves for the two individual zones show differing results (Annex D).

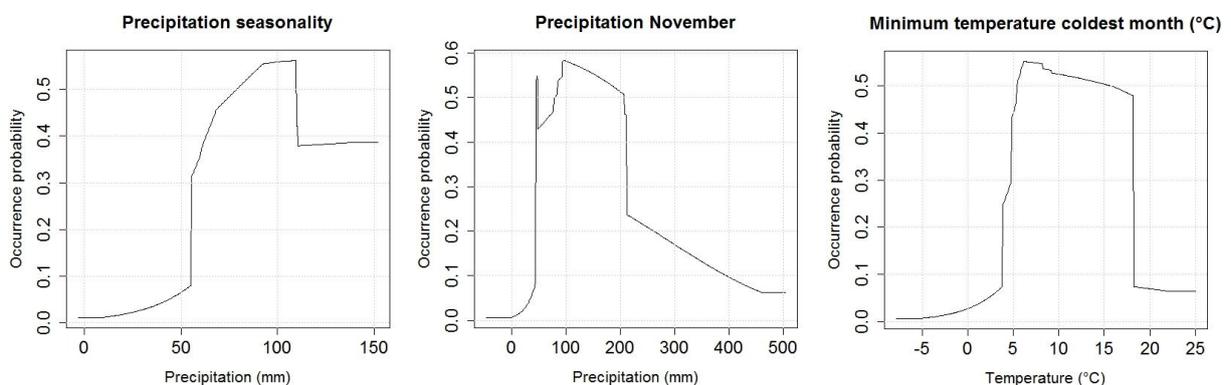


Figure 2.4 – Response curves of three environmental variables for model R. The effect of precipitation seasonality, rainfall in November, and average minimum temperature of the coldest month on the probability of occurrence for *Pterocarpus angolensis* is shown by the calculation of univariate models containing only the variable.

2.3.2 Realised distribution

The equal sensitivity and specificity threshold applied to the best model R resulted in a lower accuracy (Kappa = 0.52) than when the 10 percentile training presence threshold was applied (Figure 2.3). The Kappa coefficient obtained with the latter threshold indicated good agreement (Table 2.4) and will be used further. Commission is higher than omission and the errors occur almost all at the southern edges of the distribution. There is no obvious pattern in the location of the omission errors except that there are a relatively high number in Zambia (6 out of a total of 8 Zambian observed presence points).

Table 2.4 – Accuracies for two realised distribution maps: the potential distribution map on which a threshold was applied and the same map projected on a tree cover map of SAFARI2000 (DeFries et al., 1999). Om reflects the omission error and Com the commission error.

	Om (%)	Com (%)	Kappa
Potential distribution	14	24	0.62
Realised distribution on SAFARI2000	18	18	0.64

Addition of the recent fire history or potentially competing species as predictors to the SDM of *P. angolensis* improved the PO but not the PA validation results (Table 2.2) and they were not added to the final model. However, similar to the environmental data, the response curves of fire and the potentially competing species give useful information with regard to the occurrence of *P. angolensis*. There was a clear negative relation between fire occurrence and the species' occurrence probability for areas with 3 or more fires within the period 2000-2012. Grid cells with 6 or more fires during that period are considered as unsuitable.

The potential distributions of Manketti (*S. rautanenii*), Miombo (*B. boehmii*), and African Blackwood (*D. melanoxylon*), as well as precipitation in October, were the variables with the highest contributions to model C. The response curves indicate that with increasing occurrence probability of the two latter species, the probability of finding *P. angolensis* increases (Figure 2.5). The response is not following the line that would reflect perfect co-occurrence, but it is fairly similar especially for occurrence probabilities over 50%. There is an average probability of 55% to find *P. angolensis* in areas where *S. rautanenii* or *J. paniculata* do not occur. Most of the remaining potentially competing species have a similar response curve as *B. boehmii*, with exception of *B. africana*. The highest probability of finding *P. angolensis* is where the probability of occurrence for *B. africana* is lower than 70%.

Projection on the SAFARI2000 data gave slightly better PA validation results than the potential distribution map and a better balance between omission and commission errors. Hence, the potential distribution map projected on the SAFARI2000 data and after removal of Madagascar was selected as realised distribution map (Figure 2.6).

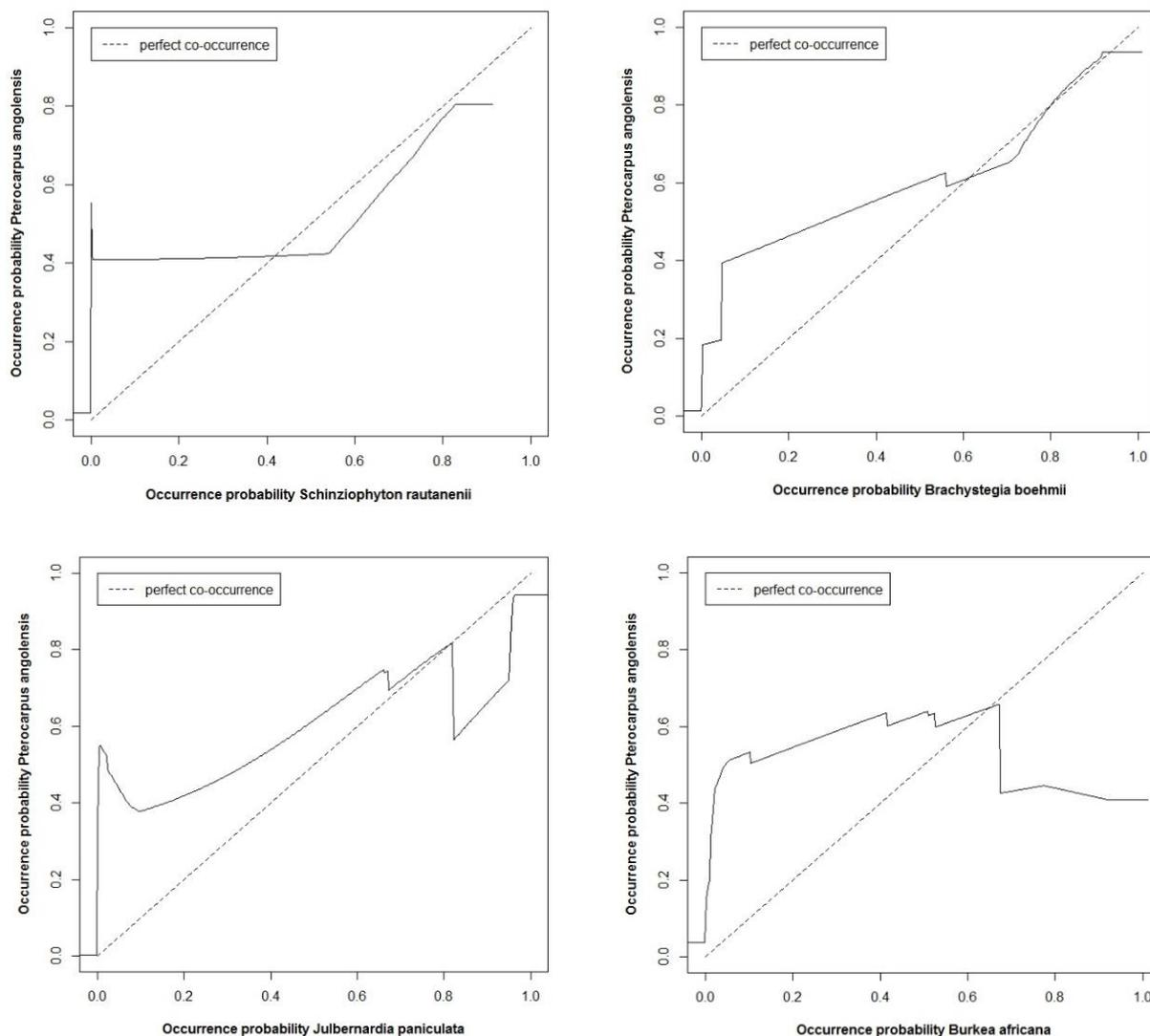


Figure 2.5 – Response curves of potentially competing tree species created by Maxent model C. The effect of potential distribution of those species on the model for *Pterocarpus angolensis* is shown by calculating univariate models containing only the considered species. The dashed lines represent perfect co-occurrence of species.

2.3.3 Future model

A Maxent model was used whereby the amount of frost days was replaced by the average rainfall in September, which contributed as 13th best to models A and W. This model gave similar validation results to that of model R with current climate data (AUC 0.825, COR 0.586). The distribution area of *P. angolensis* decreased for both 2080 scenarios: 22% for the B1 and 51% for the A2a emission scenario (Figure 2.6). The Maxent model predictions are not affected by environmental variables that are outside their training range; future values of the variables are still within the ranges of the current values for the study area.

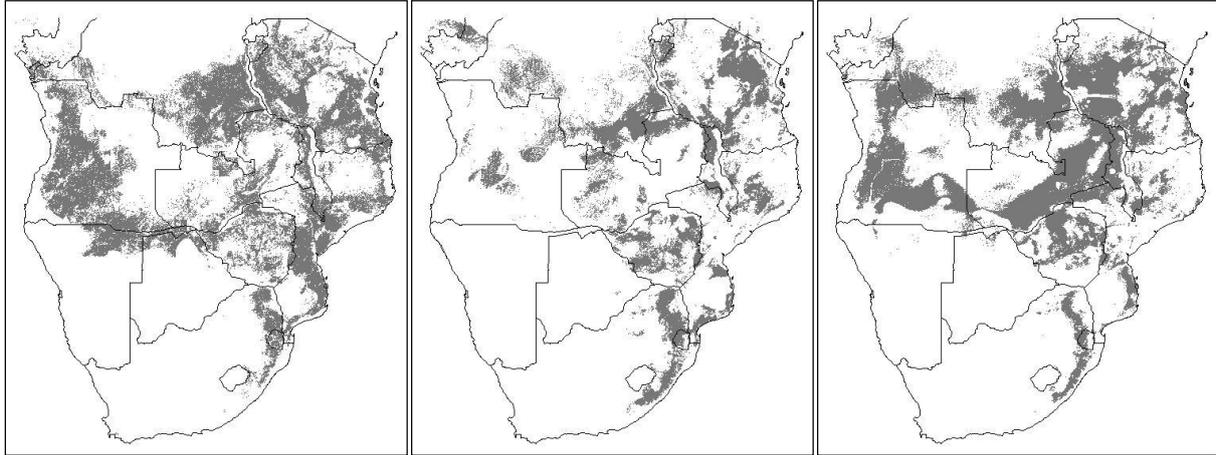


Figure 2.6 – Current and future (2080) distribution scenarios for *Pterocarpus angolensis*. Left is the current distribution, the middle uses emission data from emission scenario A2a and the right from emission scenario B1. A minimum threshold of 10 percentile on occurrence probabilities was applied to delineate species distribution.

2.4 Discussion

Potential distribution of P. angolensis

SDMs allow creating detailed distribution maps for large regions with relatively little observations. This is especially useful for large areas with limited access such as southern Africa. Creating an accurate distribution map for *P. angolensis* with only field observations would need systematic and extensive collection of occurrences in countries lacking good road infrastructure and/or on-going civil wars. The distribution models produced for *P. angolensis* show high AUC values, indicating a good discrimination of the species' presence. Deviance values are similar but slightly higher than those of Phillips and Dudik (2008), whereas correlation values are much higher indicating that there were several discrepancies between the model and PA dataset that are penalised by a larger deviance. Correlation with actual absences and presences of withheld data are good in comparison with other studies (Elith et al., 2011, 2006). It is however difficult to compare PA validation results of various studies without an objective way to characterise the absence dataset. Test runs showed that better validation results could easily be obtained by extending that part of the study area where absences were randomly selected. Currently not many SDM studies use independent PA datasets to validate their models and it may be advisable to document the location of absences in further studies.

The probability of occurrences (Figure 2.3) shows that the environmentally most suitable areas for the species are in Zimbabwe, Tanzania, South Africa, and to a lesser extent central Angola. Anecdotal references show that these areas are only partially related to a higher productivity of the species. Vermeulen (1990) and Von Breitenbach (1973) indicate that maximum heights of the species are achieved in Tanzania, but also in Zambia and Mozambique. The highest tree (27.4 m) was recorded in the Copper belt area of Zambia (Groome et al., 1957), whereas the probability of occurrences there is nowhere higher than

0.5. Stahle et al. (1999) write that the natural forests supporting adequate stocks of *P. angolensis* for industrial extraction are confined to certain areas of north-western and north central Zimbabwe. However only central parts, together with the east of Zimbabwe, are shown as high probability areas in this study. Hence, there is no indication that the environmentally most suitable areas for occurrence are also areas with high productivity.

Realised distribution

The potential and realised distribution of *P. angolensis* are very similar, with exception of Madagascar where the environmental conditions are potentially suitable for the species but where it does not occur due to the Indian ocean acting as a geographic dispersal barrier. Another area where the species does not occur, unlike indicated in the potential distribution map, is northeast of the Etosha pan in Namibia, which is a karst area (the Grootfontein-Tsumeb-Otavi triangle), as well as areas where forest has been removed, such as for example in Burundi.

Adding fire occurrences as predictor did not improve the model but this does not mean that fire frequency does not have an effect on the species' distribution. As in other studies (Archibald et al., 2008), fire occurrence was correlated to rainfall (e.g. Pearson correlation of 0.17 with $p < 0.01$ for February rainfall), causing a smaller contribution of fire history to the model that already included predictors related to rainfall. The finding that *P. angolensis* rarely occurs in areas with annual fire frequencies of over 45% could not be confirmed by literature although there are indications that where fires are too frequent, the suffrutex stage is prolonged, and there is a higher mortality in adult trees (Groome et al., 1957; Vermeulen, 1990). Several authors (Geldenhuys, 1992; Graz, 2004; Vermeulen, 1990) state that a certain amount of fire is needed to reduce competition in the sapling stage of *P. angolensis*, but this could not be derived from the model. The response curve (data not shown) showed a negative relation between fire occurrences and occurrence of *P. angolensis* for all fire frequencies.

Although the potentially competing trees did not improve the calibration of the model, their response curves provided interesting information about their interaction with the study species. Only a few of the species considered showed signs of competing behaviour with *P. angolensis*: *B. africana*, *S. rautanenii*, and *J. paniculata*. The probability to find *P. angolensis* decreases in the most suitable areas for *B. africana*, a species that is at least as fire resistant as *P. angolensis* in the Namibian open forests (Burke, 2006) and appears to have a competition advantage there. The distribution areas of *S. rautanenii* and *J. paniculata* do not overlap with the areas considered best for *P. angolensis* by the model, hence there is a good probability to find the study species in areas where those two do not occur.

The other species can be considered as co-occurring in most areas that have a higher probability (> 50%) to find *P. angolensis*, at least at a resolution of 1 km². Especially the occurrence of *B. boehmii* is an indication that there is a high probability (40 – 100%) that *P. angolensis* is in the same area. It would be interesting to test other potentially competing species, also those with ranges that do not overlap such as *Colophospermum mopane*.

The final realised distribution model has a Kappa coefficient of 0.64, indicating a good accuracy (Banerjee et al., 1999; Landis and Koch, 1977). Better results may be obtained for the realised distribution map if a more recent forest cover map than that of DeFries et al.

(1999) were available. The final map shows that the species' distribution area is largest in Angola and Tanzania (about 550,000 km² in each country). It confirms the most northerly occurrence of *P. angolensis* in the vicinity of the southern shores of Lake Victoria, Tanzania (Boaler, 1966b), and not Lake Edward, DRC (Groome et al., 1957). The most southern part of the distribution appears to run about 300 km further south than the earlier reported Itala Game Reserve in South Africa (Vermeulen, 1990). The species may not occur here because of intensive harvesting during previous centuries, considering the proximity to the seaport Durban.

The distribution map's area showed a lot of similarities to the natural range map that Therrell et al. (2007) based on older collations of records and observations (Coates Palgrave, 1983; Von Breitenbach, 1973) although it covered a smaller area (60%). This is mainly because our map provided more detail and omitted a large area in the south of the DRC, eastern Angola, and western Zambia. The omitted area is characterised by a lower altitude, a lower number of frost days and slightly higher precipitation than the areas to the east and west of it, but the limiting environmental factors for *P. angolensis* are not obvious. There is a possibility that the species occurs in the area but that there is no recent occurrence data available; Monteiro (1957) mentions that the species occurs frequently in the Moxico province of Angola, which borders Zambia, as a shrub smaller than 3 m, whereas there is a species record from 1938 at Royal Botanic Gardens, Kew for Matonchi, which is near the border of Zambia and Angola, not too far from the DRC. On the other hand, climatic conditions in the mid-twentieth century may have been different then compared to the end of the 20th century. Therrell et al. (2007) indicated that the range of the species in the southern DRC was not exactly known and our SDM showed that it did not extend as far north (Figure 2.2).

Input data of SDM

The best results were obtained by reducing the amount of input data, especially the environmental variables or predictors. Currently, the choice of predictors remains a challenge (Ashcroft et al., 2011) and it is remarkable that a lot of studies do not use an objective selection method (Acevedo et al., 2012; Elith et al., 2006; Elith and Leathwick, 2009; Phillips et al., 2006; Thuiller et al., 2006; Zimmermann et al., 2009) considering that the choice of the predictors has a significant effect on the final model (Araújo and Guisan, 2006), as was noticed during the test runs of this study. The analysis of training gain and permutation importance by Maxent provides an objective and quick tool to select predictors by evaluating their effect on the accuracy of the final model. The chosen predictors are not always obvious from existing knowledge of the species, such as for example the temperature seasonality or November rainfall for *P. angolensis*.

Early test runs of the models indicated that validation results also improved when both training and test points in Namibia and South Africa - that had a relative overrepresentation of occurrences and thus induced a bias in the data - were reduced. However, when only the training points were reduced, the model performed worse because of the bias in the test points. It is an indication of how easily results can be adapted by the choice of training and test points and confirms earlier studies that mention that biases and gaps in the input data may affect SDM results (Costa et al., 2009; Elith et al., 2011).

The soil data itself did not appear to contribute much to the final quality of the SDM, as in the study of Trabucco et al. (2010). Although this could be explained by the fact that the quality and resolution of the soil data is not good or not uniform enough for southern Africa or that soil is not an important contributor to the distribution of *P. angolensis*, it seems more likely that soil requirements are different for the species within certain zones of the distribution area. The results of the model run with training points of two subzones indicate that there are no clear soil preferences outside the Kalahari, unlike the Kalahari area where the species grows well on deep and sandy soil whereas it does not grow in the karst area of Namibia. Dividing the study area in relevant ecological zones in order to establish a SDM per zone is a challenge, and may be worth testing in further studies.

Many SDM studies focus on comparing algorithms (Elith et al., 2006; Jiménez-Valverde et al., 2011; Segurado and Araujo, 2004), but it is obvious that the quality of SDMs is at least as dependent on the quantity and quality of the input data, both occurrences and environmental predictors. Some authors do consider data quality as the most critical factor influencing model performance (Jiménez-Valverde et al., 2013; Lobo, 2008).

Environmental requirements for P. angolensis

The response curves created by Maxent can give a lot of detail on the environmental requirements of a species if the statistical response for the whole study area is similar to the ecological response of the species. They can form the basis of further ecological research into the species and possible genetic varieties. The response curves in this study showed for example that the average minimum temperature in the coldest month has to be above 4 °C for *P. angolensis*, as indicated in literature (Burke, 2006; Von Breitenbach, 1973). It is the variable that limits the distribution of the species in South Africa towards the west. Beyond that, the response curves provide information not available in literature, for example the species often occurs on slopes up to 30° and the probability to find it is highest on the steeper slopes outside the Kalahari basin and vice versa within. This may be caused by the fact that the species prefers well-drained soils (Von Breitenbach, 1973; World Agroforestry Centre (ICRAF), 2013), which are situated higher uphill in the areas of higher rainfall and permanent rivers outside the Kalahari basin. In the Kalahari basin, most soils further way from riverbeds are deep, sandy, and well drained.

The precipitation seasonality has to be higher than 55% in the distribution area. It is the main environmental variable that limits the species to occur further north, mentioned by Von Breitenbach (1973) as the border between the single-season rainfall and more northerly two-season rainfall regime. The diurnal range - mean of the difference between the monthly maximum and minimum temperature - should not exceed 18 °C, especially outside the Kalahari basin, where the best chances to find the species are at much lower ranges. Model A indicates that the probability to find the species increases sharply at an average annual rainfall of 430 mm year⁻¹ (data not shown), confirming findings for the species in Namibia (Burke, 2006; Curtis and Mannheimer, 2005). The rainy season has to be in full swing by November with at least 45 mm of rain that month. This is a limiting factor for the distribution of the species towards the south in Namibia, part of Botswana, and an area of lower altitude in central Tanzania.

There are less environmental variables that appear to influence the distribution of the species in the Kalahari Desert, and their response curves differ from those of the whole study area. For example, temperature seasonality is a limiting factor towards the south but was more important outside the Kalahari with values lower than 35 °C (Figure D.1). The temperature seasonality for the total distribution area, but especially the Kalahari, is limited to values lower than 38.7 °C. The optimal rainfall in the month of February is about 160 mm for the Kalahari basin, while *P. angolensis* can be found with a similar probability outside the basin for a February rainfall above 300 mm. There should be no rainfall in the driest month in the Kalahari, while this can be up to 2.7 mm for the whole study area. *P. angolensis* has to handle much more extreme environmental conditions in the western part of its study area than in the wetter eastern part.

Adding a climate extreme like number of frost days did improve the model as also indicated by other studies (Bykova et al., 2012; Zimmermann et al., 2009). Our model shows that *P. angolensis* grows in areas with up to 19 frost days per year, especially in the Kalahari basin. Bykova et al. (2012) indicated that temperatures during the development of the flowers and seed maturation – indicated as spring frost in this study - may be an important factor to determine reproduction niche and thus species distribution, but it does not seem to be an important factor for *P. angolensis*.

Future distribution of P. angolensis

Both future models indicate that the distribution area of *P. angolensis* will decrease under global climate change, with a clear northward shift for the western part. The main causes of the northward shift are rainfall in October and November that are projected to decrease. HadCM3 is considered as one of the “drier” models (Midgley et al., 2005; Wolski, 2013), but the decreasing summer rainfall in the west of southern Africa is a consistent trend in other climate change studies (Hewitson, 2006). This makes a northward shift of the species’ distribution a realistic scenario by the end of 21st century although the rate maybe slower than indicated by both scenarios in Figure 2.6, especially considering that summer rainfall is a limiting factor for the species in that area. Other authors (Midgley et al., 2005; Thuiller et al., 2006) also predicted a decrease in the tree cover and biomass in northern Namibia, southern Angola, and eastern Botswana by 2080 using the HADCM3 model, emission scenario A2, and the Sheffield Dynamic Global Vegetation Model (Woodward and Lomas, 2004). However, biomass increased in the border area of eastern Namibia and Zambia when the fertilisation effect of rising atmospheric CO₂ was taken into account. The authors (Midgley et al., 2005; Thuiller et al., 2006) did admit a high degree of uncertainty in estimating the impact of the fertilization effect on projections for the future.

According to one of the high emission scenarios (A2a) of global climate change, the species may even disappear in large areas of its western distribution, including Namibia and Botswana. The large reduction of the distribution area in Angola has its origin in the increase of the diurnal range. It should however be mentioned that there are few climate stations in the eastern and central parts of southern Africa for which temperature range data was available to establish the WorldClim layers (Hijmans et al., 2005). The interpolations between stations can cause inaccuracies that may have a large effect on a SDM.

Under emission scenario B1, the species' distribution area would actually increase in Zambia (+78%) and Malawi (+8%). Other studies (Midgley and Thuiller, 2011; Scheiter and Higgins, 2009) predict a gain of forest or woodland cover by 2100 in the same area. Rising minimum winter temperatures and decreasing rainfall in February may cause a slight southward respectively eastward migration in South Africa. The increase in winter temperatures is another consistent trend in African climate change scenarios (Hewitson, 2006).

Recently, the emission scenarios were replaced with Representative Concentration Pathways (RCPs) (IPCC, 2014). The B1 emission scenario can best be compared by RCP4.5 as it gives a similar median temperature increase by 2100, and the A2a scenario is most similar to RCP8.5 (Rogelj et al., 2012).

Currently, no evidence is available of a decrease of the species in the southwest of its distribution area or of an increase in Zambia. It will be difficult to collect considering the long lifespan of the species but could be supplied by long-term field research into mortality and regeneration rates, especially in Namibia, Botswana and in comparison with neighbouring areas. This would support policy makers and managers in the region who currently have few research based facts to support their decisions with regard to potential climate effects on dry forests (Midgley and Thuiller, 2011).

2.5 Conclusions

Potential and realised distributions of *P. angolensis* are very similar. A distribution map with fairly good accuracy (Kappa 0.64) can be obtained with SDM for *P. angolensis* that gives much more detail than the range extent and environmental requirements described in the literature. More occurrence points for Zambia and Mozambique and a more recent forest map may improve the model, whereas more absence data along the distribution area's margins, especially in the north and Zambia, will increase the validity of the PA statistics. The distribution of the species is mainly influenced by the amount of rainfall in November and February, by the minimum temperature in winter, by temperature seasonality, and by its preference for well-drained soils. Environmental requirements are slightly different for the species within the Kalahari basin compared to the area outside.

Using fire occurrence and distribution maps of potentially competing species as predictor variables did not improve the final distribution maps of *P. angolensis*, however allowed to learn more about those factors with regard to the distribution of *P. angolensis* and provide interesting starting points for further ecological studies. Global climate change can decrease the species' distribution area 20% to 50%, with Namibia and Botswana most exposed. Unmitigated climate change clearly is another threat to the species, together with unsustainable logging, unmanaged fires, and deforestation. Future studies should explore the effect of using other climate models in combination with the new RCPs (IPCC, 2014).

The distribution models can assist in assessing the conservation status of the species on a regional scale, especially by allowing to derive area of occupancy and range size for listing on the IUCN Red List of threatened species (Gaston and Fuller, 2009; Master et al., 2009). They can assist the identification of suitable areas for regeneration trials or forest inventories and aid in assessments of historical logging operations. The future models can point out the regions where the species is most sensitive to climate change and thereby contribute to detect early signs of climate change in the field.

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Chapter 3 - Patterns of forest composition and their long term environmental drivers in the tropical dry forest transition zone of southern Africa

Adapted from:

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VDC did part of the recent forest inventory, performed the data analysis, and drafted the manuscript.

Abstract

Tropical dry forests cover less than 13% of the world's tropical forests and their area and biodiversity are declining. In southern Africa, the major threat is the increasing population pressure, while climate change is a potential threat in the drier transition zones to scrubland. Large decreases in rainfall are projected for this transition zone, especially in the open forests of northern Namibia and southern Angola. Monitoring impacts of climate change is challenging because the available information on forest composition does not allow disentangling them from other drivers of environmental change. This study combined data of various forest inventories covering an area of 21,000 km² and collected over four decades to distinguish late succession tree communities, to understand their dependence on site factors, and to detect trends in the forest composition over the last 40 years.

The studied forests in Namibia and Angola are dominated by six tree species that represent 84% of the total basal area and can be referred to as *Baikiaea* - *Pterocarpus* forests. A boosted regression tree analysis revealed that late succession tree communities are primarily determined by climate and topography. The *Schinziophyton rautanenii* and *Baikiaea plurijuga* communities are common on small inclined dune or valley slopes and have the highest basal area (5.5 – 6.2 m² ha⁻¹). The *Burkea africana*, *Guibourtia coleosperma*, and *Pterocarpus angolensis* – *Dialium englerianum* communities are typical for the sandy plateaux and have a higher proportion of smaller stems caused by a slightly higher fire frequency. A decrease in overall basal area or a trend of increasing domination by the more drought and cold resilient *Burkea africana* community was not confirmed by the historical data, but there were significant decreases in basal area for *Ochna pulchra* and the valuable fruit tree *D. englerianum*. The slope communities are more sheltered from fire, frost, and drought but are more susceptible to human expansion. The community with the important timber tree *Pterocarpus angolensis* can best withstand high fire frequency but may be most susceptible to climate change. Conservation and climate adaptation strategies would need to include protection of the slope communities through the creation of refuges. Follow-up studies are needed on short term dynamics, especially near the edges of the transition zone towards scrubland.

3.1 Background

Tropical dry forests represent approximately 8 to 13% of the world's tropical forests (Bodart et al., 2013; Hansen et al., 2013). Next to the provision of important ecosystem services such as climate regulation and carbon storage, they support millions of poor people through timber and non-timber forest products (Blackie et al., 2014; Shackleton et al., 2007; Snyder et al., 2004). They are an important safety net for human and animal populations by providing food during dry years (Chidumayo and Gumbo, 2010). Virtually all remaining tropical dry forests are threatened by deforestation and degradation and should be given high conservation priority (Hansen et al., 2013; Miles et al., 2006). However, they are among the least studied forest ecosystems, which hampers sustainable forest management and adequate forest policy (Blackie et al., 2014).

The main threat to tropical dry forests, especially in Africa, is an increasing population inducing changes in land use practices, land cover, and fire regimes (Cabral et al., 2011; Leadley, 2010; Miles et al., 2006; Sloan and Sayer, 2015). It is unclear how climate change will affect Africa's dry forests as projected changes vary at the regional level while increasing CO₂ and drought can have opposite effects on tree cover (Hély et al., 2006; Leadley, 2010; Liu et al., 2013; Lucht et al., 2006; Thuiller et al., 2006). Rainfall has a large effect on woody cover in the transition zone where open dry forest gradually changes into shrub and grassland (Figure 3.1). This effect is pronounced until the zone where mean annual rainfall reaches about 650 mm (Sankaran et al., 2008, 2005). More drought in combination with the increasing fire occurrences (Pricope and Binford, 2012) and population pressure, may provide enough stress to induce changes towards other vegetation types in the transition zone and affect the communities that depend on forest resources.

There are several global climate change scenarios that project temperature rises of 1.0 to 4.9 °C by the end of the 21st century (IPCC, 2014; Rogelj et al., 2012). According to one of the low impact scenarios, the largest changes in rainfall by 2080 for the African dry forest transition zones can be expected in northern Namibia, Angola, Botswana, and South Africa with reductions of over 15% (Figure 3.1). Thuiller et al. (2006) simulated how the range of deciduous broad-leaved trees will reduce in Namibia, for both constant and elevated CO₂ concentrations. De Cauwer et al. (2014) showed that climate change will cause a northward shift of the important timber species *Pterocarpus angolensis*' range in south-western Africa. Monitoring the forest composition in the transition zones can provide an early warning system for climate change. However, there is not sufficient adequate information on the current state of those forest ecosystems to disentangle climate change from other environmental effects, as is the case for many other tropical dry forest areas (Blackie et al., 2014). Knowledge about forest composition is a necessary prerequisite for monitoring of change. The use of passive remote sensing offers only limited options because the spectral signal from the open forests is influenced by fire scars and shrub and grass cover, which all have a high annual variability (De Cauwer, 2015; FAO, 2001; Ganzin et al., 2005).

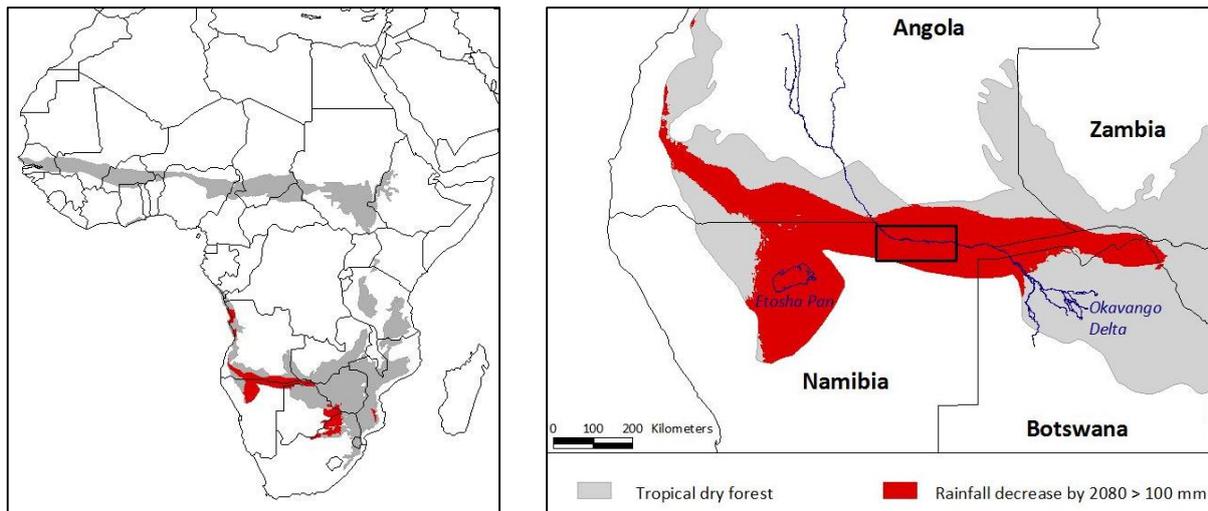


Figure 3.1 – Left: Tropical dry forest ecozone in Africa (FAO, 2000) with areas susceptible to drought. The susceptible areas are situated in the transition zone to scrubland where the largest decrease in mean annual rainfall (MAP) is predicted by 2080. The transition zone is defined as the tropical dry forest area where woody vegetation cover is mainly influenced by rainfall (Sankaran et al., 2005). Right: Study area indicated as rectangle in the dry tropical forest transition zone. MAP in 2080 is based on the B1 SRES emission scenario for 2080 (WorldClim).

This study aims to provide more insight in the patterns of forest composition of African tropical dry forest for an area where one of the largest reductions in rainfall is predicted. It concerns the open *Baikiaea* forests at the south-western edge of the Miombo ecoregion (Figure 3.1). The area has a different forest composition from the wetter Miombo forests more northwards, as well as a lower population density. The forests contribute directly to national economies through ecotourism focused on large mammals, the provision of fuel and timber wood and fodder (Barnes et al., 2010).

Some detailed studies on forest composition in this area do exist but focus on smaller study areas (Aarrestad et al., 2011; Childes and Walker, 1987; Revermann and Finckh, 2013; Strohbach, 2013; Strohbach and Petersen, 2007), whereas there are barely any long-term studies explaining patterns in late succession forest composition (e.g. Mosugelo et al., 2002). Detecting forest patterns in the study area is complicated by the facts that 1) there are no obvious environmental gradients with exception of a few rivers and dunes and 2) distinguishing tree communities is difficult with small datasets (< 200 plots) (Childes and Walker, 1987; De Cauwer, 2013; Strohbach, 2013). Regional studies indicate that forest dynamics are mainly driven by fire, drought, and browsing (Archibald et al., 2008; Burke, 2006; Fanshawe, 2010). The long-term effect of fire on forest composition remains controversial, especially because it depends on many other variables, such as soil, browsing, or the amount of rainfall (Bond et al., 2003; Sankaran et al., 2008). The impact of elephant populations on woody vegetation is well studied in the eastern *Baikiaea* forests of Botswana and Zambia (Aarrestad et al., 2011; Holdo, 2007; Kalwij et al., 2010; Loarie et al., 2009; Makhabu et al., 2006), but elephants are less common in the western parts and cattle are the most important large herbivores.

The lack of information does not only make it difficult to monitor impacts of climate change and develop climate change adaptation strategies, but also to make informed forest management and land use planning decisions, e.g. as in recent cases of tobacco and *Jatropha curcas* plantations (Jull, 2007; Namwoonde, 2010). This study combines data of different forest inventories collected over four decades to identify tree communities over a large area and study their long-term interactions with site variables, including disturbances. Larger trees will be used to distinguish the communities because their abundance accumulates the effect of past climate variation (Thijs et al., 2014; Zhu et al., 2014). The dataset is the most extensive and quantitative ever used for the study area.

This study aims at (1) distinguishing late succession tree communities in the western *Baikiaea* forests and describing their composition; (2) determining which environmental variables including disturbances have shaped the communities and their species composition; (3) detecting trends in the composition of the tree communities over the last 40 years; and (4) comparing the population structure of *P. angolensis* with the population structure of the remainder of the forest.

3.2 Methods

3.2.1 Study area

The study area covers a territory of about 21,000 km² in the open forests of Namibia and Angola that are classified as “*Baikiaea* woodlands” (Olson et al., 2001; Timberlake and Chidumayo, 2011) (Figure 3.1). Most of the area is communal land with some parts managed as community forests or state forest. The study area is situated within the Kavango Zambezi Trans-frontier Conservation Area (KAZA TFCA), the largest trans-frontier conservation area in the world (WWF, 2012). It is a flat landscape with very gradual slopes where the main topographic features are the valley of the Okavango river and its tributaries, which are dry, fossil rivers. Permanent parallel dunes, only a few meters higher than the surrounding areas, can be found in the south-western part of the study area (Graz, 1999). The soil consists of aeolian sediments forming Arenosols, with exception of the floodplains and fossil rivers where clay and silt contents are higher. The sand soils have low amounts of carbon and nitrogen and a low nutrient level (Gröngröft et al., 2013).

Mean annual rainfall in the study area is approximately 560 mm, with increasing rainfall towards the north. Seasonal rainfall variability is high with most rainfall concentrated in the period November - April. More details on the physical environment of the study area are given in Table 3.1.

The Okavango river is associated with a wetland system as described by Strohbach (2013). The vegetation outside the river valley is open forest according to FAO definitions, with an average canopy cover of 25% and canopy heights of 10 to 15 m. It is characterised by a low standing stock (Table 3.1) and tree species such as *P. angolensis*, *B. plurijuga*, *B. africana*, and *Schinziophyton rautanenii*. The shrub layer has a mean coverage of 25% and is characterised by species such as *Baphia massaiensis*, *Bauhinia petersiana*, *Ochna pulchra*, *Combretum psioides*, *Terminalia sericea*, and *Strychnos pungens*. The herb layer has only a mean coverage of 6% to which the suffrutex *Diospyros chamaethamnus* contributes a large

part. Grass cover is seasonal with a higher coverage in the wet season; the mean coverage of the forest inventory data, which included measurements in the dry season, was 30%. It is often dominated by annuals or unpalatable grasses such as *Aristida stipitata* and *Melinis repens*, although palatable climax grasses are present (Strohbach, 2013; Strohbach and Petersen, 2007). In Namibia, the vegetation is referred to as northern Kalahari dry forests and woodlands (Giess, 1998) and in Angola as *B. plurijuga* woodland savannah with stands of *S. rautanenii* (Diniz, 1973). The open forests extend northwards where they gradually change into typical miombo forest dominated by *Julbernardia paniculata*, *Brachystegia bakeriana*, and *B. spiciformis* (Coelho, 1967, 1964; Fanshawe, 2010; Santos, 1982). Southwards, the tree layer becomes more open and intermingled with *Acacia* species (Burke, 2002). About 20% of the study area burns every year in the months of August and September, towards the end of the dry season and mainly because of human ignition (Stellmes et al., 2013b).

Table 3.1 – Physical environment and forest characteristics in the study area: range of the variables in the sample plots. SD is the standard deviation. Climate data were derived from WorldClim (Hijmans et al., 2005) and CRUTS (Harris et al., 2013).

	Minimum	Maximum	Mean	SD
Latitude (°)	-19.09	-17.49	-18.10	0.18
Longitude (°)	18.45	20.45	19.65	0.60
Altitude (m)	1077	1173	1127	21
Sand fraction in topsoil (%)	52	95	94	4
Annual rainfall (mm)	531	625	564	15
Minimum temperature coldest month (°C)	5.8	7.5	6.3	0.6
Maximum temperature warmest month (°C)	34.0	34.6	34.2	0.1
Frost (days year ⁻¹)	8	11	10	1
Maximum tree diameter at breast height (cm)	20	189	49	20
Basal area all trees (m ² ha ⁻¹)	0.3	22.3	4.7	2.5
Stem density (ha ⁻¹)	7	493	112	59

Since the 1960s, the population in the Namibian part of the study area grew exponentially (e.g. from 116,830 to 222,500 persons (+ 90%) in the Kavango regions during the period 1991 – 2011 (NPC, 2011), fuelled by refugees of the civil war in Angola (Giro, 1998; Mendelsohn, 2009) and expanded along roads and dry riverbeds. Forests are cleared for agriculture, despite the less fertile soils, resulting in a yearly deforestation rate of 3.9% for the period 1943-1996 (Mendelsohn, 2009). Charcoal is not produced and shifting cultivation is not practiced; farmers remain on the same fields and use fallow periods (Pröpper et al., 2010). At 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 of their villages, mainly as firewood and for construction. Commercial logging focuses on large individuals of a few species, mainly *P. angolensis* but also *B. plurijuga*. Legal harvesting in Namibia is currently restricted to community forests, but illegal logging does take place (Kabajani, 2013; Pröpper & Vollan, 2013; own observations). Harvesting of timber in Angola is on the increase and the wood is often transported through Namibia (Karen Nott, pers. comm.).

3.2.2 Forest inventory data

Forest inventory data was obtained for the study area from various sources: (1) research data: own data collected in 188 sample plots during the period 2011 – 2014 along transects representing an increasing distance from human settlements and rivers (mean distance between plots on transects: 520 ± 400 m); (2) forestry data: data of the Namibian Directorate of Forestry and the Namibian Community Forestry programme in 650 plots, collected by systematic grid sampling during the period 1998 – 2008 (mean distance between plots in grid: 720 ± 300 m) (Chakanga and Selanniemi, 1998; Kamwi, 2003; Kanime, 2003; Rechberger, 2008); and (3) historical data of the Department of Forestry of South Africa, then in charge of forestry in Namibia, collected in 492 sample plots in a systematic grid design in the Kavango region over the period 1972 – 1974 (mean distance between plots in grid: 3.0 ± 2.8 km) (Geldenhuys, 1992).

The sample plot design varied for the different datasets (Annex E). This resulted in different sampling intensities per diameter at breast height (DBH) class. To minimise differences in sampling intensities and to avoid the inclusion of early succession tree communities, trees with a minimum DBH of 20 cm were used for the tree community classification. The most common tree species require approximately 40 to 70 years from the last resprouting occurrence to reach this diameter (Therrell et al., 2007; Van Holsbeeck et al., 2016; Worbes, n.d.). Trees with minimum DBH 20 cm were measured in plots with a radius of 20 m for the research and forestry data and 30 m for the historical dataset (Burke, 2002; Geldenhuys, 1992). A Monte Carlo analysis shows that the β -diversity - the variation in species composition among sites (Whittaker, 1972) - of the historical dataset falls within range of the research data and that the difference between the research and forestry data is higher (Table 3.2). Structural composition was described for each community using all data with a DBH threshold of 10 cm.

Table 3.2 - Monte Carlo analysis of β -diversity for the three data sources. Mean, variance, and confidence interval (CL; $p = 0.05$) are calculated for 500 iterations with subsamples of 50 plots.

Dataset	Beta	Monte Carlo Analysis			
	Diversity	Mean	Variance	Lower CL	Upper CL
Historical	3.8	3.7	0.05	3.3	4.2
Research	4.6	4.6	0.14	3.9	5.4
Forestry	7.1	7.0	0.26	6.0	8.0

The data collected for the trees in the sample plots included species, DBH, and tree height. Some *Commiphora* and *Strychnos* species were only included at genus level because species identification for some inventories was questionable. Tree height was measured with a Vertex hypsometer. Tree cover, shrub cover, grass cover, and damage caused by cattle, humans or fire were determined at plot level for the research data. Tree cover was determined with the Bitterlich gauge technique (Friedel and Chewings, 1988) and shrub and

grass cover with the line intercept method (e.g. Kabajani, 2016). Dead trees were included in the recent (research and forestry) inventories.

There were no accurate coordinates available for the sample plots of the historical dataset and approximate locations were derived after georeferencing scanned forest maps of Kavango of 1971 with scale 1:75,000 on which the points were indicated during the planning phase of the inventory. Error of the rectification varied between 9 m and 29 m, but the positional error of the sample points is much larger, mainly because determining geographic coordinates in the field could not be done accurately in the 1970s. The historical plots were randomly clustered in groups of four and at a maximum distance of 500 m of the central sample point (Annex E).

3.2.3 Site variables

An overview of all site variables used is given in Table 3.3. Elevation data from the Shuttle Radar Topography Mission (SRTM) of NASA were used to derive slope, aspect, and landscape curvature at landscape level. The latter quantifies the shape of the landscape surface and determines high and low points (Jenness, 2006). Human intervention in the forest was indirectly reflected by distances to villages, tracks, roads, riverbeds, agricultural fields, and major towns because human activities are concentrated there (own observations; Schneibel et al., 2013). GIS data based on orthophotos from 1996 were updated with information from Google Earth for the period 2011 to 2013. The extent of cleared land in 1972 (Mendelsohn and Obeid, 2004) was used to determine distances to agricultural fields for the historical dataset. Fire frequency – the portion of years for which a fire was recorded – could be determined for the recent datasets based on AVHRR for the period 1981 - 1991 (Barbosa et al., 1999), Landsat Quicklooks for the period 1991 - 2004 for the Namibian plots (Verlinden, 2004), and based on MODIS burned area products for 2000 - 2012 (Stellmes et al., 2013b).

3.2.4 Data analysis

The forest inventory data allowed to derive several abundance measures per tree species: stem density (number of stems per ha), basal area per ha, and presence/absence. Tree community classification was tested on all three abundance measures. Distribution of basal area data was skewed and hence log converted to improve assumptions of normality and focus on relative quantities of species (McCune et al., 2002). Outliers and species that only occurred in three plots or less were removed. Outliers consisted of species and plots situated at more than two standard deviations from the grand mean Sørensen distance measure. For each of the abundance measures, the sample plots were hierarchically clustered into groups using a Sørensen distance measurement and flexible beta linkage ($b = -0.25$) (McCune and Mefford, 2011).

Table 3.3 – Overview of predictors for the tree communities. Data representing damage classes and dunes had an ordinal scale, and all other data an interval scale. Resolution is indicated for raster data. A glossary of terms is in Annex A.

Variables	Source	Period	Resolution
Temperature (temp.) seasonality, Max. temp. warmest month, Min. temp. coldest month, Precipitation (prec.) warmest quarter, Annual prec., Prec. seasonality, Annual prec., Temp. annual range, Diurnal range, Prec. wettest quarter, Prec. February, Prec. October, Prec. November	WorldClim (Hijmans et al., 2005) http://www.worldclim.org	Mean of 1950/1960 - 1990/2000 (depending on dataset)	30 arc sec (± 920 m at equator)
Elevation, Slope (derived in GIS), Aspect (derived in GIS), Landscape curvature (derived in GIS)	Shuttle Radar Topography Mission http://srtm.csi.cgiar.org		3 arc sec (± 90 m)
Soil-pH, Sand fraction, Organic Carbon, Cation Exchange Capacity (CEC), soil class, nutrient availability	Harmonised World Soil Database (FAO/IIASA/ISRIC/ISSAS/JRC, 2009)		30 arc sec
Frost days	Climatic Research Unit time- series datasets (CRUTS v.3.10.01) (Harris et al., 2013) Barbosa et al., 1999 - AVHRR	Mean of 1941-2002	30 arc min (± 55 km at equator)
Fire frequency	Verlinden, 2004 - Landsat TM Quicklooks Stellmes et al., 2013 - MODIS Burned area	1981 - 1991 1991 - 2004 2000 - 2012	1 km 350 m 500 m
Enhanced vegetation index (EVI)	Stellmes et al., 2013b - MODIS	Mean of 2000 - 2012	500 m
Distance to Okavango river, non-perennial rivers, agriculture, tracks, main roads, towns and villages	GIS data digitised in Google Earth (2013, 2014) and derived from Atlas of Namibia (Mendelsohn et al., 2002) and Okavango river (Mendelsohn and Obeid, 2004)	2014	
Dunes, Cattle density, Ground water depth			
Tree cover, Shrub cover, Grass cover, Fire damage class, Human damage class, Cattle damage class	Own forest inventory data in nested plots with maximum radius of 30 m	2006 - 2014	

Indicator Species Analysis was applied to determine indicator species for the different groups (Dufrene and Legendre, 1997). The occurrence of single species and species combinations were evaluated based on their positive predictive value A and their sensitivity B (occurrence frequency in plots of that community), which give the indicator value IV when multiplied (De Cáceres et al., 2010). Differences between groups and homogeneity within groups were tested with multi-response permutation procedures (MRPP) using the Sørensen distance measure. The test statistic T of the MRPP procedure describes the separation between groups and the statistic A the within-group homogeneity. A is larger than 0 if the emerging groups are significantly more homogeneous than expected by chance (McCune and Mefford, 1999). Communities were identified based on the results of indicator species analysis and MRPP, both performed in PC-ORD version 6.08.

The impact of site variables on tree communities was explored by developing a boosted regression tree model (BRT) for each tree community as the abundance matrix was too sparse to allow the randomisation test for more conventional ordination methods (McCune and Mefford, 2011). BRT modelling is one of the top performing species distribution modelling methods, together with other machine learning methods such as Maxent and random forest (Elith et al., 2006; Leathwick et al., 2006; Moisen et al., 2006; Opper et al., 2012; Stohlgren et al., 2010). Its use for modelling the occurrence of communities in function of site variables is less common but has been successfully applied in recent studies (Duff et al., 2014; Luo et al., 2014; Rodil et al., 2014). BRT models combine a large number of simple tree models to optimise performance (Elith et al., 2008). Although BRT models can handle collinear predictors through a reliable identification and modelling of interactions between the predictors (Elith et al., 2008; Leathwick et al., 2006), we simplified the BRT models by dropping those variables that did not increase model performance. This is relevant for small datasets where redundant predictors can degrade predictive performance by increasing the variance (Elith et al., 2008). All forest inventory data were used for developing the models because this resulted in the best predictive performance, despite the lower positional accuracy of the historical plots.

Performance of the models was evaluated by 10-fold cross-validation of deviance and correlation (Elith et al., 2008; Leathwick et al., 2006). Deviance measures how well calibrated the prediction values are and 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 visualise the marginal effect of the selected variable on the model prediction, while the dependency of the remaining variables is neutralised (De'Ath, 2007; Ridgeway, 2014). All differences between structural characteristics or site variables and the communities were tested with Kruskal-Wallis and pairwise comparisons using the Wilcoxon rank sum test and the Bonferroni adjustment for multiple tests. Certain tests could only be performed for the recent data because site variables were not available for the historical data. Spearman rank correlations were determined between all variables. BRT modelling and statistical tests were performed with R, including the *gbm* package (Ridgeway, 2014) and functions written by Elith et al. (2008).

For detection of trends in forest composition over the last 40 years, two analyses were performed: (1) comparison of DBH distributions between the three datasets with Kolmogorov-Smirnov, and (2) comparison of historical with recent plots - if situated within a radius of 1 km - with regard to structural and species composition and distance to agricultural fields. Variables selected to reflect structural composition were the total amount of stems, mean DBH and basal area for stems with minimum DBH of 10 cm, and stems and basal area of the DBH class 10 to 20 cm. The species composition was analysed through the basal area of the most common tree species with minimum DBH of 20 cm. Differences were tested for significance with the t-test for normally distributed data and Wilcoxon signed rank test for the non-parametric tests.

The population structure of the forest and that of *P. angolensis* were compared with the size class distribution method described by Lykke (1998). A linear regression was applied to the population structure data with the middle of each DBH class of 5 cm as independent variable and the ln transformed number of stems per ha ($\ln(N_i+1)$) as dependant variable. The slopes

of the linear regressions were compared with the Student's t-test ($p < 0.05$). The slope was used to describe the shape of the population structure (Sop et al., 2011).

3.3 Results

3.3.1 Tree communities

The original data of all inventories indicate that six species contribute 84% of the wood basal area in the study area (Annex F). The mean basal area for trees with minimum DBH of 10 cm was $4.5 \text{ m}^2 \cdot \text{ha}^{-1}$ and the stem density $109 \text{ stems} \cdot \text{ha}^{-1}$. About 4% of the plots did not have any trees with DBH of 20 cm or larger and were removed before classification. After removal of outliers and uncommon species, the final dataset used for vegetation classification comprised of 1230 sample plots and 19 tree species and had a β -diversity of 5.4. The abundance measure with the best classification results was log converted basal area, yielding five tree communities of which four were characterised by only one important indicator species (Table 3.4). Differences between the communities ($A = 0.33$, $T = -496.4$) were larger than those between the data sources ($A = 0.02$, $T = -38.4$) or location within the study area ($A = 0.08$, $T = -76.9$).

The use of basal area resulted in communities with large differences in structural composition (Table 3.5). Shrub, grass and herb cover did not show significant differences between the communities. There was a significant but low correlation between the density of dead trees and fire frequency for the periods 1981 - 1991 ($r_s = 0.11$, $p = 0.002$) and 1991 - 2004 ($r_s = 0.16$, $p < 0.001$). *T. sericea* was the species with the highest ratio of dead versus living trees (106%), followed by *Dialium englerianum* (31%) and *B. africana* (19%).

Table 3.5 - Structural characteristics of the tree communities. The mean of each variable is based on all trees with minimum diameter at breast height (DBH) of 10 cm²; standard error of the mean is between parentheses. Letters represent significant differences between groups at level $p < 0.05$. The proportion of stems with DBH 10-20 cm is the proportion of all stems with minimum DBH of 10 cm that falls in the diameter class 10-20 cm for that community. EVI is the Enhanced Vegetation Index. A glossary of terms is in Annex A.

	<i>Schinziophyton rautanenii</i>	<i>Baikiaea plurijuga</i>	<i>Burkea africana</i>	<i>Guibourtia coleosperma</i>	<i>Pterocarpus angolensis</i> - <i>Dialium englerianum</i>
Maximum tree DBH (cm)	64 (22) ^a	51 (16) ^b	34 (11) ^c	52 (21) ^b	41 (14) ^d
Mean tree DBH (cm)	23 (4) ^a	24 (7) ^a	19 (6) ^b	21 (5) ^c	20 (5) ^b
Basal area ($\text{m}^2 \cdot \text{ha}^{-1}$)	6.2 (2.7) ^a	5.5 (2.7) ^b	2.8 (1.5) ^c	4.6 (2.0) ^d	3.9 (1.7) ^e
Stem density ($\text{stems} \cdot \text{ha}^{-1}$)	118 (50) ^b	109 (60) ^{ab}	96 (62) ^b	115 (59) ^a	116 (62) ^a
Proportion of stems with DBH 10-20 cm (%)	54 (20) ^a	44 (25) ^b	62 (28) ^c	59 (22) ^c	60 (24) ^c
Dead tree density ($\text{stems} \cdot \text{ha}^{-1}$)	21 (25) ^a	9 (15) ^b	17 (25) ^a	18 (27) ^a	18 (26) ^a
Tree cover from field observations (%)	29 (12) ^b	31 (12) ^{bc}	19 (9) ^a	26 (7) ^{ab}	22 (12) ^a
Mean EVI 2007-2012	0.274 (0.014) ^b	0.281 (0.015) ^c	0.266 (0.011) ^a	0.267 (0.012) ^a	0.266 (0.013) ^a

² The table is based on a larger dataset than that used for community classification, which used a minimum DBH of 20 cm.

Table 3.4 – Tree communities derived from forest inventory data with minimum DBH of 20 cm. Indicator species are listed with positive predictive value (A), sensitivity or frequency of occurrence (B) and indicator value (IV). Single indicator species are included when $p < 0.05$ and indicator species combinations when they have a higher A than the best single indicator species.

	A	B	IV (%)
Schinziophyton rautanenii community (230 plots)			
<i>S. rautanenii</i>	0.92	1.00	92
<i>S. rautanenii</i> + <i>Erythrophleum africanum</i>	1.00	0.07	7
<i>E. africanum</i>	0.53	0.07	3
Baikiaea plurijuga community (278 plots)			
<i>B. plurijuga</i>	0.75	1.00	75
<i>B. plurijuga</i> + <i>Combretum psidioides</i>	0.85	0.16	14
<i>C. psidioides</i>	0.48	0.16	8
<i>B. plurijuga</i> + <i>Commiphora</i> spp.	0.81	0.09	8
<i>B. plurijuga</i> + <i>Philenoptera nelsii</i>	0.96	0.07	7
<i>Commiphora</i> spp.	0.72	0.09	7
<i>P. nelsii</i>	0.56	0.07	4
Burkea africana community (168 plots)			
<i>B. africana</i>	0.29	0.99	28
<i>Terminalia sericea</i>	0.30	0.16	5
<i>B. africana</i> + <i>Acacia erioloba</i>	0.87	0.02	2
<i>A. erioloba</i>	0.51	0.02	1
Guibourtia coleosperma community (249 plots)			
<i>G. coleosperma</i>	0.61	1.00	61
Pterocarpus angolensis - Dialium englerianum community (305 plots)			
<i>P. angolensis</i>	0.32	0.88	28
<i>P. angolensis</i> + <i>B. africana</i>	0.38	0.70	26
<i>Dialium englerianum</i>	0.43	0.40	17
<i>D. englerianum</i> + <i>Combretum collinum</i>	0.66	0.06	4
<i>D. englerianum</i> + <i>Strychnos</i> spp.	0.57	0.05	3

The BRT models for the different tree communities explained between 6 and 27% of the deviance, with the best model for the *B. plurijuga* community (Annex G). Abiotic variables appeared to have a more important effect on tree composition than anthropogenic variables. Elevation was considered an abiotic variable as it was only correlated to climatic variables (e.g. rainfall in wettest quarter: $r_s = -0.77$, $p < 0.001$) and groundwater level ($r_s = 0.46$, $p < 0.001$). The distance to the Okavango river was correlated to both abiotic and anthropogenic variables (e.g. burned area for 1981 – 2004 ($r_s = 0.66$, $p < 0.001$), diurnal range ($r_s = -0.59$, $p < 0.001$)).

The Kruskal-Wallis tests of site variables (Annex H) indicated that three communities - the *Burkea africana*, *Guibourtia coleosperma*, and *Pterocarpus angolensis* – *Dialium englerianum* communities - were typical for the sandy plateaux that are 20 to 40 meters higher than the valleys. The two others were found nearer to dry riverbeds, the old floodplain of the Kavango river or dune areas and are referred to as the slope communities, despite the fact

that most slopes were very gradual and often invisible in the field. A new BRT model was created for the distinction of sand and slope communities that yielded a better deviance (31%) and correlation (0.61). The most important predictor of the model is cattle density (Table 3.6), a proxy for both abiotic variables (e.g. rainfall in the warmest quarter: $r_s = 0.58$, $p < 0.001$) and disturbances (e.g. distance to villages: $r_s = -0.75$, $p < 0.001$). Fire frequency was not selected as a predictor by the model. The effects of the predictors were studied through the partial dependence plots of which some are illustrated in Figure 3.2. They illustrate straightforward relations that can easily be described, for example, the probability to find the sandy community decreases with cattle density and it can especially be found in areas with cattle density lower than 8 animals per km². The slope community is mainly found on slopes with a northern aspect. Impacts of other variables are included in Annex I, a description of the communities based on the BRT models, the site variables (Table H.1) and structural characteristics (Table 3.5).

*Table 3.6 – Predictor variables of the boosted regression tree model to distinguish sandy plateau from slope communities. The sandy plateau communities are the *Burkea africana*, the *Guibourtia coleosperma*, and the *Pterocarpus angolensis* – *Dialium englerianum* communities. The slope communities are the *Schinziophyton rautanenii* and the *Baikiaea plurijuga* communities.*

	Range	Relative importance (%)
Cattle density	0 - 14 km ⁻²	13
Temperature seasonality	30.2 - 35.7 °C	12
Elevation	1077 - 1173 m	10
Distance to fossil rivers	0 - 22 km	9
Aspect	0 - 359°	9
Distance to the Okavango river	0 - 49 km	8
Distance to main roads	0 - 35 km	8
Mean temperature warmest quarter	25.2 - 26.0 °C	7
Slope	0 - 4.3 °	6
Annual rainfall	531 - 625 mm	5
Landscape curvature	-	5
Rainfall warmest quarter	144 - 195 mm	5
Rainfall seasonality	102 - 111 %	4

Most plots on communal land belonged to the slope communities (59%), while those in the community forests were mainly sand plateau communities (83%). Stem density within the more protected state forest consisted of 41% small stems compared to 55% on average.

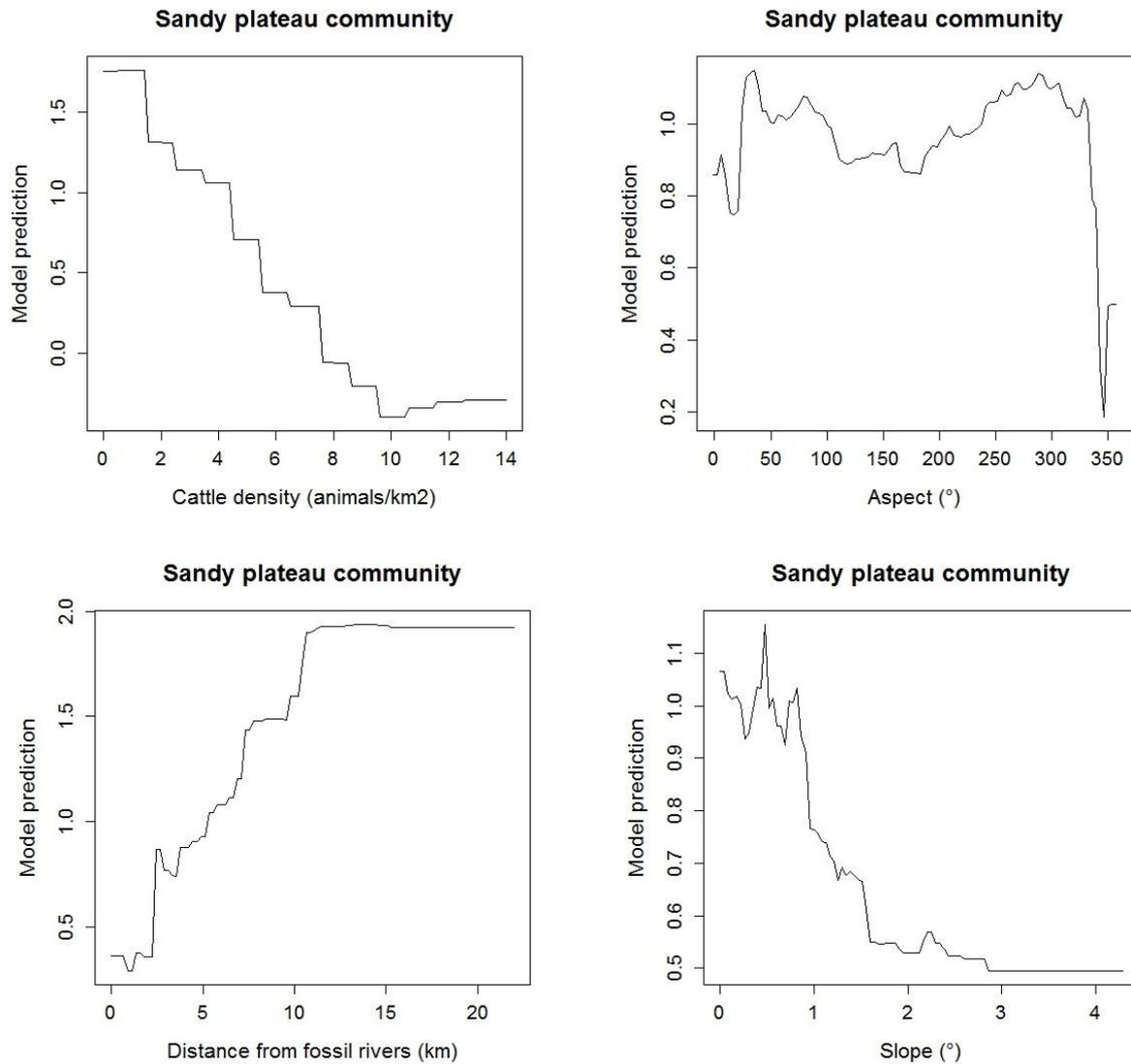


Figure 3.2 – Partial dependence plots of predictor variables for the sandy plateau communities. The plots show the dependencies of the presence models on predictors. The Y axis represents the mean prediction values of the model using a log-odds scale for presence and a log scale for the other plots (Ridgeway, 2014). When model prediction for the presence of the sandy community is high, prediction for presence of the slope plateau community is low and vice versa. An aspect of 0° and 180° is a northern, respectively southern exposure.

3.3.2 Historical trends in tree community composition

The size class distributions of the three datasets showed no significant differences (Figure 3.3). Fifty-five historical plots were situated within a distance of 1 km from recent plots. Structural variables of late succession communities did not change significantly over the last 40 years (Figure 3.4). The only significant differences in composition were a decrease in the basal areas of *B. africana* ($p < 0.05$), *D. englerianum* ($p < 0.01$), and *Ochna pulchra* ($p < 0.01$). The distance to agricultural fields also decreased significantly ($p < 0.001$), confirming the agricultural expansion of the last decades.

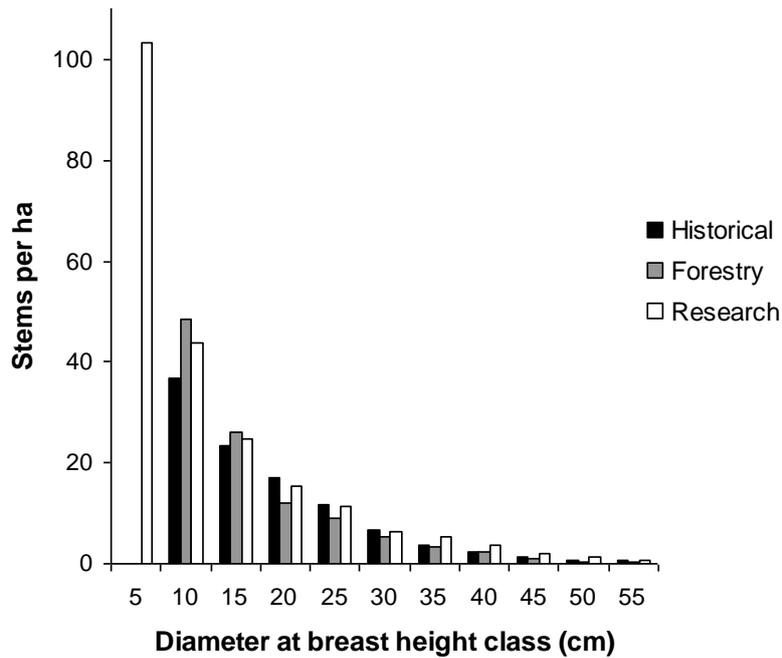


Figure 3.3 – Distribution of diameter at breast height classes for the three datasets.

3.3.3 Population structure of *P. angolensis*

The linear regressions describing the population structure of *P. angolensis* and the population structure of all woody species both showed negative slopes but were significantly different (Table 3.7). *P. angolensis* had a less negative slope as its population structure does not follow the typical reverse J-shape curve of a healthy population (Sop et al., 2011) (Figure 3.5).

Table 3.7 – Linear regressions describing the population structure of all woody species and of *P. angolensis*. The regressions have the form $\ln(\text{stems per ha}) = \alpha + \beta \cdot \text{DBH}$ with DBH the diameter class at breast height.

	Intercept α	Slope β	Adjusted R- squared	p-value
All woody species	4.697068	-0.07812	0.9628	<0.001
<i>Pterocarpus angolensis</i>	2.054356	-0.03551	0.9814	<0.001

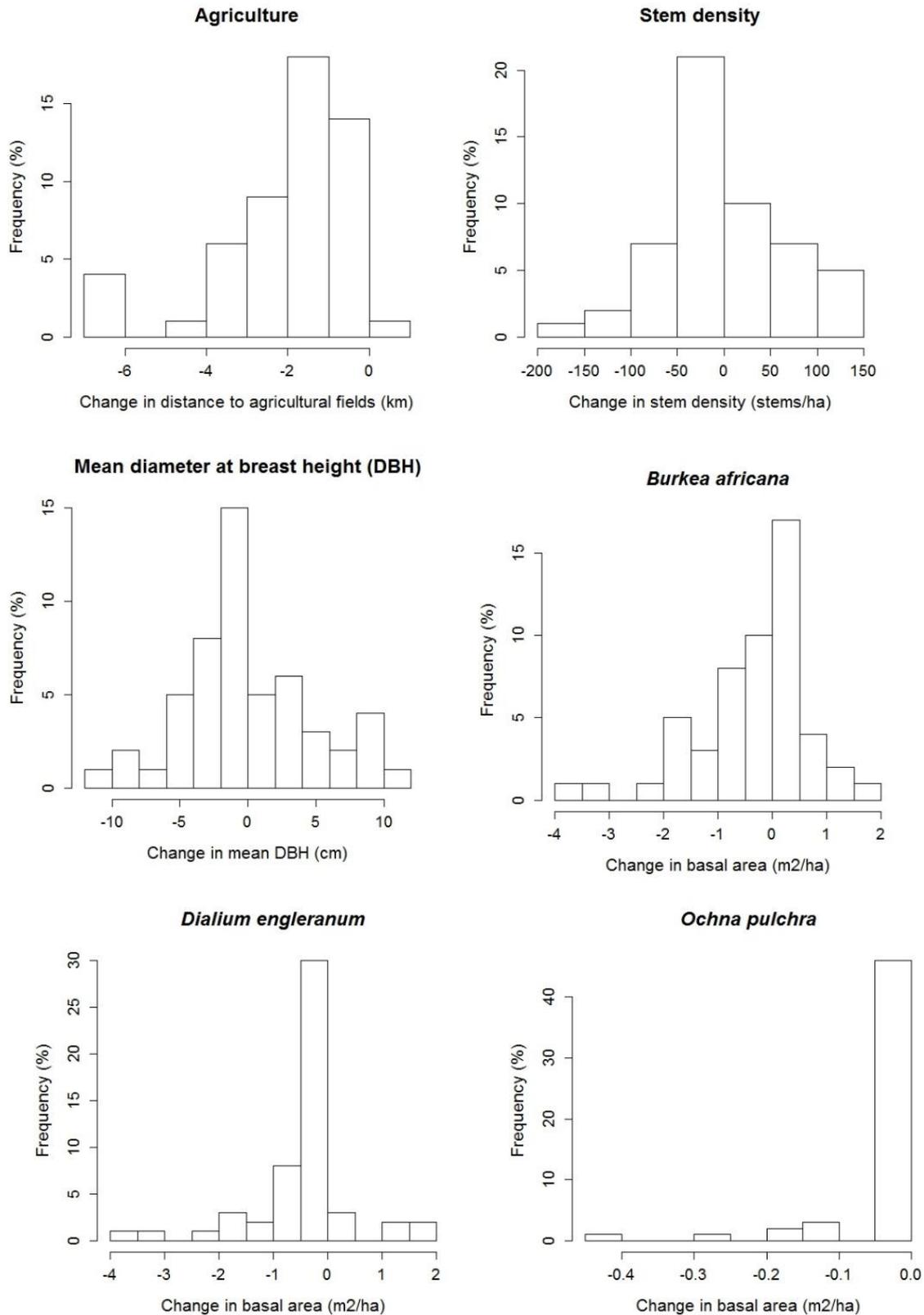


Figure 3.4 – Histograms showing the differences between historical and recent plots. Change in stem density is for all stems with minimum diameter at breast height (DBH) of 10 cm. Change in basal area for *Burkea africana*, *Dialium englerianum*, and *Ochna pulchra* is for all stems with minimum DBH of 20 cm.

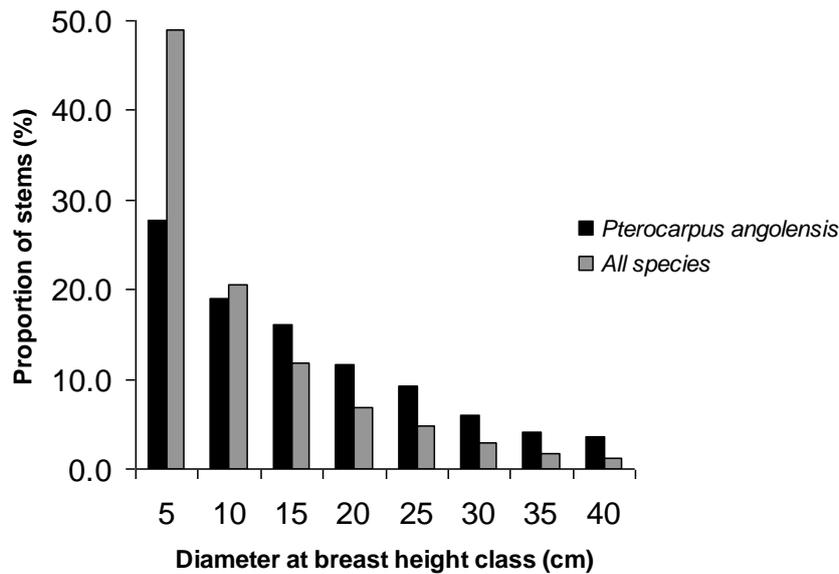


Figure 3.5 – Population structure of *P. angolensis* compared to that of all woody species.

3.4 Discussion

3.4.1 Species and structural composition in the study area

The western *Baikiaea* forests do not show a large variability in woody species composition and are dominated by six species that represent 84% of the total basal area (Table F.1). The five tree communities were fairly equally represented in the study region (Table 3.2) with the *B. africana* community least common. *B. africana* was however the most represented canopy tree species (29% of all stems) because it was often present in other communities. The *B. africana* community appears to be the undifferentiated phase of the forests.

The best represented community was the *P. angolensis* – *D. englerianum* community. *P. angolensis* was an indicator species through its abundance; it was present in 88% of the plots (Table 3.3). It was also often present in the slope (55 – 67% of the plots) or *G. coleosperma* (62% of the plots) communities, supporting the high degree of species interspersion reported by Graz (2006). Despite the light demanding character of the species (Vermeulen, 1990), it may be able to tolerate more competition after the crucial establishment phase. *P. angolensis*, the most important timber tree in the region, was the second most common species in the study area with 8 stems ha⁻¹ (19%) on average. Other authors indicated that both *P. angolensis* and *B. africana* are common in north-eastern Namibia and there was a suggestion to name the forests the *Burkeo - Pterocarpetea* (De Raedt, 1961; Strohbach and Petersen, 2007). *P. angolensis* is an indicator species through its abundance. It was often present in other communities, supporting the high degree of species interspersion reported by Graz (2006). The biggest contributors to total basal area were *B. plurijuga* and *B. africana* (Table F.1). *B. plurijuga* is another important timber tree, however it was not as abundant in

the study area as in the *Baikiaea* forests further towards the east (Childes and Walker, 1987; Mitlöhner, 1993).

We are aware of the limitations of using a threshold DBH of 20 cm to perform tree community classifications for the historical data set. However, the alpha diversity or average number of species per plot ($\alpha = 3$) was very similar to that for the recent data with DBH threshold of 10 cm ($\alpha = 3.6$). The communities distinguished were also very similar to those obtained during earlier test runs performed on the recent dataset alone with threshold DBH of 10 cm. The main difference was the lack of a community characterised by *Acacia erioloba*, *Terminalia sericea*, and *Combretum* spp.; a community combining an early succession vegetation with vegetation at the fringes of depressions, dry riverbeds, and dune valleys (Burke, 2006, 2002). The main aim of the study, to distinguish long-term patterns in later succession tree communities, is therefore possible with the DBH threshold of 20 cm.

3.4.2 Impact of abiotic variables on forest composition

The available information allowed creating predictive models for tree communities that explained up to 31% of the deviance, which is in the range of other studies (Elith et al., 2008; Froeschke et al., 2010). The system has an inherent stochastic component because of the unpredictable rainfall events (Holdo, 2006), which in turn affect the extent of the burned area (Archibald et al., 2008). Overall, abiotic variables influenced the late succession tree communities more than anthropogenic induced disturbances.

The slope communities had lower temperature seasonality and slightly higher minimum temperatures in the coldest month (Annexes H and I), suggesting that the communities are more frost sensitive than the sandy plateau communities. This explains their preference for slopes (cold air descends to the valley floors) and a northern aspect. Other authors have indicated that *B. plurijuga* is often found on slopes because it is frost sensitive and does not tolerate waterlogging (Childes and Walker, 1987; Holdo and Timberlake, 2008). The open *B. africana* community can be found in areas with the most extreme conditions: in areas with lowest rainfall, lower temperatures, more frost, and further away from fossil rivers. The community is often exposed to the east, the major wind direction. The *B. africana* community appears to be an earlier succession stage than the other communities with *T. sericea* a typical pioneer. *B. africana* and especially *T. sericea* have shallow root systems and can handle frost well (Childes and Walker, 1987; Holdo, 2006). The earlier succession stage explains the higher mortality rates of *T. sericea* (106%) and *B. africana* (19%) as trees with DBH over 20 cm are relatively old and succumb to natural self-thinning. Childes and Walker (1987) also found a high mortality (63%) for *T. sericea* trees with DBH > 6 cm.

Globally, one of the most visible effects of climate change is tree mortality caused by warming and drought, which is on the increase (Allen et al., 2010). The historic forest inventory did not include dead trees and so an increasing mortality trend could not be shown in our study. However, the high mortality of mature *D. englerianum* trees of recent years is alarming and will need further investigation. The species has the narrowest distribution of the six indicator species within the study area (Curtis and Mannheimer, 2005), which coincides with a slightly lower maximum temperature of the warmest season compared to the rest of the study area. Warmer summers and an increasing temperature seasonality may affect this species, but another possibility is that the species cannot handle

the fires in the late dry season, as shown by Geldenhuys (1977). *D. englerianum* is valuable to the local population for its edible fruits, seeds, and its wood (Mannheimer and Curtis, 2009). The other indicator species of the community, *P. angolensis*, did not show high mortality rates. However it did in a study area more southwards with slightly lower rainfall (Strohbach and Petersen, 2007), which could be caused by gradually decreasing summer rainfall and increasing temperature seasonality to which the species is vulnerable (De Cauwer et al., 2014). *P. angolensis* did also show an unhealthy population structure. The lower amount of regeneration compared to other species was also found in the same study area for seedling density (Kabajani, 2016). The lower regeneration may be a consequence of climate change, but can also be caused by the fire frequency that is higher than that in other communities. Trees need a period of about 6 years without fire to grow from seedling into sapling stage (Bond, 2008). Monitoring tree mortality and regeneration at the edge of the transition to scrubland may show a clearer trend. This would also contribute to global predictions on the distribution of dry forests, something which is currently lacking (Liu and Yin, 2013).

3.4.3 Impact of disturbances on forest composition

The expansion of agriculture and human infrastructure primarily threatens the slope communities. Strohbach (2013) indicated that 90% of the *Acacia erioloba* – *S. rautanenii* community in the Okavango river valley has already been cleared for agriculture. Environmental impact studies for agricultural development projects should advise preservation and establishment of corridors and islands of natural forest, especially for the *B. plurijuga* and *S. rautanenii* communities. The better soils and denser canopies of the slope communities allow a higher moisture retention capacity (Wallenfang et al., 2015). The corridors and islands can therefore also act as a refuge for drought sensitive species during drier conditions and can be part of a climate adaptation strategy (Liu and Yin, 2013).

Effects of livestock on late succession forest composition were not obvious as there was little evidence of livestock damage. The high contribution of cattle density to the predictive model is best explained by its correlation to other variables, such as the distance to villages. Areas with high cattle density are often bush encroached areas with few large trees, and were thus not included in this study. A study of the effect of livestock on forest succession in the slope communities, situated in the highest cattle density areas, may give more insight.

Fire frequency was slightly higher in the sandy plateau communities compared to the slope communities, causing a higher proportion of small stems, which is typical for areas with frequent fires in the late dry season (Higgins et al., 2007). The *P. angolensis* – *D. englerianum* community was found in the highest fire frequency areas for the period 1981-2004. The main indicator species, *P. angolensis*, has a strong fire resistance and needs a minimum amount of fire to favour regeneration (Banda et al., 2006). There was no relation between the open *B. africana* community and fire frequency, confirming the results of a fire trial study of Geldenhuys (1977) and that the occurrence of the *B. africana* community is influenced by abiotic variables.

The *B. plurijuga* community had the lowest fire frequency, confirming that the community can only evolve if fire frequency is low enough (Childes and Walker, 1987; Geldenhuys, 1977). It should however be indicated that the community was situated on slightly better

soils and closest to agricultural fields, as observed by other authors (Mitlöhner, 1993; Revermann and Finckh, 2013; Wallenfang et al., 2015). Areas closer to agricultural fields had lower fire frequency in the period 1984 - 2004 (r_s 0.70, $p < 0.001$), a common occurrence (Archibald et al., 2008; Lavorel et al., 2007), and can thus act as a refuge for more fire sensitive species. The protection of large, mainly uninhabited areas as national parks, such as Bwabwata in Namibia, may be a disadvantage for the *B. plurijuga* community because of the higher fire frequencies that can be expected and are also observed (Pricope and Binford, 2012). Establishment of fire refuge areas should be considered within the newly established Kavango Zambezi Transfrontier Conservation area.

3.4.4 Trends in forest composition over the last 40 years

Despite the human population increase of the last 40 years, no changes in the structural composition of the forest were detected for DBH classes of 10 cm and more. It may be that the total impact of disturbances, especially fire and harvesting of trees, remained similar as legal timber harvesting decreased after the 1980s. There were however significant changes in species composition of trees with a minimum DBH of 20 cm. The decrease of *O. pulchra* may be explained by the fire sensitivity of the species (Geldenhuys, 1977), although more evidence is needed. The decrease in basal area of *D. englerianum* was caused by a much rarer occurrence of large trees (DBH > 40 cm) in the recent data compared to the historical data. It confirmed the high mortality rate of the species, especially the larger individuals, probably as a consequence of climate change and/or fire. The slightly decreasing basal area of *B. africana* over the last 40 years cannot be explained by climate change as the species' range extends to areas with climate conditions similar to those predicted by projected climate changes (Curtis and Mannheimer, 2005; De Cauwer et al., 2014), in fact the opposite trend could be expected. It may indicate a trend towards later forest succession stages and would need to be confirmed by revisiting more historical plots.

3.5 Conclusions

The western *Baikiaea* forests of southern Africa are characterised by six tree species that represent 84% of the total basal area and can be appropriately described as *Baikiaea* - *Pterocarpus* forests. The available site variables allowed the development of predictive BRT models for the tree communities that explained up to 31% of the deviance (correlation 0.61). Abiotic variables influenced the tree communities more than human induced disturbances. Despite the fairly uniform topography and soil of the study area, tree communities have exploited small differences in the landscape. The *Schinziophyton rautanenii* and *Baikiaea plurijuga* communities were more common on dune slopes, within a range of a few kilometres from - mainly dry - river valleys and had higher basal areas (5.5 – 6.2 m² ha⁻¹). They are more sheltered from frost, fire, and drought. The *Burkea africana*, *Guibourtia coleosperma* and *Pterocarpus angolensis* – *Dialium englerianum* communities were typical for the sandy plateaux and showed a lower basal area (2.8 – 4.6 m² ha⁻¹). They occurred in areas with a slightly higher fire frequency (21 – 34%). All communities were well presented with *Pterocarpus angolensis* - *Dialium englerianum* the most common community and *Burkea africana* the most abundant tree species. Comparison between recent and historical data did not show large changes over the last four decades; stem densities, mean

DBH, and basal area remained similar, whereas some species showed a decline in basal area. More of the historical plots need to be revisited to confirm the trends observed. The slope communities are most threatened by human expansion. The *Pterocarpus angolensis* – *Dialium englerianum* community shows less resilience towards climate change, illustrated by mortality rates of the indicator species and a decreasing basal area of *Dialium englerianum*. The community with most resilience towards climate change is the *Burkea africana* community, an open, undifferentiated, earlier succession stage forest type that can handle more extreme conditions, such as lower rainfall and more frost. Conservation of all tree communities will require establishment of refuges to protect the slope communities from anthropogenic activities, and of the *Baikiaea plurijuga* community and possibly the species *Dialium englerianum* from fire and drought. Follow-up studies are needed to study short term dynamics, especially mortality and regeneration near the edges of the transition zone between dry forest and scrubland, as is required for all tropical dry forests.

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Chapter 4 - Predicting site productivity of the timber tree *Pterocarpus angolensis*

Adapted from:

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VDC collected half of the local sample data, did 2/3th of the growth ring measurements for Namibia, performed the data analysis, and drafted the manuscript.

Abstract

Pterocarpus angolensis is an important timber tree of the Miombo forests of Sub-Saharan Africa. The species grows in natural mixed forests and little is known about its productivity potential. This study aims at investigating the productivity of *P. angolensis* on a local scale in Namibia and Angola and on a regional scale in southern Africa. Stem diameter increment was used to study productivity at a regional scale based on own and other studies' growth ring measurements. 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 using 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. Trees are sensitive to light competition until they reach canopy height and sensitive to root competition at sites with stand basal area larger than 4 m² ha⁻¹. Mean annual diameter increment in the open forests of Namibia was 0.51 cm after 50 years compared to a mean of 0.47 cm in southern Africa. 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 0.71 vs. 0.54 and 0.59 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, temperature annual range below 27.4 °C, a slope of less than 1°, a stand basal area between 6 and 10 m² ha⁻¹, and were situated close to agricultural fields (1-3 km) and far from main roads (> 10 km). 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.

4.1 Introduction

Pterocarpus angolensis is among the most important indigenous timber species in southern Africa (Takawira-Nyenyanya et al., 2010; Vermeulen, 1990). 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 (Shackleton, 2002; Vermeulen, 1990; Von Breitenbach, 1973). The species can be found where a dry season contrasts with a single wet

season, and where mean annual rainfall varies between 400 and 1250 mm (Curtis and Mannheimer, 2005; Von Breitenbach, 1973). Its distribution coincides roughly with the revised Miombo Ecoregion, which includes the typical Miombo, as well as open *Baikiaea* and *Burkea* forests at its southern edges (Olson et al., 2001; Therrell et al., 2006; Timberlake and Chidumayo, 2011) (Figure 4.1). The tree is threatened by land use changes, overharvesting and/or frequent intense fires in many countries (Caro et al., 2005; Leadley, 2010; Pröpper and Vollan, 2013; Shackleton, 2002; Stellmes et al., 2013b). Additionally, 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 because the tree grows only in natural mixed forests. Earlier attempts to establish plantations have been largely unsuccessful (Caro et al., 2005; Vermeulen, 1990). 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 are missing (Burke, 2006; Graz, 2004; Shackleton, 2002; Vermeulen, 1990). More knowledge on the productivity of *P. angolensis* would allow improved forecasts of its growth, mortality, recruitment, and timber yield and possibly assist in the establishment of plantations.

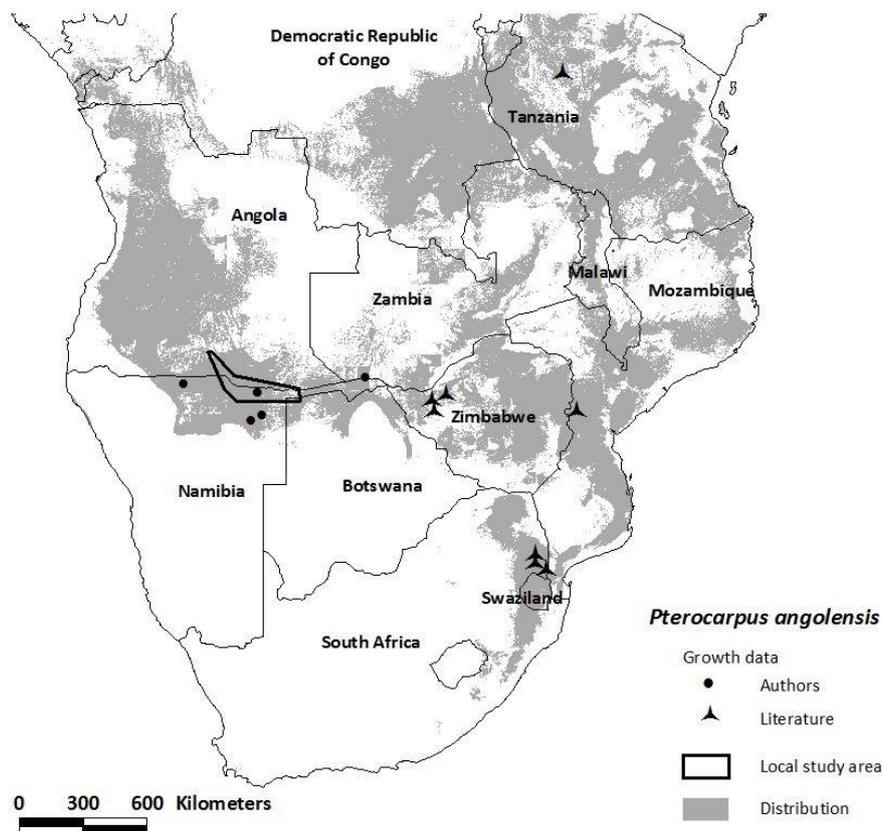


Figure 4.1 – Location of regional diameter growth data and local study area with indication of the distribution of *Pterocarpus angolensis* according to De Cauwer et al. (2014). The authors of this article measured the growth data in Namibia. Sources of growth data from literature are listed in Table 4.3.

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

Site or stand productivity can also be approached from a different angle and be considered in function of site factors, especially geo-climatic variables (Bontemps and Bouriaud, 2014; Pokharel and Froese, 2009). This approach allows upscaling productivity and mapping and predicting it on a larger scale. In this study, we explore 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.

4.2 Material and methods

4.2.1 Study area

The regional study focused on locations within southern Africa for which growth data were collected by the authors or for which relevant growth data could be found in the literature (Figure 4.1). Details on all locations, as well as the authors of the literature consulted, are listed in the results (Table 4.3). 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 4.1). 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 4.1.

The soils in the local study area are mainly nutrient poor, deep Kalahari sand (Gröngröft et al., 2013). The vegetation outside the Okavango river valley is open forest with a canopy coverage 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*. 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).

Table 4.1 – Range of environmental characteristics in the study area (based on WorldClim (Hijmans et al., 2005)). A glossary of terms is in Annex A.

	Local scale : Namibia and Angola		Regional scale: southern Africa	
	Minimum	Maximum	Minimum	Maximum
Altitude (m)	1047	1207	324	1224
Annual precipitation (mm)	539	712	478	1085
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)	30.2	35.6	11.8	37.8

The human population in the Namibian part of the study area increased rapidly in the last decades - from 116,830 to 222,500 persons (+ 90%) in the Kavango regions of Namibia during the period 1991 – 2011 (NPC, 2011) - and settlement expanded from the Okavango river valley to the forest, especially along roads and dry fossil rivers. Forest clearing for agriculture resulted in an annual deforestation rate of 3.9% in the period 1943 – 1996 in the Kavango regions (Mendelsohn and el Obeid, 2003). At the Angolan side, people have been returning since the end of the civil 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 (CBNRM) programme, but illegal logging does take place (Kabajani, 2013; Pröpper & Vollan, 2013; own observations). Harvesting of timber in Angola is on the increase as more Angolan wood is being transported through Namibia (K. Nott, pers. comm., IRDNC, 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., 2013b). The majority of the fires have an anthropogenic origin (Stellmes et al., 2013b).

4.2.2 Data

Diameter growth data

Diameter growth rate in Namibia was estimated through measurements in two permanent sample plots (PSP’s) of 1 ha and from growth rings (Table 4.2). The PSP’s were measured at the start and end of a period of 8 years (De Cauwer, 2006; Van Holsbeeck, 2015). Stem increment cores and stem discs were collected from five locations in Namibia (Figure 4.1). The growth ring data from the Zambezi and Oshana regions have previously been described in a dendrochronological study (Fichtler et al., 2004). The annual nature of the growth rings of *P. angolensis* has been proven (Fichtler et al., 2004; Stahle et al., 1999; Therrell et al., 2006; van Daalen et al., 1992; Worbes, n.d.) and was also confirmed by three successful cambial markings made on trees in Kavango West (Figure 4.2). More cambial markings were made but were not found in the wood after harvesting. Removing the cambial marking is complicated when not felling the tree (Figure 4.3).

Table 4.2 – Material used for measuring diameter increment of *Pterocarpus angolensis* in Namibia. GR stands for growth rings.

Source of material	Region	Method	Number of trees	Number of radii per tree
Fichtler et al., 2004	Oshikoto/Ohangwena	GR on stemdiscs + LINTAB	8	3 - 4
Fichtler et al., 2004	Zambezi	GR on stemdiscs + LINTAB	3	3 - 4
Own data	Kavango West	Diameter measurements in permanent plots	12	
Own data	Kavango West	GR on cores + LINTAB & CDendro	5	3
Own data	Kavango West	GR on stemdiscs + magnifying glass/ruler	3	3
Own data	Otjozondjupa	GR on cores + LINTAB & CDendro	4	3
Moses Moses, 2013	Kavango East	GR on stemdiscs + magnifying glass/ruler	2	3

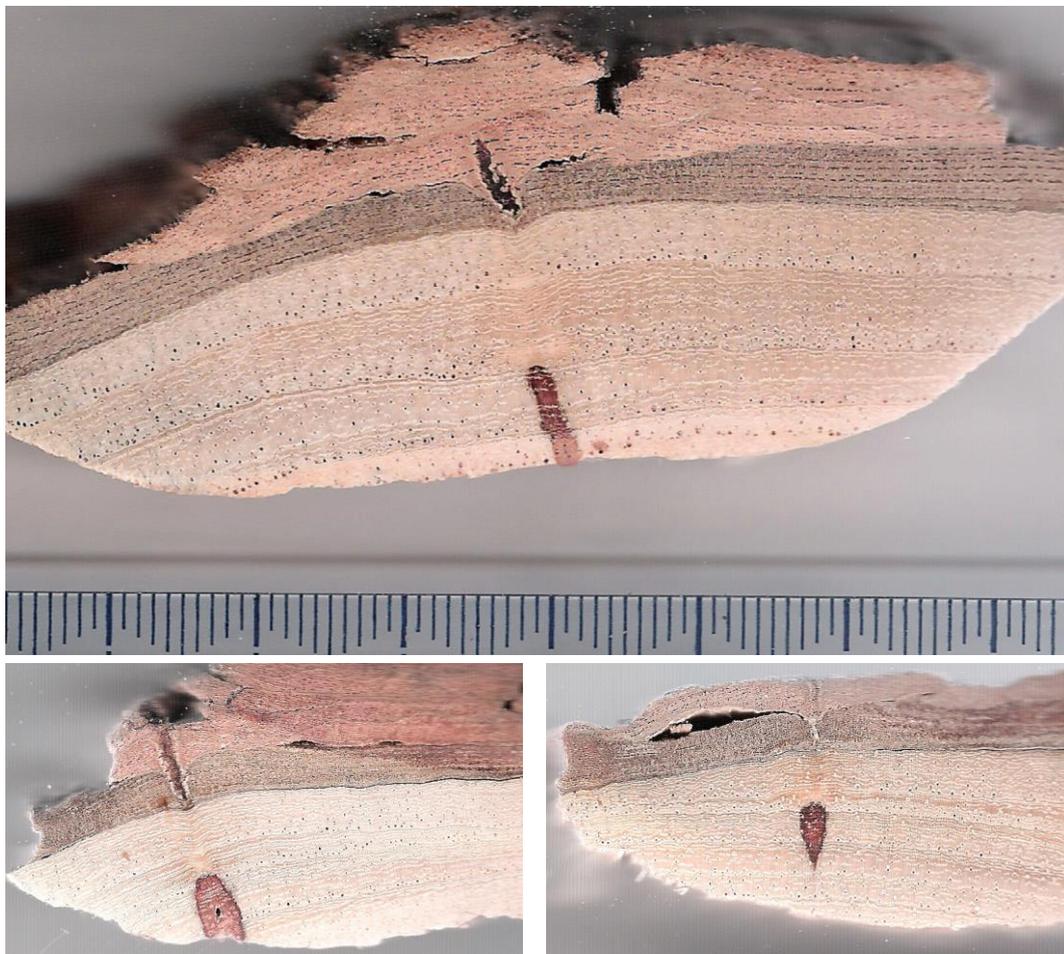


Figure 4.2 – Cambial markings made by V. De Cauwer on three mature (diameter at breast height > 20 cm) *Pterocarpus angolensis* trees in August 2010 (dry season). The wood samples were collected in May 2012 (end of wet season). Rainfall in the wet seasons of 2010 - 2011 and 2011 - 2012 was above average (> 510 mm based on CRUTS).



Figure 4.3 – Removal of cambial marking without harvesting the tree. The red resin is very sticky making the use of a saw difficult. A fungicide was applied on the wound after harvesting the cambial marking.

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). Growth rings were counted and measured with the assistance of LINTAB equipment (Rinn and Jäkel, 1997), the software CDendro (Cybis Elektronik & Data AB, 2014), or a magnifying glass and ruler for the stem discs. Two to three samples (radii or cores) were measured per tree. The average ring width after the first 50 years of cambial growth was compared with that of growth data available from the literature for southern Africa (Groome et al., 1957; Stahle et al., 1999; Therrell et al., 2007; van Daalen et al., 1992). Growth rates were compared for a reference age of 50 years because annual diameter increment (ADI), DBH, and age are 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 suffrutex stage (definition: Annex A), during which it dies back in the dry season and resprouts in the wet season, a normal phenomenon in miombo woody species (Ryan and Williams, 2011; Von Breitenbach, 1973). 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 growth ring 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 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) (Annex E, sample design for research data). The forest inventory data include all woody plants with minimum DBH of 5 cm. Main measurements per tree were circumference at breast height and tree height. Main measurements per plot were plot

centre coordinates, tree, shrub, grass, and herb cover. All variables derived from the forest inventories and used as predictors for the productivity models are listed in Annex J.

Site variables

For the local study, site factors were collected in the field and from existing or compiled geodatabases. These included abiotic variables, anthropogenic disturbance as well as stand variables. An overview of the variables and their sources is provided in Annex J. **Abiotic** site factors included climate, soil, and topography variables. Topography was described by altitude, aspect, slope, and landscape curvature.

Both direct and indirect indicators were used for **anthropogenic disturbance**. Direct measures were for example cattle density and severity of fire damage on the woody vegetation. Indirect measures included the distance to villages and tracks.

Stand variables were mainly related to tree competition and were based on data collected in the field: stand basal area (BA), coverage of grass, herbs, shrubs and trees, the competition index (CI), and H/H_{max} . Stand basal area reflects below-ground competition with the ability of trees to capture nutrients decreasing with the total basal area of all neighbouring trees, not only taller trees (Coomes and Allen, 2007; Seifert et al., 2014b). Grass, herb and shrub cover are also related to below-ground competition, and tree cover is a measure of above-ground or light competition. CI and H/H_{max} are both individual tree competition indices that reflect the social status of the tree and hence above-ground competition. CI is calculated as DBH of *P. angolensis* divided by the quadratic mean diameter of the plot or the DBH of the tree with mean basal area. H/H_{max} is the tree height (H) of *P. angolensis* divided by the maximum tree height (H_{max}) in the plot (Eid and Tuhus, 2001; Namaalwa et al., 2007). A last stand variable was the enhanced vegetation index (EVI), a vegetation index related to vegetation cover, density and condition that was derived from MODIS satellite images for the period 2007 - 2012 (Huete et al., 2002; Stellmes et al., 2013b). Waring et al. (2006) demonstrated its relation to site index.

For the analysis on a regional scale, only the abiotic site factors listed in Annex J, except dunes, were used. FAO data layers with the “occurrence of forest, cropland, pasture, and browse” were also used (FAO, 2007); each pixel displays the portion covered by a specific land use, for example cropland.

4.2.3 Data analysis

Basal area (BA), proportional BA (proportion of the BA of *P. angolensis* compared to the total stand BA), and site form of *P. angolensis* 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.

BA, proportional BA or site form were modelled with a two-step approach to avoid skewed data with many zero's (Fletcher et al., 2005). First species presence, defined as the occurrence of *P. angolensis* within a radius of about 60 m around the plot centre, was modelled. CI and H/H_{max} were not used as predictors in the presence model as they directly

reflect the presence of *P. angolensis*. Then BA, proportional BA or site form were modelled for the plots in which the species was present.

The reference tree diameter for site form was selected by inspecting the height - DBH relationship of the data (Figure 4.4). 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: SF25 and SF30. SF30 was also used by Angombe (2004) in Namibia.

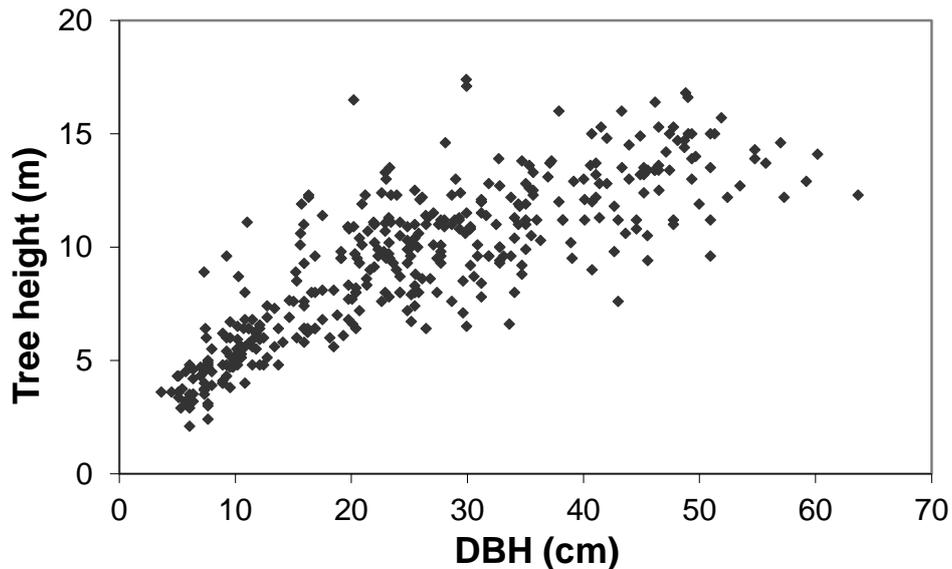


Figure 4.4 – Relationship between diameter at breast height (DBH) and tree height for 385 *Pterocarpus angolensis* trees from forest inventory data in 217 plots in northern Namibia and southern Angola.

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 modelling often outperforms other ecological modelling methods (Aertsen et al., 2010; Elith et al., 2006; Leathwick et al., 2006; Moisen et al., 2006) and has been successfully used to model site index (Aertsen et al., 2009) and abundance, including tree basal area (Moisen et al., 2006; Pittman et al., 2009). It combines a large number of simple tree models to optimise performance (Elith et al., 2008). A Bernoulli distribution was used to model the presence-absence data and a Gaussian distribution for BA and proportional BA (Moisen et al., 2006; Pittman et al., 2009; Ridgeway, 2014). The latter two variables were fourth root transformed to obtain a normal distribution. The BRT models were simplified by dropping variables 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 (Elith et al., 2008; Leathwick et al., 2006). Deviance not only measures how well calibrated the prediction values are, but also penalises errors in scaling of prediction values (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 in the software R (R Core Team, 2012) 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 because there were not enough data to model interactions with all site factors. The Spearman correlation ρ (rho) with the different site factors was explored and linear regressions were tested for the factors with the best correlations.

4.3 Results

4.3.1 Growth data

The mean annual diameter increment of *P. angolensis* at 50 years varied between 2.9 and 6.6 mm in southern Africa and was on average 4.7 ± 1.0 mm (Table 4.3). Namibian mean diameter increment was 5.1 ± 1.7 mm y^{-1} and was consistent for the different methods (Table 4.2) used. None of the climatic or soil variables showed a significant correlation ρ with annual diameter increment on a regional scale. The only variables with significant correlations ($p < 0.05$) were altitude ($p = 0.66$), forest occurrence ($p = -0.62$), and pasture occurrence ($p = 0.65$). Significant linear regressions were obtained for forest and pasture occurrence (Figure 4.4).

Table 4.3 – Mean annual diameter increment at 50 years (MDI50) with indication of number of trees sampled.

Source	Country	Latitude	Longitude	MDI50 (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, 1957	Tanzania	-4.7000	32.4000	5.9	10
Own data Kavango East	Namibia	-19.1280	19.9140	6.6	2
TOTAL					121

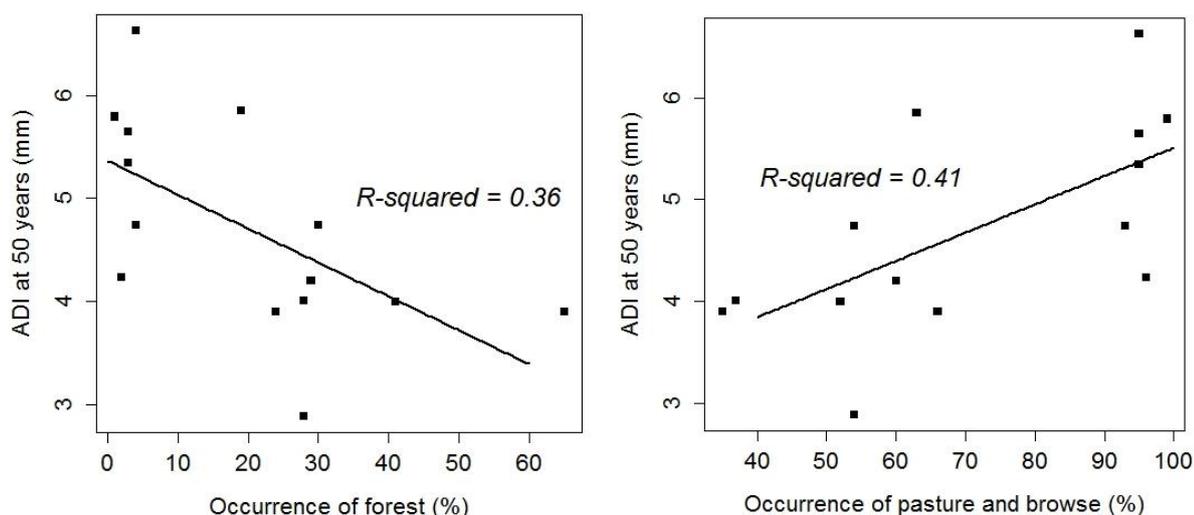


Figure 4.4 – Relation between mean annual diameter increment (MDI) of *Pterocarpus angolensis* in sub-Saharan Africa at 50 years and occurrence of forest (left) or pasture and browse (right) according to FAO (2007).

4.3.2 Boosted regression tree models

P. angolensis trees (DBH ≥ 5 cm) were present in 126 of the 217 plots. 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 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 better than the BA models. Table 4.4 shows that the deviance of the presence model did not improve much with the addition of disturbances or stand factors, whereas adding stand factors or disturbances explained relatively more deviance of the BA and proportional BA model.

Table 4.4 – 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.

	% Deviance explained			Correlation
	Site factors used for models			
	Abiotic	Abiotic Disturbances	Abiotic Disturbances Stand	Abiotic Disturbances Stand
Presence	38	40	44	0.71
Basal area	13	17	32	0.54
Proportion of stand basal area	8	15	30	0.59

Variables with the greatest contributions to the models differed for the presence and abundance models (Table 4.5). Temperature annual range was the most important abiotic variable and CI the most important stand variable. There are 16 partial dependence plots for the predictors. They illustrate straightforward relations that can easily be described; only a few of them are shown in Figure 4.5. *P. angolensis* was mainly found in areas with EVI below 0.29 (Figure 4.5a), with annual temperature range below 28.3 °C, more than 1 km away from fossil rivers, and with cattle density below 7 animals km⁻². Cattle density however is a proxy for certain abiotic variables, hence the limited improvement of the model by adding this disturbance factor (Table 4.4). The highest BA of the species was found in areas where *P. angolensis* had a competition index higher than 0.9 and H/Hmax between 0.6 and 0.9, and where stand BA was higher than about 9 m² ha⁻¹ (Figure 4.5b), annual temperature range below 27.4 °C, more than 6 km away from main roads, a northern to north-eastern aspect (0° – 45°), and temperature seasonality below 34.5 °C (Figure 4.5c). Highest proportions of the species in stand BA were in plots where *P. angolensis* had a competition index higher than 0.9 (Figure 4.5d) and H/Hmax between 0.6 and 0.9 (Figure 4.5e), and that were located on plains (slope < 1°) with stand BA lower than about 5 m² ha⁻¹ (Figure 4.5f), far away from roads (> 10 km), close to agricultural fields (1 – 3 km), and with annual temperature range below 27.4 °C.

Table 4.5 – Site factors affecting presence and productivity of *Pterocarpus angolensis* in Namibia and Angola: (1) contribution of predictors (%) to the boosted regression tree model with all site and stand factors and (2) correlation ρ with site form ($p < 0.05$). BA stands for basal area and % BA for proportional BA. Site form is tree height at a reference diameter, H is tree height, and Hmax is the maximum tree height in the plot. A glossary of terms is in Annex A.

	(1) BRT models			(2) Site Form	
	Presence	BA	% BA	SF25	SF30
Temperature annual range	35	14	10		
Competition index CI		20	20		
Total basal area stand		17	17		
H/Hmax		20	13	0.42	
Enhanced Vegetation Index (EVI)	26				
Distance to fossil rivers	22				-0.44
Distance to main roads		9	12		
Aspect		10	10		
Cattle density	17				
Temperature seasonality		11			
Slope			10		
Distance to agricultural fields			8		
Tree cover				-0.36	
Wet season EVI					0.47
Fire damage					-0.44

4.3.3 Site form

There were 31 plots that contained at least one tree with DBH of $25 \text{ cm} \pm 1 \text{ cm}$; their mean height was 9.7 m. Of these, there were 23 plots with at least one tree with DBH of $30 \text{ cm} \pm 1 \text{ cm}$ and with mean height of 11.1 m. There were only few significant correlations with site factors and many of these factors were different to the main predictors of the BRT models (Table 4.5). The regressions for both SF25 and SF30 were not significant.

4.4 Discussion

Diameter increment data for a tree of 50 years were derived for 14 locations in southern Africa (Table 4.3). These locations represented a wide range of climatic factors (Table 4.1), however there was hardly any other site information that could contribute to our understanding of the differences in growth rates. The most remarkable conclusion is the lack of a relationship between mean diameter increment and rainfall at a regional scale. Namibia, which has the lowest rainfall of the species' distribution range, shows a higher mean diameter increment (5.1 mm y^{-1}) compared to other areas (Shackleton, 2002; Stahle et al., 1999; Therrell et al., 2007; van Daalen et al., 1992). Other authors found relatively high growth rates for Namibia; 5.4 mm y^{-1} in northern Namibia (Lückhoff, 1969, unpublished report cited in van Daalen et al., 1992) and $7.1 \pm 3.8 \text{ mm y}^{-1}$ for Kavango West (Van Holsbeeck et al., 2016). Growth rate was negatively related with forest occurrence on a regional scale and showed the highest mean diameter increment for areas with less than 5% of forest. However, the forest occurrence dataset (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) that are difficult to detect by remote sensing (De Cauwer, 2015; Ganzin et al., 2005; Verlinden and Laamanen, 2006). It can therefore be concluded that the correlations of mean annual diameter increment with forest and pasture occurrence indicate a better growth rate of *P. angolensis* in open forests.

The preference of the species for open forests is supported by the negative relationships found at a local scale between proportional BA and stand BA, and between SF25 and forest cover. It confirms the theory that *P. angolensis* is a light demanding species (Vermeulen, 1990) and is negatively affected by competition. Light competition appeared to play only a role until the tree height has reached the canopy ($H/H_{\text{max}} = 0.9$) and its DBH is almost equal to the quadratic mean diameter of the neighbouring trees ($CI = 0.9$; average quadratic mean diameter was 21 cm). It explains why SF25 was correlated to a predictor reflecting competition (tree cover), unlike SF30. At a DBH of 25 cm, the tree has not reached its full height yet (9.7 m) and competition is fiercer than when the species has a DBH of 30 cm and has almost reached full height (11.1 m).

SF30 reflects the differences in site characteristics better because of lower interference with stand factors, affirming the selection of a reference DBH of 30 cm for site form by Angombe (2004). Root competition – measured by stand BA (Seifert et al., 2014b) – played a role from a stand BA of $3 \text{ m}^2 \text{ ha}^{-1}$ (Figure 4.5f). The species may have a lower competitive ability, doing well in areas where other species struggle due to less favourable environmental conditions

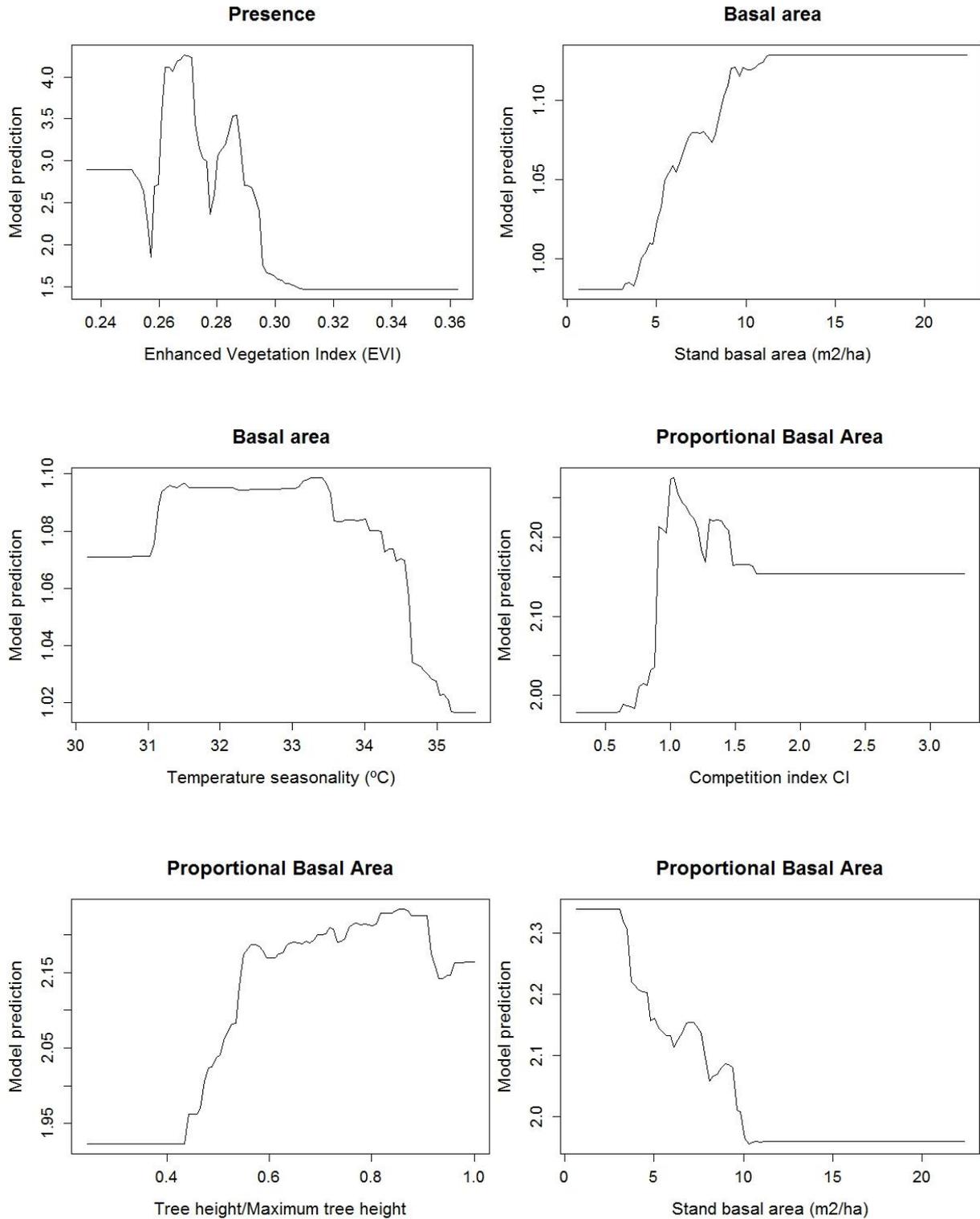


Figure 4.5 – Partial dependence plots for predictors of the (a) presence, (b-c) basal area, and (d-f) proportional basal area models for *Pterocarpus angolensis* in Namibia and Angola. The plots show the marginal effect of the variable on the model prediction. The Y axis represents the mean prediction values of the model using a log-odds scale for presence and a log scale for the other plots (Ridgeway, 2014).

and hence conform to the inclusive niche theory (McGill, 2012). De Cauwer et al. (2014) showed 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.

We did 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 life time of *P. angolensis* and the limited variability in the fire frequency data. We did find a negative correlation between fire damage and tree height at a reference DBH of 30 cm (Table 4.5).

There was a large variation in diameter increment at 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.

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. The better performance in less extreme temperature conditions is in accordance with the poorer performance observed 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 on 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 concurring with the presence of *P. angolensis* in eastern Africa (Annex D) is the same as the upper limit for an high proportional basal area of *P. angolensis* in the study area (Figure 4.5c).

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*³ species and *Terminalia sericea* (Strohbach and Petersen, 2007). Another reason is that people prefer to cultivate 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 away 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, no growth models exist with exception of a simple matrix model established for the species in Tanzania (Schwartz et al., 2002). This model has several limitations, especially the fixed time steps of 50 years and the use of a diameter increment of 0.5 mm, about 1/10th of other values in literature (Table 4.3). 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, 2006). Forest managers who aim to maximize wood production of *P. angolensis* should focus their interventions, including fire management (e.g.

³ Has been renamed *Vachellia* but *Acacia* is still officially used in Namibia (Klaassen and Kwembeya, 2013).

as discussed by Ryan and Williams (2011)), on stands with the highest abundance and performance of *P. angolensis*.

4.5 Conclusions

At a regional scale, no positive relationship between rainfall and diameter growth rate of *P. angolensis* was determined. The study area in Namibia showed a higher mean annual diameter increment (5.1 mm) than a lot of other areas in the distribution range with higher mean annual rainfall. This can be explained by the better productivity of the species in open, and often drier, forest where there is less tree competition as long as there are no other limiting factors such as a too low summer rainfall or too high temperature seasonality. The high variability of diameter increment at stand level and within the region illustrates the potential impact of stand factors and opens up possibilities for forest management to improve growth of the species.

At a local scale, species presence was better explained by site factors, mainly abiotic, than the measures of site productivity. *P. angolensis* is mainly found in areas with an annual temperature range below 28.3 °C, more than 1 km away from dry fossil rivers, with cattle density below 7 animals km⁻², and with an Enhanced Vegetation Index below 0.29. The study used site form as a measure of productivity of a species at a site. Site form for a reference DBH of 25 cm reflected mainly stand characteristics, while site form for a reference DBH of 30 cm (SF30) was mainly 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*. Satisfactory models could be established for BA and proportional BA, especially with addition of stand factors reflecting competition. Future studies on diameter increment should aim to collect stand-level information and be spread over more locations with similar geo-climatic variables to provide more insights. The areas with the highest abundance and best performance of *P. angolensis*, most relevant for forest management, are mainly found in the west of the study area, more than 10 km away from main roads, with stand BA between 6 and 10 m² ha⁻¹, and within a range of 1 to 3 km from agricultural fields. These areas have preferably a minimal slope (< 1°) and otherwise a northern to north-eastern aspect. This information can be upscaled to establish forest productivity maps and to establish growth models for *P. angolensis*.

Acknowledgements

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Chapter 5 – Individual tree growth and yield models for the African timber tree *Pterocarpus angolensis*

Abstract

Pterocarpus angolensis is an important timber tree of sub-Saharan Africa that reaches its southern limits in the open forests of South Africa, Botswana, and north-eastern Namibia. In Namibia, it is considered the most valuable timber in the country, but no yield models or estimations for the growing stock exist on a national level. Harvesting bans are put in place because harvest rates are considered unsustainable but this is not supported by hard data. Allometric relations and growth models would allow to establish sustainable harvest rates and yield, and contribute to assessing the biomass storage potential of Namibia's forests. This study established individual tree models for total and timber volume, biomass, heartwood portion, age-diameter relations, and radial growth of *P. angolensis* based on all data currently available for Namibia. Several modelling methods were tested to compensate for heterogeneity in the data. Site variables were added to improve the models and to investigate factors affecting productivity. The impact of increasing atmospheric CO₂ on growth rate was explored. Results showed that models with only diameter at breast height (DBH) as predictor gave good results for the prediction of total wood biomass, total wood volume, wood volume of stem and branches, as well as timber volume at national level (adjusted R² > 0.9). The best model for the dark heartwood portion of the wood was a linear model with DBH and latitude as predictors (adjusted R² = 0.47). The age-diameter relation was well described by a mixed effects (ME) model that allows to derive sustainable harvest rates. Mean radial stem growth per year was 5.5 ± 1.9 mm and was almost constant for all diameter classes up till 74 cm, pointing to the negative effect of competition in the juvenile stage on growth. The basal area increment models showed that stem diameter explains most of the variance (76 %) and that the tree reaches the senescence stage at a stem diameter of 60 cm or approximately 100 years. There was proof of an effect of increasing atmospheric CO₂ on growth for areas with higher mean annual rainfall. Forest inventory data of the Kavango regions allowed to demonstrate how the models allow to derive yearly yield of *P. angolensis* (e.g. mean annual yield of 196 kg biomass per ha). The study gives more insight in conditions of optimal growth, which may inspire forest management and silvicultural treatments of the species.

5.1 Introduction

Pterocarpus angolensis is an important timber tree in sub-Saharan Africa. Its wood has many names, such as Kiaat, Mukwa, Muninga, and Dolf, and it is sought after for furniture, decking, and woodcraft because of its beautiful grain, colour, and good stability. Its density is about 440 to 680 kg.m⁻³ (air dry) (Vermeulen, 1990). The species reaches the edge of its southern range in Namibia, Botswana, and South Africa, which is also the southern edge of the Miombo Ecoregion (De Cauwer et al., 2014; Olson et al., 2001; Timberlake and Chidumayo, 2011).

Namibia has about 70,000 km² of open forests in the north-east of the country of which the majority are *Baikiaea-Pterocarpus* forests with a mean wood volume of about 21 m³.ha⁻¹ (De

Cauwer, 2015; De Cauwer et al., 2016; FAO, 2014). *P. angolensis* reaches its bioclimatic limits there, but contributes more to the total basal area of those forests, approximately 16% in the Kavango regions (Annex F), compared to the less than 1% in typical Miombo forest (Banda et al., 2008; Kalaba et al., 2013; Syampungani, 2009). In the suboptimal climate conditions of this region the tree is still a medium sized tree with an average height of 11 m, sometimes reaching up to 18 m. It is the most valuable timber species in the country, especially because most individuals have a straight, non-hollow stem unlike other canopy species. Annual revenue of the commercial harvest of Namibian timber, *P. angolensis* and *Baikiaea plurijuga*, was estimated at NAD/ZAR 1.3 million or USD 100,000 (2016 values with www.inflationcalc.co.za) for the period 1993 - 2000 (Chakanga and Kojwang, 2001); no more recent data are available. The timber use value of *P. angolensis* is larger than its carbon value (Moses, 2013). However, the largest value is in its local use for construction, firewood, crafts, and medicines and represents approximately 77% of the total Namibian wood value (Chakanga, 2000).

Despite its importance, there are no accurate estimations for the growing stock of the species on a national level because of the outdated data on forest cover and limited availability of forest inventory data (De Cauwer, 2015; FAO, 2014). Another obstacle is the high degree of uncertainty associated with yield models available for *P. angolensis* in Namibia (Angombe, 2004; De Cauwer, 2015; Julin, 2002). A few allometric relations were established on a regional level with 9 to 18 trees per region (Julin, 2002), while Moses (2013) used a larger dataset for Kavango East. There is however no biomass or wood volume equation at national level, nor a model to estimate timber volume. A timber volume equation is relevant as the saw log is often the only part used of commercially felled *P. angolensis* trees (Moses, 2013). Most Namibian forest inventories estimate timber by calculating the saw log volume with the volume of a cylinder and the estimated saw log length. An age-diameter model would allow to derive simple harvest guidelines. Equally relevant is a relation between the stem diameter and the heartwood diameter, as the darker and stronger heartwood is the part that carpenters are interested in. It is not known if the equations derived for the species in eastern Africa (Shackleton, 2002; Therrell et al., 2007) apply to Namibian and southern Angolan trees. There is no growth model established for the species in Namibian conditions and forest management plans of community forests (Mulofwa et al., 2003; Otsub and Omoro, n.d.) base allowable harvest rates on rough estimates of yearly diameter increment by Worbes (n.d.).

Also outside Namibia little work has been done on yield prediction of *P. angolensis*. Therrell et al. (2007) established an age-diameter model for eastern Africa but advised caution for its use because of growth variability within and among stands. Two simple matrix growth models have been established for the species; for Tanzania (Schwartz et al., 2002) and for South Africa. The Tanzanian model cannot be applied in Namibia because its time of passage through diameter classes is based on an annual diameter increment of 0.5 mm, about 1/10th of other values in literature (Table 4.3). None of the models have explored site factors that affect growth. Little is known about the conditions that influence the productivity of the species, except that it performs best on well-drained soils, in open forests due to its high light demand (De Cauwer et al., in press; Vermeulen, 1990), and better in mixed stands than in monocultures (Vermeulen, 1990).

The lack of knowledge on optimal growth conditions does not encourage silvicultural interventions to increase timber yield, something which is currently not done in Namibia or most other countries where *P. angolensis* is found. The lack of accurate data on growing stock and a good growth model make it difficult to prove claims that the present forest resources are not adequate to sustain a timber economy (Chakanga, 2000), or that current timber harvest is unsustainable. The latter is the main reason for regular logging bans on the species in Namibia (Bjorkman, 1999; Hailwa, 2012) and for restricting harvest to local use and community forests, although illegal logging does take place (Kabajani, 2013; Pröpper & Vollan, 2013; own observations). Deriving the productivity of the species would allow comparison with agricultural yields on the poor forest soils. Clearing forest for subsistence and cash-crop agriculture is the main reason for deforestation in most regions of Namibia. Detecting growth trends over the long-term would contribute to solving uncertainties related to the impact of atmospheric CO₂ fertilisation on tree biomass in Namibia (Midgley et al., 2005; Thuiller et al., 2006). Increasing growth trends over the last five to ten decades have been linked to climate change and increased global CO₂ concentration for trees in temperate regions (Cole et al., 2010; Martinez-Vilalta et al., 2008).

This study aims at developing individual tree models that can calculate current wood volume and biomass of *P. angolensis* and allow predicting growth and hence future wood volume and biomass based on forest inventory data in Namibian conditions. The models will combine all data available for Namibia, which is possible with the most recent modelling techniques that can take into account different sites or sampling methods (Chave et al., 2004; Seifert and Seifert, 2014; Zuur et al., 2009). We evaluate if site variables can improve the models, especially as this may compensate for regional differences, determine the role of competition or disentangle factors influencing short-term versus long-term growth. The growth model should be able to predict when the maximum growth rate can be expected as this is relevant for harvesting.

Specifically, this study will (1) model biomass, total wood and timber volume of *P. angolensis* in Namibia, (2) model the relation between heartwood portion and stem diameter for Namibia and southern Angola, (3) model the age-diameter relationship in Namibia and southern Angola, (4) create a deterministic model for annual diameter growth of *P. angolensis* in Namibia and southern Angola that allows to predict future standing stock based on forest inventory data, (5) investigate if site variables can improve the models, and (6) investigate if increasing atmospheric CO₂ has an impact on diameter growth.

5.2 Methods

5.2.1 Study area

Data were collected in the *Baikiaea-Pterocarpus* forests of northern Namibia and just across the border in southern Angola (Figure 5.1). The study area consists of dry, open forest according to FAO definitions (Annex A), 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 soil outside the valleys of the Okavango and ephemeral rivers consists of nutrient poor, deep Kalahari sand as described by Gröngröft et al. (2013). Mean annual rainfall is between 480 and 700 mm (Table 5.1).

The human population has increased rapidly in the last decades, from 386,900 to 557,700 (+ 44%) in the Kavango, Ohangwena and Zambezi regions during the period 1991 – 2011 (NPC, 2011), and settlement expanded from the Okavango river valley to the forest, especially along roads and dry fossil rivers (Mendelsohn, 2009). Most villagers harvest small quantities of wood within a radius of about 5 km of settlements and agricultural fields, mainly as firewood and for construction. Commercial logging focuses on large individuals of *P. angolensis* and to a lesser extent *B. plurijuga*. Harvesting of timber in Angola is on the increase (Karen Nott, pers. comm.). Every year, approximately 20% of the area burns, mainly towards the end of the dry season (Stellmes et al., 2013b).

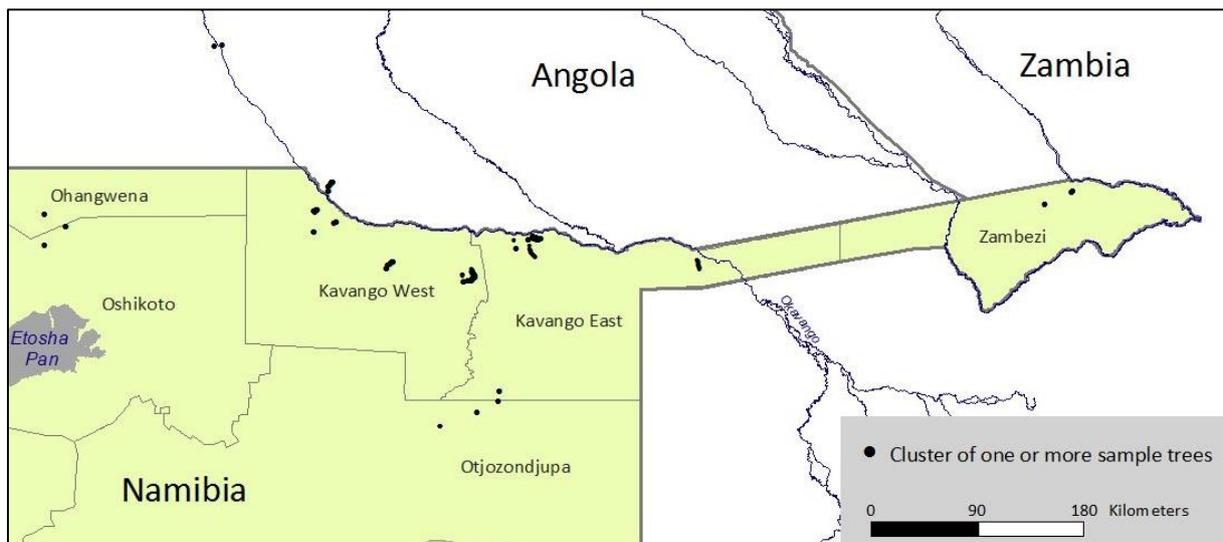


Figure 5.1 – Location of study area and sample trees to determine growing stock, biomass and growth.

5.2.2 Wood volume and biomass data

Wood volume and biomass can be calculated in various ways, mainly depending on the inclusion of branches. Models were established for:

- Total above ground wood biomass (B_{tot}): the dry weight biomass of all over bark wood components of the tree, including branches;
- Total wood volume (V_{tot}): the total over bark wood volume of the tree, including all branches;
- Wood volume of stem and branches (V₁₀): the over bark wood volume up to branches with a diameter of 10 cm;
- Timber volume (V_{tim}), also called merchantable volume: over bark wood volume of the stem that can be used as saw wood (bole). No minimum top diameter was defined as this is dependent on the size of the tree (Figure 5.2). For the smaller trees, it concerns the part of the stem that can be used as a straight pole or that has the potential to be used as saw wood.

Two datasets are available in Namibia for Btot, Vtot and V10 that were collected by (1) the Namibia Finland Forestry programme (NFFP) (Chakanga et al., 1996), and (2) Moses (2013) (Table 5.1) in several regions of northern and north-eastern Namibia (Figure 5.1). The data of Moses (2013) was collected for trees in open forest stands, but it is unknown if the trees included in the NFFP data were in forest stands or single individuals along roads and agricultural fields. Both projects used destructive sampling, which typically generates more precise data. The volume of the trees was based on measurements of diameters and lengths of tree sections with bark and calculated with the Smalian formula. Biomass was estimated based on samples of stem and branches with bark. Volumes of the samples were determined by the water displacement method and basic wood density was estimated through their oven-dry mass. Mean basic wood density for the stem up to branches of 10 cm and including bark, differed significantly per region. It varied between 532 kg.m⁻³ in Otjozondjupa and 631 kg.m⁻³ in Kavango East (Moses, 2013) to 729 kg.m⁻³ in Zambezi.

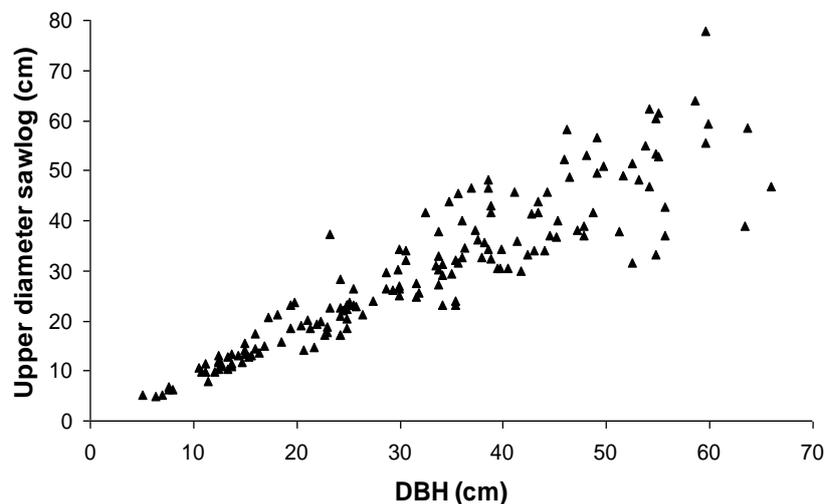


Figure 5.2 – Top diameter of the tree bole in function of diameter at breast height (DBH) as measured from a distance with a laser dendrometer. Data was collected by De Ruytter (2015) and the author in Namibia and southern Angola. More information on the 173 trees measured is in Table 5.1 (NUST team).

A quality check was performed on the two datasets based on the total tree form factor F , which is the fraction of the volume of a cylinder with diameter DBH and tree height that represents V_{tot} (Cannell, 1984). F normally varies between 0.5 and 1 (Chave et al., 2014; Colgan et al., 2014) whereby trees with a higher proportion of branches show a higher F and can even exceed 1 with values up to 1.7 (Cannell, 1984; Henry et al., 2010). For all except 1 of the 13 trees measured in the Oshikoto and Ohangwena regions, F was higher than 1 with an abnormally high mean of 3.6. Hence the Oshikoto/Ohangwena data was not used in the modelling. The average total form factor F for the remaining data was 0.70 ± 0.25 .

For V_{tim} , the datasets of Moses (2013) and NFFP were complemented by volume data of 173 trees collected by NUST through non-destructive sampling (Table 5.1) (e.g. De Ruytter,

2015). Tree diameters were determined at several heights along the saw log by measuring the circumference at the heights of 0.3 and 1.3 m and by measuring the diameter with a laser dendrometer at 2.3 m and higher. Timber volume over bark was calculated with the Smalian formula.

Table 5.1 – Study sites in Namibia and Angola with sample trees for volume and growth measurements. MAP is the mean annual precipitation and DBH diameter at breast height (cm). Sample collection teams are Göttingen-Stellenbosch (GO), M. Moses (MM), Namibia Finland Forestry Programme (NFFP), and Namibian University of Science and Technology (NUST).

Region	Location	MAP (mm)	Sample collection team	Volume measurements		Growth measurements		
				Number of trees	Mean DBH	Number of trees	Mean age	Mean DBH
Otjozondjupa	Kanovlei	478	NUST			6	59	40
	West Tsumkwe	492	NFFP	18	45			
Oshikoto	Oshikoto	522	NFFP	8	42	7	88	45
Ohangwena	Ohangwena	526	NFFP	5	30	2	85	53
Kavango West	Katope	540	NUST	18	28	0		
	Hamoye	553	NUST/GO	86	31	29	56	36
Kavango East	Mashare	576	NUST	36	33	15	48	36
	Kahenge	582	NUST	15	30			
	Divundu	588	NUST			10	47	35
	Karukuvisa	502	MM	40	47	11	75	48
Zambezi	Katima Mulilo	671	NFFP	9	31	4	71	34
Cuando Cubango (Angola)	Cuangar	612	NUST	16	42	4	68	35
	Caiundo	707	NUST	2	48			
TOTAL				253		88		

5.2.3 Diameter growth data

Growth models are often established after monitoring permanent sample plots (PSP's) over a long time period. There are however very few PSP's in Namibia and most are too recent (De Cauwer, 2006) or data are not available. Therefore stem diameter increments derived from growth-ring series for 88 trees were used to model diameter growth (Table 5.1). Growth-ring series were derived by the author, with exception of data of 13 trees that formed part of a dendrochronological study by Fichtler et al. (2004) in Namibia based on the NFFP stem discs (Table 5.1). Both stem discs and cores were used that were collected at stump height. A second core sample was collected at breast height (1.3 m) for trees in state forests linked to research stations, but not in communal forests to minimise the damage to wood belonging to the communities.

The growth rings of *P. angolensis* have proved to be annual in previous studies (Fichtler et al., 2004; Stahle et al., 1999; Therrell et al., 2006; Worbes, n.d.), as can be expected from a tree with strong deciduous behaviour. They were confirmed by cambium markings for Namibia (Figure 4.2). Frequent wedging rings at the stem base hamper the measurement of annual rings, even on stem discs (Stahle et al., 1999; Therrell et al., 2007; van Daalen et al.,

1992). This can be solved by cross-dating techniques but was only done to a limited extent in this study as the main goal was to estimate age-diameter relationships at different sites, which is possible without cross-dating (Therrell et al., 2007).

Dried cores and discs were progressively sanded with sanding paper up to fine grit and scanned at 2000 dpi resolution with a photo scanner. Ring widths were measured with CooRecorder (Cybis Elektronik & Data AB, 2014). The distance to pith for off-centre cores was estimated with the “Set distance to pith” tool. Ring widths could be cross-dated and averaged per tree in CDendro (Cybis Elektronik & Data AB, 2014) when more than one radius per tree was measured. Cross-dating of growth-ring series from the same site was not successful and resulted in low t-values for most trees (t-value < 2 with the Baillie-Pilcher method (Trouet et al., 2010)). The main aim of this study is the determination of growth patterns and we thus used the complete collection of not cross-dated (per site), not detrended growth-ring series. Records for the age classes for which less than 3 observations per age class were available were removed, which was ages over 113 years. All growth data reflect the growth of the tree since the last resprouting event. *P. angolensis* seedlings go through a phase during which they die back each dry season and resprout in the wet season (Von Breitenbach, 1973). This suffrutex phase (definition: Annex A) can last from 0 to 14 years and 9 years on average in Namibia (Kayofa, 2015; Vermeulen, 1990).

5.2.4 Volume and biomass modelling

Tree allometry data are strongly heteroscedastic showing an increasing variation with increasing DBH, and hence were ln transformed (Seifert and Seifert, 2014). Linear models were established for the ln transformed data, resulting in a common allometric relation for wood volume:

$$\ln Y = \alpha + \beta X + \varepsilon$$

with lnY the natural logarithm of Btot in kg.m⁻³ or Vtot, V10 or Vtim in m³, X the predictor variables with as main predictor DBH in cm, α and β the intercept and slope to be estimated by the regression, and ε the residuals. Tree height was not added as predictor because it does not significantly improve the models for species of savannah woodlands and open forests (Abbot et al., 1997; De Ruytter, 2015; Hofstad, 2005), unlike models for many (taller) tree species of temperate and wet tropical regions. Moreover, tree height data were not always available for all Namibian forest inventories and show inaccuracies, even when made with a laser dendrometer.

The dataset showed other sources of heterogeneity than DBH for Vtim: the region where the data was collected, the collector of the data or the method used to collect the data (destructive versus non-destructive). The heteroscedasticity and apparent nested data structure of Vtim was addressed by testing both a generalised least squares (GLS) and mixed effects (ME) model structure. For the GLS model, a variance structure was used for the residuals to compensate for heterogeneity caused by the different regions, collectors or methods. The ME model adds a random component reflecting differences caused by region, collector or method (Zuur et al., 2009).

5.2.5 Model for the proportion of heartwood

The proportion of heartwood was defined as the width of the heartwood relative to the stem diameter without bark. The growth measurements described in Table 5.1, excluding those of Fichtler et al. (2004) on the NFFP discs, were used to derive the heartwood portion. Heartwood portion could be modelled with a linear model.

5.2.6 Radial growth models

The relation between growth and predictors was first explored with a **cumulative diameter increment** model; a relationship between cambial age and stem diameter. GLS and ME model structures were tested because the growth data have a nested data structure; they are correlated per tree and possibly per location or region (Free et al., 2014; Zuur et al., 2009).

For the annual growth model, radial stem growth was expressed as basal area increment (BAI, cm²):

$$BAI_i = \pi \cdot (R_i^2 - R_{i-1}^2)$$

with R the radius of the tree (cm) determined by the cumulative width of the growth rings at the end of the growing season in year i. BAI showed a skewed distribution and was therefore ln transformed. To compensate for the inaccuracies caused by missing or wedging growth rings (Stahle et al., 1999; Therrell et al., 2007), the dataset was aggregated in age classes of 5 years. BAI, diameter increment and CO₂ were averaged over each period of 5 years. The use of time classes is equivalent to calculating average growth rates from PSP's between two measurements separated by 5 years. The classes showed slightly better correlations to the site variables than the original data and gave better model results. The BAI model was applied to trees with a minimum DBH of 5 cm, the minimum tree size for Namibian forest inventories, which also reduced errors caused by off-centre coring.

Explorative BAI models were established to study the impact of stem diameter and other predictors on BAI. A two-step approach adapted from Kint et al. (2012) was used. Two models were established: (1) a site model SM based on the natural logarithm of BAI, stem diameter and site variables (SM), (2) a long-term model LM based on the natural logarithm of BAI, stem diameter, site variables, and long-term increase in atmospheric CO₂ :

$$LM = \ln BAI_{ij} = SM + \eta Z_i + \varepsilon_{ij} = \alpha + \beta D_{ij} + \gamma X_i + \eta Z_i + \varepsilon_{ij}$$

with BAI_{ij} (cm²) the BAI of tree i in year j, D a linear function of stem diameter (cm) derived from the cumulative growth ring widths, X representing site variables including mean climatic characteristics at the site, Z the atmospheric CO₂ concentration, and ε the residuals. More information on the predictors used for X and Z is given in section 5.2.8.

Data on forest structure was measured for 47 % of the trees in the database (see 5.2.8) and were added to the site variables in a second site model (SM_F). However, forest structure is variable over time and we therefore used the last two age classes of 5 years per tree only, restricting the model data for SM_F to 8% of the original records. BAI in this reduced dataset was not skewed and no ln transformation was needed. Models SF and SF_M are most relevant to understand site productivity, but can also contribute to understanding the sensitivity of the species' growth to climate change if predictors include climate variables.

Model LM aims to analyse if the increase in atmospheric CO₂ has a fertilising effect on the species. Generalised additive modelling (GAM), which is appropriate for non-linear data, was used for all explorative models.

Next to the explanatory models, a **predictive BAI model** was established for SM. Both GLS and ME model structures were tested for the predictive model. The predictive BAI model in combination with the wood volume and biomass models allow to **predict yield** based on forest inventory data. This was demonstrated with the research data used in Chapter 3.

All modelling was done in R (R Core Team, 2012) with use of the packages nlme (Pinheiro et al., 2012) and mgcv (Wood, 2011).

5.2.7 Model evaluation

Model comparison and selection was done with the Akaike information criterion (AIC). Only models where all coefficients were significant ($p < 0.05$) were kept. A bias correction was applied for the back transformation of $\ln Y$ to Y as outlined by Baskerville (1972):

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

with σ equal to the standard error of the residuals in log units. The same was done for the back transformation of $\ln BAI_{ij}$ to BAI_{ij} . The adjusted coefficient of determination R^2 was used to compare the performance of linear models. The residual standard error (RSE) of all models was derived from the model predictions and actual tree data and used as a measure of absolute error (Colgan et al., 2014). The relative error (RSE_{rel}) was determined by dividing RSE by the mean of the observations and allows 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 was calculated on all data (calibration) and through 10-fold cross-validation, as described by other authors (e.g. Aertsens et al., 2010).

5.2.8 Model predictors

Table 5.2 gives an overview of the site variables tested as predictors in the models. For the volume and biomass models, only bioclimatic variables (Hijmans et al., 2005), the long-term climatic water deficit (CWD), and the environmental stress factor (E) were evaluated (definitions: Annex A). Chave et al. (2014) showed that E has an important impact on the diameter-height relationship of trees. The climate variables are available as averages over the time period indicated. Variables describing topography were included, but no soil data as they were not accurate enough to detect differences between sites. Forest inventory data were collected by the author according to the national forest inventory method for Namibia (Burke et al., 2001) (see research sample design in Annex E). The inventory allowed deriving competition indices at stand level (e.g. stand basal area, tree cover, BAL) and at tree level (e.g. competition index CI) (definitions: Annex A). Predictors for the models were selected based on their Spearman correlation to the variable modelled, the variance inflation procedure (Zuur et al., 2009), and their significance in the models.

Table 5.2 – Predictor variables tested in the models. All predictor data are on an interval scale, except for the names of collectors, sites or regions that are on a nominal scale. Spatial resolution is indicated for raster data. A glossary of terms is given in Annex A.

Variables	Source	Period	Resolution
Bioclimatic variables: Temperature Seasonality, Max Temperature Warmest Month, Min Temperature Coldest Month, Precipitation Warmest Quarter, Annual Precipitation	WorldClim (Hijmans et al., 2005)	Mean for 1950/1960 - 1990/2000 (depending on dataset)	30 arc sec (± 920 m at equator)
Frost days	Climatic Research Unit time-series datasets (CRUTS v.3.10.01) (Harris et al., 2013)	Mean for 1941-2002	30 arc min (± 55 km at equator)
Climatic Water Deficit (CWD), Environmental Stress Factor (E)	chave.ups-tlse.fr/pantropical_allometry (Chave et al., 2014)	Mean for 1960-1990	2.5 arc min (± 4.6 km at equator)
Atmospheric CO ₂ concentrations	Law Dome Ice Core + Cape Grim (CSIRO Oceans and atmosphere, 2015)	Time series 1850 - 2014	
Altitude, Slope (derived in GIS), Aspect (derived in GIS), Landscape curvature (derived in GIS)	Shuttle Radar Topography Mission (SRTM), NASA		3 arc sec (± 90 m)
Distance to perennial and non-perennial rivers, distance to agriculture	GIS data digitised in Google Earth and derived from the Atlas of Namibia (Mendelsohn et al., 2002)	2014	
latitude, longitude, diameter at breast height (DBH), for some datasets: Tree height (H), H.DBH ⁻¹	Namibia-Finland Forestry Programme (NFFP), Fichtler et al. (2004), De Ruytter (2015), Van Holsbeeck (2015)	1997 - 2015	
latitude, longitude, DBH, H, H.DBH ⁻¹ , Crown diameter (CD), CD.DBH ⁻¹ , Collector, Name of Site, Name of Region	Moses (2013)	2012	
latitude, longitude, DBH, Tree density, H, H.DBH ⁻¹ , CD, CD.DBH ⁻¹ , Crown class, Stand basal area (BA), Tree cover, Shrub cover, Grass cover, BA larger trees (BAL), Competition Index (CI), Maximum tree height in plot (Hmax), H.Hmax ⁻¹ , Quadratic Mean Diameter, Collector, Name of Site, Name of Region	Own forest inventory data in nested plots with maximum radius of 30 m	2006 - 2014	

5.3 Results

5.3.1 Wood volume and biomass models

Table 5.3 illustrates that linear models gave good results for the prediction of wood volume and biomass with only DBH as predictor. Adding a quadratic component of DBH did not improve the models. The model predictions include the bark; average bark thickness of all trees was 2.7 ± 0.9 cm. The biomass model is illustrated in Figure 5.3 and compared with two species generic biomass models: a pantropical and a Miombo model (Chave et al., 2014; Chidumayo, 2013).

Table 5.3 - Volume and biomass models with form $Y = \exp(\alpha + \beta_1(\ln DBH))$. LM is a linear model and ME a mixed effects model. α includes the Baskerville correction factor. All regression coefficients are significant with $p < 0.001$. RSE is the standard error, RSErel the relative error of the residuals, and SD is the standard deviation. RSE was calculated for the fixed effects of the ME model for timber volume.

	n	AIC	Intercept α	DBH β_1	SD per region	Adjusted R^2	RSE	RSErel (%)	RSE	RSErel (%)
							Calibration		Validation	
Range variable				9 - 73 cm						
Mean variable	67			44 cm						
Biomass (B) - LM (kg)		17	-1.6509	2.2317		0.92	283	28	290	29
Total Volume (Vtot) - LM (m ³)		11	-8.2846	2.2905		0.93	0.49	29	0.51	30
Wood volume (V10) - LM (m ³)		23	-9.8902	2.6577		0.94	0.41	29	0.42	30
Range variable				5 - 76 cm						
Mean variable	240			36 cm						
Timber volume (Vtim) - ME (m ³)		40	-8.4656	2.0890	0.35 - 1.0		0.21	51	0.21	51

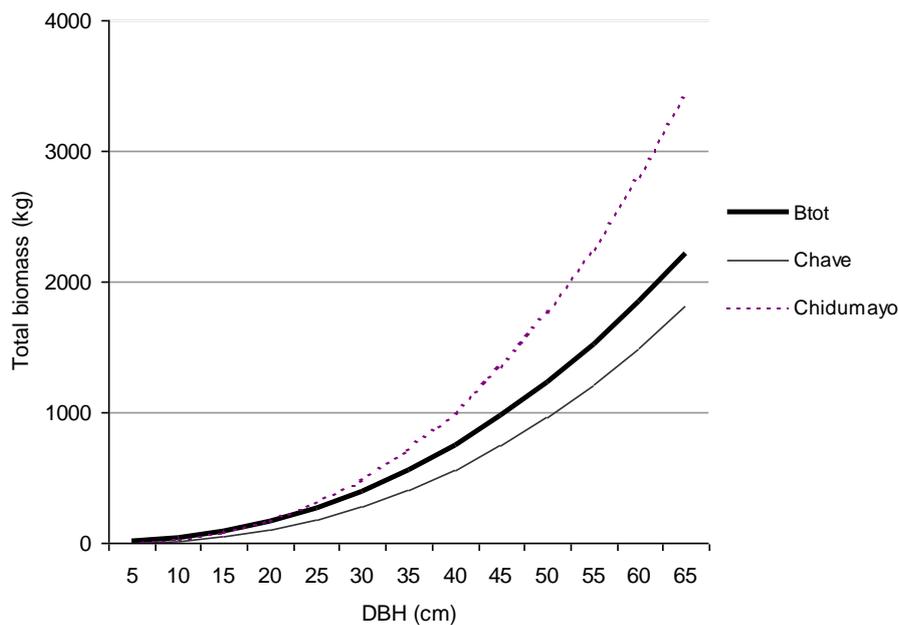


Figure 5.3 – Biomass model (Btot) compared with the generic models of Chave et al. (2014) for tropical forest and Chidumayo (2013) for Miombo forest. The Chave model without tree height was used with as mean Environmental Stress Factor (E) 0.8806 and mean wood density of 618 kg.m⁻³.

A ME model managed to solve the heterogeneity for V_{tim} ; random effects were of the format $1+DBH+DBH^2$ per region, with the highest standard deviation for the intercept (0.54). The random part is ignored when using the model for predictions. Variation of V_{tim} is highest in Zambezi and lowest in Kavango West.

5.3.2 Proportion of heartwood

The mean heartwood portion of the sample trees, that had stem diameters of 20 to 70 cm, was $64 \pm 18\%$. The best linear model to estimate the amount of heartwood contained only two predictors ($p < 0.001$):

$$\text{Heartwood proportion (\%)} = -287.78 + 41.41 \cdot \ln(\text{DBH}) - 11.01 \cdot \text{Latitude}$$

with DBH (cm) including bark, and latitude in decimal degrees. Calibration gave a RSE of 12.9% (RSErel 20%) and validation a RSE of 13.2% (RSErel 21%). Most of the variance was explained by DBH (adjusted R^2 of 39% compared to 47% for the model including latitude). Figure 5.4 illustrates the model.

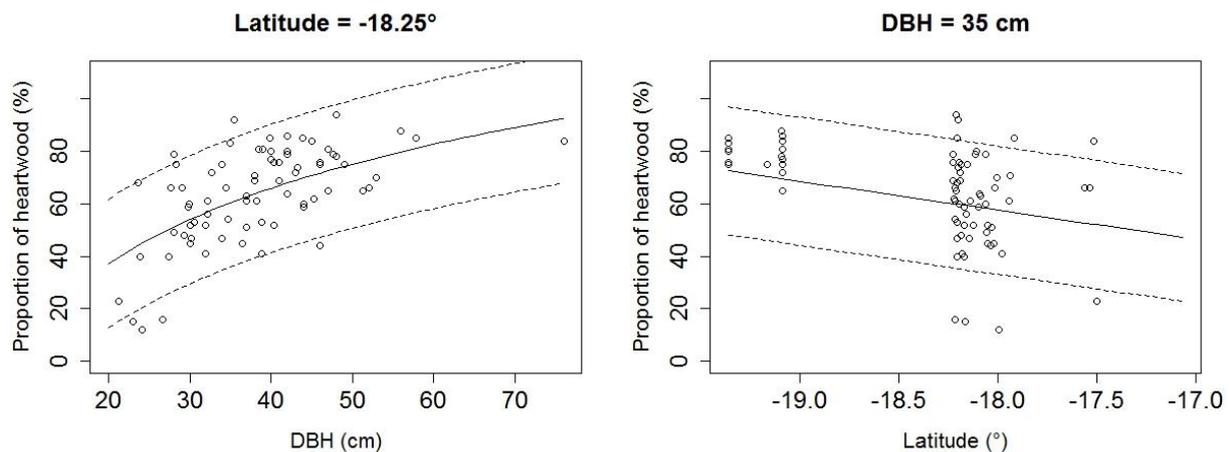


Figure 5.4 – Linear model for the proportion of heartwood with indication of the 95% confidence intervals and the fitted values of the actual observations ($n=75$).

5.3.3 Age – diameter relationship

The age – diameter relationship showed different trajectories depending on the tree (Figure 5.5). A ME model with an exponential variance structure and a random effect per tree gave the best results to determine the cambial age (years) or the age of the bole of the tree:

$$\text{Cambial age} = -0.8601 + 2.0166 \cdot X - 0.0052 \cdot X^2$$

with X the stem diameter (cm) without bark. Variance of the residuals was $\sigma^2 \cdot e^{0.0023 \cdot DBH}$. Random effects were of the format $1+X$ per tree with standard deviations of 3.37 and 0.44 for intercept and slope respectively; they are ignored when using the model for predictions.

Calibration gave a RSE of 9.7 years (RSErel 28%) for the fixed effects and for the complete model 1.8 years (RSErel 5%). As in the previous models, validation gave similar results: RSE 9.7 years for fixed effects and 1.9 years for the complete model. The ME model structure solved all heterogeneity per location. Adding other predictors did not improve the model.

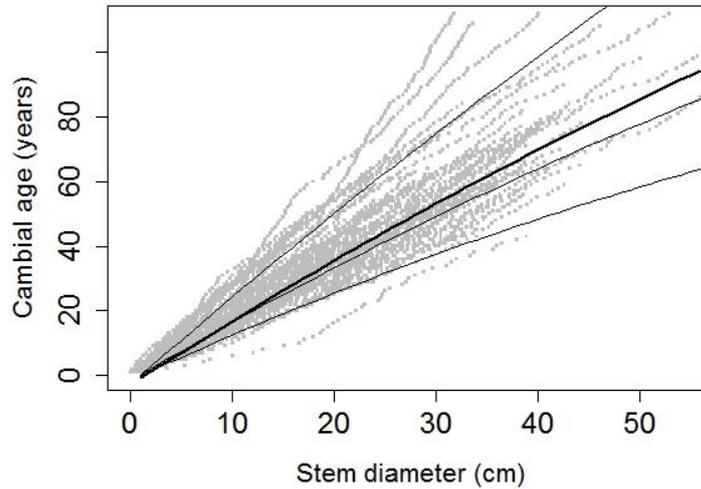


Figure 5.5 – Relationship between stem diameter and cambial age for 88 Pterocarpus angolensis trees. The grey points are the actual observations. The lines indicate the mixed effects model with the bold line the population model and the other lines model results for a few trees.

5.3.4 Explanatory BAI models

The mean values of stem diameter increment and BAI per year were 5.5 ± 1.9 mm and 18.2 ± 13.2 cm² respectively. BAI increased with time until the stem diameter reached 60 cm but diameter increment was very constant (Figure 5.6). Stem diameter explained most of the variance in the BAI models: 76% (data not shown) compared to 79% for the site model SM (Table 5.4). The explanatory models SM and LM gave high relative errors but appear robust for predictions, unlike model SM_F.

5.3.5 Predictive BAI model

The best predictive model had a GLS structure and is illustrated in Table 5.5. The model does not capture the decrease of BAI for stem diameters larger than 60 cm (Figure 5.6). However, a model with higher-order functions of stem diameter decreased the performance of the model significantly. Differences between locations were smaller than differences between individual trees and therefore a correlation per tree was added.

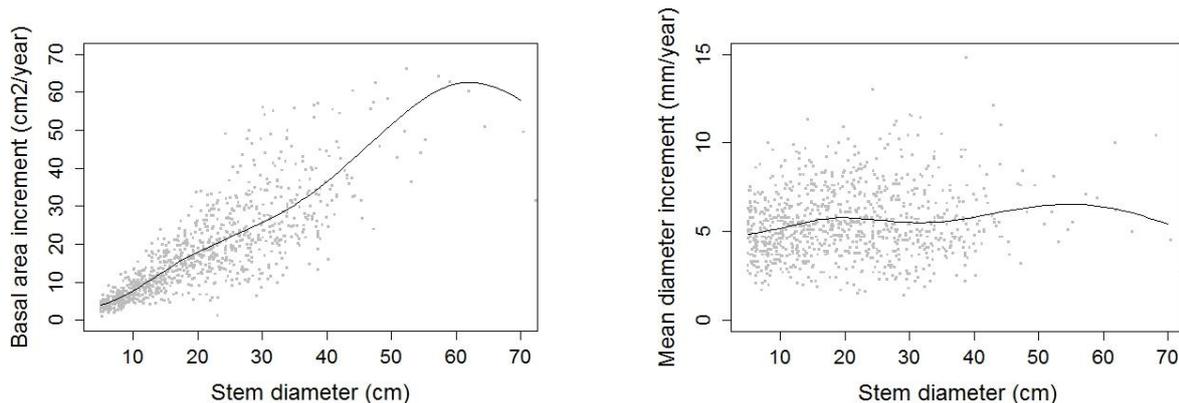


Figure 5.6 – Stem growth of 88 *Pterocarpus angolensis* trees based on growth ring measurements. The grey points are the actual observations ($n = 935$). The lines are the generalised additive models for basal area and diameter increment.

Table 5.4 – Basal area increment models for *Pterocarpus angolensis*. The site (SM) and long-term (LM) models have as form $BAI = \exp(\alpha + s(D) + \gamma X)$ with the intercept α including the Baskerville correction factor, D the stem diameter, and X other predictor variables. The site model with forest structure variables (SM_F) has as form $BAI = \alpha + s(D) + \gamma X$. They are generalised additive models with $s(X)$ representing the smoother or non-linear function. All regression coefficients are significant with $p < 0.01$. RSE is the standard error and RSErel the relative error of the residuals. A glossary of terms is added in Annex A.

	Range predictor	SM	SM_F	LM
n		935	23	935
Intercept		31.7366	83.7291	27.6963
Stem diameter (cm)	5 - 73.6	smoother	smoother	smoother
Temperature seasonality (°C)	30.2 - 37.8	-0.2391		-0.1477
Minimum temperature coldest month (°C)	4.2 - 7.4	-0.8148		-0.5736
Maximum temperature warmest month (°C)	33.2 - 34.9	-0.4183		-0.2962
Precipitation warmest quarter (mm)	128 - 241	-0.0097		-0.0457
Shrubcover (%)			-0.4592	
Basal area larger trees (BAL) (cm ²)			3.3058	
Maximum tree height in stand (Hmax) (m)			-3.5262	
Atmospheric CO ₂ concentration (ppm)	286 - 395			-0.0159
Precipitation warmest quarter*Atmospheric CO ₂				0.0001
Adjusted R ²		0.79	0.45	0.80
Calibration RSE (cm ²)		7	8	7
Calibration RSErel (%)		40	28	40
Validation RSE (cm ²)		8	13	8
Validation RSErel (%)		46	47	45

Table 5.5 – Generalised least squares model for basal area increment (BAI) with as form $BAI = \exp(\alpha + \beta D + \gamma X)$. The intercept α includes the Baskerville correction factor, D is the stem diameter, and X are the other predictor variables. All regression coefficients are significant with $p < 0.0001$. RSE is the standard error and RSErel the relative error of the residuals.

	Range predictor	Mean predictor	SM
n			935
Correlation per tree			0.58
Exponent variance			0.01
Intercept			26.3548
ln (Stem diameter) (cm)	5 - 73.6	19	1.0852
Maximum temperature warmest month (°C)	33.2 - 34.3	34.0	-0.3972
Temperature seasonality (°C)	30.2 - 37.8	35.0	-0.2119
Minimum temperature coldest month (°C)	4.2 - 7.4	6.1	-0.7405
Precipitation warmest quarter (mm)	128 - 241	155	-0.0086
Calibration RSE (cm ²)			7.5
Calibration RSErel (%)			41
Validation RSE (cm ²)			7.6
Validation RSErel (%)			42

5.3.6 Simulation of yield prediction

The predictive BAI model in combination with the wood volume and biomass models allow to predict yield based on forest inventory data. Table 5.6 illustrates the annual yield of *P. angolensis* in the Kavango regions.

Table 5.6 - Estimation of the yield of *Pterocarpus angolensis* in the Kavango regions based on 188 plots (sample design in Annex E for research data). Basal area increment (BAI, cm²), increment of timber volume (VTI, dm³), and increment of biomass (BII, kg) are given per year and per ha.

DBH class	Stems	BAI	VTI	BII
5 - 10	5.8	33	11.18	15
10 - 15	3.9	40	13.94	20
15 - 20	3.4	49	17.63	27
20 - 25	2.4	46	17.10	27
25 - 30	1.9	46	17.14	28
30 - 35	1.2	35	13.32	22
35 - 40	0.9	29	11.16	19
40 - 45	0.7	28	11.01	19
45 - 50	0.3	15	5.92	10
50 - 55	0.1	6	2.53	4
55 - 60	0.0	2	0.69	1
60 - 65	0.0	1	0.31	1
TOTAL	21	329	122	193

5.4 Discussion

5.4.1 Wood volume and Biomass

The study established allometric relations to determine the wood volume and biomass of *P. angolensis* based on forest inventory data. The models can be used on a national level as they showed no heterogeneity in wood volume and biomass between regions. The relative error for V_{tot} , V_{10} , and B_{tot} was approximately 30%, which compares well to other local and pantropical studies (Chave et al., 2014; Colgan et al., 2014). There were, however, indications that the dataset did not capture the variety of tree shapes and wood densities of the species in Namibia. A first indication was that the relative error for V_{tim} was much higher (50%) despite the larger dataset for V_{tim} . Subjectivity in defining the saw log may play a role in the error of V_{tim} because of the differences in variance per collector, but different bole shapes per region can also explain differences in V_{tim} as the best model added a random model element per region. Another indication that the dataset is too small is the fact that there were no significant differences for B_{tot} per region, whereas the wood density showed large differences. Wood density was lowest in the driest areas, opposite to what can be expected as higher wood densities are often found in environments with more drought stress (Chave et al., 2006; Wiemann and Williamson, 2002). Finally, Angombe (2004) demonstrated different height-diameter relations per region in northern Namibia with a larger forest inventory dataset, which points to different tree shapes but could also be the result of different species compositions.

The large total tree form factors F found for Ohangwena and Oshikoto are probably caused by measuring errors but may need further investigation. Chave et al. (2014) found that F was negatively related to CWD and mean annual rainfall and that it was higher (0.6) in dry forests compared to the moist and wet forests of their pantropical study. Their F value is slightly lower than what we found (0.7), explaining the lower values obtained by Chave et al.'s model (Figure 5.3). The higher F factor can be expected for our study area because it has more open and drier forests than the sites used in Chave et al.'s study (2014). Colgan et al. (2014) however did not find that inter-specific biomass variation was caused by differences in F but rather by variation in wood density in a dry forest in eastern South Africa.

The difference between our and the pantropical model (Chave et al., 2014) results was smaller than that with a model established for Miombo forest in neighbouring country Zambia (Chidumayo, 2013) (Figure 5.3). The use of the latter model in Namibia would give overestimations of biomass for *P. angolensis*, especially considering the fact that it did not include branches smaller than 5 cm in diameter.

5.4.2 Heartwood portion

The mean heartwood portion increased with DBH, as shown by other authors (Shackleton, 2002; Therrell et al., 2007), and decreased with latitude. Our model explains the same amount of variance as that of Therrell et al. (2007), and much less than that of Shackleton (2002) that is based on data collected in a smaller study area. The driest areas of the distribution range of *P. angolensis* (Curtis and Mannheimer, 2005; De Cauwer et al., 2014) appeared to have the highest heartwood portions in our study. If harvesters want to collect 30 cm of heartwood at stump height, they would need to harvest trees with a stem diameter of 40 cm and 47 cm at latitudes of -19° and -17.5° respectively. It may explain why most commercial concessions of the 1960s and 1970s in Namibia were situated at lower latitudes.

The heartwood portions at the lower latitudes in Namibia are similar to those in south-eastern Africa where, at latitudes between -15° and -25° , harvest of trees with diameter of 40 to 41 cm are required to obtain 30 cm of heartwood (Shackleton, 2002; Therrell et al., 2007). The equation proposed for Namibia and southern Angola can be used in table form by forest extension officers and harvesters that aim to assess the portion of heartwood of a tree. This would assist in eliminating the harmful practice of axing through the bark to assess the heartwood portion, thereby creating entry points for pathogens and fire (Krynauw, 1998; Shackleton, 2002).

5.4.3 Growth

The annual growth increment of *P. angolensis* did not show a typical trend with increasing size or age. Most species show initially a fast annual diameter increment that slows down from a specific age or diameter depending on the species (Bowman et al., 2013). For pioneer species, this is typically early and before the tree is 20 years old (Cole et al., 2010; de-Miguel et al., 2013; Subedi and Sharma, 2013). Diameter increment of *P. angolensis* remained practically constant for all diameter classes although there was a slight decreasing trend with age as also observed by other authors for the species (Stahle et al., 1999; Therrell et al., 2007). The relatively low diameter increment of small trees can be explained by root and light competition of other trees. Free et al. (2014) showed a similar age-diameter curve for *Swietenia macrophylla*, a late successional tree of the Amazon that has in common with *P. angolensis* that it is a long-living, light-demanding canopy tree. The annual BAI of *S. macrophylla* decreases with increasing competition and its maximum BAI is only reached after it reaches a diameter of 50 to 100 cm, depending of the tree's crown position (da Cunha et al., 2016). The growth trends of *P. angolensis* therefore underline the fact that the species is sensitive to competition until it reaches maturity, that it is long-living and only becomes senescent (Bowman et al., 2013) at a diameter of approximately 60 cm which corresponds to an age of about 100 years. However, very few trees get older than 100 years in Namibia and there are hardly any trees with DBH over 50 – 60 cm to be found (De Cauwer et al., 2016; Hilbert, 1986). The main reasons are commercial harvesting and accumulated fire damage at the stem base caused by late dry season fires that cause the trees to topple over.

BAI was only weakly related to any other predictor than stem diameter and all predictors were related to climate and not topography. The influence of some predictors on BAI is consistent with our other results (Chapters 3 and 4), for example sites with a higher mean temperature seasonality and maximum temperature in the warmest month showed a lower growth rate. This also concurs with the results of other studies on *P. angolensis* and on another southern African tree species *Brachystegia spiciformis* (Stahle et al., 1999; Therrell et al., 2007; Trouet et al., 2006) that showed that growth is positively related to rainfall and negatively to high temperatures in summer.

However, other predictors showed unexpected or counterintuitive trends. For example, BAI was higher at sites with a lower mean for the minimum temperature of the coldest month and a lower precipitation in the warmest quarter. It could be that these sites, which are mainly towards the south of the study area, are areas where *P. angolensis* has less competition of other trees. This could not be explored in detail with the site model that included forest structure (SM_F) because it included only a few of the trees at those sites.

SM_F did indicate the negative effect of shrub cover and stand height (Hmax) on the growth of *P. angolensis*. One of the predictors of SM_F does however contradict the competition theory. BAL increased when there were more trees larger in DBH than the sample tree (BAL) and hence more competition for light (Coomes and Allen, 2007). In the dataset, a large BAL was often caused by *Schinziophyton rautanenii*, a tree that can obtain a very large DBH. This tree grows in areas with slightly better soil conditions and slightly less fires (De Cauwer et al., 2016), which are conditions that can positively influence growth.

The model showed a positive effect of the increasing atmospheric CO₂ concentration in areas with higher mean rainfall. The interaction effect between summer rainfall and CO₂ concentration (Table 5.5) results in an increased growth for areas with a mean rainfall higher than 135 mm in the warmest quarter, excluding the Otjozondjupa region, and confirms the fertilising effect shown or predicted in other studies (Cole et al., 2010; Thuiller et al., 2006). It illustrates that the CO₂-induced growth is limited by moisture (Cole et al., 2010; Laubhann et al., 2009) in the study area.

Growth variability was better explained at tree level than at regional level. Therrell et al. (2007) also found a high variability within and stands in south-eastern Africa. The high variability at tree level (Figure 5.5) is best explained by forest structure, but possibly also by genetic factors. Forest management could aim to increase individuals with high growth rates by collecting cuttings and seeds from individuals with high growth rates and removal of slow growing individuals.

The age-diameter relationship can be used in the study area to propose sustainable harvest rates. It shows that the time of passage for each DBH class of 10 cm decreased from 19 years for the DBH class 5 – 15 cm to 14 years for DBH class 55 – 65 cm. This is quicker than most times of passages found by Therrell et al. (2007) for several study areas in south-east Africa (with data up till DBH class 30 – 40 cm). It is similar to the times of passages for *S. macrophylla* in the Amazon (18 to 11 years for DBH classes up till 60 cm) (Free et al., 2014). In fact, growth appeared so constant in our study area, that it is also possible to calculate diameter growth with an average of 5.5 mm y⁻¹ for all DBH classes. This value is higher than the values of 3.4 – 3.7 mm y⁻¹ reported by a consultancy study of Worbes (n.d.) for the Namibian Directorate of Forestry. They were based on growth ring counts on stem discs that formed part of the samples used for this dissertation. A dendrochronological study on the same discs indicated however a higher mean value of 4.9 mm y⁻¹ (Fichtler et al., 2004).

The minimum harvest size of *P. angolensis* in Namibia is a DBH of 45 cm, corresponding a biomass of approximately 970 kg and a total wood volume of approximately 1.5 m³ of which 0.6 m³ is timber wood according to our models. The age-diameter model indicates that it will take 79 years after the seedling phase to reach this diameter, or 88 years for the total tree age (Kayofa, 2015). Many local communities assume that a tree grows twice or three times as quick as this. Local information campaigns can include this information to raise awareness about the need to protect the tree or to plant it for future generations, something that is currently not done. Several authors consider the species not suitable for plantation forestry and advise to manage it within its natural environment (Vermeulen, 1990; Von Breitenbach, 1973). Although there are some reports of successful establishments of plantations outside south-western Africa (Vermeulen, 1990), there are no follow-up reports on how these plantations fared. The fact that the species is light demanding and also a nitrogen fixer (Högberg, 1990), however, makes it a good candidate for agroforestry

purposes. Plantations of the species can produce more biomass per year on the nutrient poor soils than traditional agriculture methods (potential maize yield 250 to 600 kg ha⁻¹) (Pröpper et al., 2015). This is illustrated by the annual yield of *P. angolensis* that is approximately 190 kg per ha (Table 5.6) in natural forests of the Kavango regions. This yield represents only a fraction, approximately 16%, of the total tree yield (Annex F). It is based on the growth rate in natural conditions and could be increased when thinning and pruning is applied, a labour extensive investment compared to traditional agriculture.

5.5 Conclusions

We successfully developed reliable models that can be used in Namibia and southern Angola to estimate the total wood biomass, total wood volume, wood volume of stem and branches, and timber volume of *P. angolensis* based on a single predictor: diameter at breast height (DBH) adjusted $R^2 > 0.9$). However more data on wood volume, biomass and density is needed to reduce the relative residual error that varied between 30 and 50%. The heartwood portion increased logarithmically with DBH and decreased with latitude; it was the highest in the driest areas of its range in Namibia. Further study is required into the extent and the reason of the lower heartwood portions found at a latitude of -18° in Namibia. The models showed that the variations in stem diameter growth are mainly at individual tree level, rather than per region or site. The differences were compensated by model structures that added a random factor or correlation structure for individual trees. The age-diameter relationship was described by a mixed effects model that allows to derive times of passage in diameter classes (14 – 19 years per 10 cm DBH class) and thus sustainable harvest rates. The annual diameter increment (ADI) of the stem was on average 5.5 ± 1.4 mm. It remained almost constant with increasing DBH pointing to the sensitivity to competition in the juvenile phases of growth. Basal area increment (BAI) only reached a maximum at a diameter of approximately 60 cm. BAI was mainly explained by stem diameter (76%) and improved only slightly with addition of climate variables or variables related to forest structure. Our dataset did not contain enough measurements to make a robust model that included forest structure variables and more forest inventory in combination with growth data need to be collected to explore this further. There was proof of an effect of increasing atmospheric CO₂ on growth in areas where mean summer rainfall is larger than 135 mm. The biomass and growth models allow predicting the annual yield for *P. angolensis* (190 kg per ha in the natural forests of Kavango) and provide input into matrix models that aim to derive the future standing stock. The study shows that diameter growth can be increased during the juvenile stages by reducing competition, which may initiate silviculture of the species.

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Chapter 6 - Conclusions

The overall aim of the study is to contribute to the sustainable management of *Pterocarpus angolensis*, particularly in the *Baikiaea* – *Pterocarpus* forests, by using state-of-the-art ecological methods and modelling techniques that give insight in general patterns of occurrence and productivity over large areas.

6.1 Environmentally suitable area for *Pterocarpus angolensis*: where does the species occur?

The environmental suitable area for *P. angolensis* was determined for the complete range in southern Africa as part of the SDM (Chapter 2). This results in a distribution map of *P. angolensis* that covers a smaller area (60%) than the existing maps based on collations of observations (Coates Palgrave, 1983; Therrell et al., 2007; Von Breitenbach, 1973). Our map provides more detail and omitted a large area in the south of the DRC, eastern Angola, and western Zambia. The SDM study allowed to provide more quantitative and objective measures than available in literature. The environmental suitable areas within the *Baikiaea* - *Pterocarpus* forests of the study area confirmed the important impact of abiotic variables on the species occurrence (Chapter 4). Drivers of occurrence as determined by our study are summarised in Box 1.

Box 1 – Drivers of occurrence of *Pterocarpus angolensis* are:

(A glossary of terms is given in Annex A.)

- Mean annual rainfall > 430 mm per year;
- Rainfall in February, the middle of the wet season, between 50 and 250 mm;
- Rainfall at start of wet season: > 5 mm in October and > 40 mm in November;
- Rainfall in driest month < 30 mm, only relevant for areas outside the Kalahari;
- Rainfall seasonality > 55%, reflecting the variation in rainfall over the year and thus a marked difference between dry and wet season;
- Temperature seasonality < 38.7 °C and outside the Kalahari < 35 °C;
- Diurnal range, the difference between monthly maximum and minimum temperature, < 18 °C;
- Minimum temperature of the coldest month > 4 °C, relevant outside the Kalahari;
- Less than 19 frost days per year;
- Well drained soils, avoiding flat terrain (slope > 0.5°) outside the Kalahari and preferring sandy soils in the Kalahari.

Within the study area in the *Baikiaea* – *Pterocarpus* woodlands (Kalahari):

- Temperature annual range < 28.3 °C;
- Distance from fossil rivers > 1 km;
- Cattle density < 7 animals per km².

Occurrence of *P. angolensis* is to a large extent determined by the rainfall amount and seasonality. The requirement for the minimum temperature in the coldest month ($> 4\text{ }^{\circ}\text{C}$) was the only one already clearly, quantitatively, and consequently mentioned in literature (Burke, 2006; Von Breitenbach, 1973) prior to our study. All other environmental ranges in literature (Takawira-Nyenyanya et al., 2010; Vermeulen, 1990) were broader and less explicit, while some ranges mentioned, such as that for mean temperature, appear not important to determine the species' distribution in our study. In general, *P. angolensis* is exposed to much more extreme environmental conditions (frost and drought) in the Kalahari basin of south-western Africa than in the wetter eastern part. This points to a high genetic variety within the species. Genetic studies of *P. angolensis* have been done, but only for provenances outside the Kalahari (Amri and Mamboya, 2012; Chisha-Kasumu et al., 2009).

6.2 Forest composition and population structure

P. angolensis is an important and characterising tree in the *Baikiaea – Pterocarpus* forests of the study area. It is an indicator species for the most common of the five tree communities, the *Pterocarpus angolensis – Dialium englerianum* community. The community shows a lower maximum DBH (mean of 41 cm) and tree cover (22%) than most other communities. It has a high proportion of smaller stems (60%) in the DBH class 10 – 20 cm compared to the mean for the study area (55%), a sign of frequent fires in the late dry season (Higgins et al., 2007). Our large dataset showed that *P. angolensis* is the second most common canopy tree species in the study area with 8 stems per ha (19%) and that it represents 16% of the mean basal area. The population structure was however less healthy than that of most other woody species, with less trees in the DBH class of 5 to 10 cm (Figure 3.5). This is consistent with findings of Kabajani (2016) for the seedlings in the study area, but has also been observed in other areas than our study area (Caro et al., 2005; van Daalen, 1991; von Malitz and Rathogwa, 1999). Two potential reasons can be pointed out for our study area: (1) the species occurs in the areas with the highest fire frequencies in the study area; (2) the species is sensitive to climate changes. Both reasons are elaborated further (sections 6.4 and 6.5).

6.3 Site productivity of *Pterocarpus angolensis*

Site productivity is a quantitative estimate of the ability to produce plant biomass, including wood, at a site. Because *P. angolensis* grows only in natural, mixed forests, its productivity is as much influenced by its abundance as by its growth rate. The productivity was therefore evaluated in different ways within the study area in the *Baikiaea – Pterocarpus* woodlands: through measures of abundance (basal area and proportional basal area) and measures of growth rate (stem diameter increment and site form).

Productivity in the Baikiaea – Pterocarpus forests compares well to that in typical Miombo

P. angolensis is at the edge of its bioclimatic range in Namibia and yet showed a high relative abundance and productivity. The mean basal area of the species is 1.7 m^2 per ha and it represents 16% of the basal area of trees with minimum DBH of 10 cm. The species is much more common in the study area than in typical Miombo forest where it rarely exceeds 1% of

the basal area (Banda et al., 2008; Kalaba et al., 2013; Syampungani, 2009). The mean diameter increment of the species in Namibia (5.5 mm per year) is at the higher end of the increment range found by other studies in southern Africa (2.9 to 6.6 mm per year) (Groome et al., 1957; Stahle et al., 1999; Therrell et al., 2007; van Daalen et al., 1992).

Drivers of productivity are different from drivers of occurrence

Most environmental drivers of productivity are different from those of occurrence with exception of temperature seasonality (Box 2). This is consistent with the inclusive niche structure that is based on a trade-off between competitive ability and environmental tolerance (Bertness and Callaway, 1994; Holmgren et al., 1997; McGill, 2012). A species may be adapted to a range of environmental conditions, but its abundance in the most optimal environments depends on its competitive abilities. A competitively weaker species is often more abundant in the less optimal conditions of its environmental range and *P. angolensis* appears to fit well into this category. The fact that environmentally perfect suitable areas are not necessarily areas with a high abundance or productivity was clearly demonstrated by the SDM. Areas with the highest occurrence probability do not show an obvious correlation with diameter growth or maximum height, nor have they any obvious environmental or topographical factors in common. The lower competitive ability of the species in optimal environments also explains why productivity is less well explained by abiotic factors and why additional information on anthropogenic disturbances or on forest structure is needed (Chapters 3, 4, and 5). Differences in diameter growth in southern Africa cannot be related to a climate or topographic variable, but shows a preference of the species for open forests.

The most common denominators for areas with good productivity are related to temperature, tree competition and anthropogenic disturbances. The species does not handle light and root competition well until it has almost reached canopy height, confirming the fact that the species is light-demanding (Vermeulen, 1990). The species performs best in areas with less extreme temperature conditions however it has to compete there with other tree species. Within the study area, it competes with species of the slope communities, where *P. angolensis* is common as well: in 67% of the plots of the *Schinziophyton rautanenii* and 55% of the plots of the *Baikiaea plurijuga* community, compared to 88% of the plots in the community where it is the indicator species.

The information presented in Box 2 is, to our knowledge, comprehensively described for the first time. It includes information from chapters 3 to 5.

Tree competition affects growth during the juvenile phase

The study found an almost constant diameter increment per year over all diameter and age classes, similar to what other studies found in south-eastern Africa (Stahle et al., 1999; Therrell et al., 2007). It points to the sensitivity of *P. angolensis* towards competition during its juvenile phase and confirms that the social status affects productivity (Box 2). It is consistent with our finding in Chapter 4 that the height of trees with a reference DBH of 25 cm is much more influenced by competition than that of trees with a reference DBH of 30 cm.

Box 2 – Drivers of productivity of *Pterocarpus angolensis* within the *Baikiaea* – *Pterocarpus* forests are:

(A glossary of terms is given in Annex A.)

Areas with high abundance:

- Temperature seasonality of < 34.5 °C;
- Annual temperature range < 27.4 °C;
- Preference for a western to northern aspect;
- Flat terrain (slope < 1°);
- A high fire frequency in the period 1981 – 2004 (> 30% or more than 7 fires);
- Cattle density < 7 animals per km²;
- Further away from fossil river beds (> 6 km) and the Okavango river (> 30 km);
- Further away from main roads (> 6 km);
- Stand basal area between 6 and 10 m² ha⁻¹;
- Stands where *P. angolensis* has a good social status and is close to canopy height (i.e. > 60% of maximum tree height in the stand).

Areas and trees with relatively higher growth rates:

- Lower temperature seasonality;
- Lower minimum temperature in the coldest month;
- Lower rainfall in the warmest quarter;
- Lower maximum temperature in the warmest month;
- Lower tree cover (also relative to other areas in southern Africa);
- Lower shrub cover;
- Higher wet season EVI;
- Lower maximum tree height within stand;
- Trees that have a good social status (close to maximum tree height in stand);
- Trees with minimal fire damage.

Basal area increment reaches a maximum at stem diameter of 60 cm and age of 100 years

Annual basal area increment reaches only a maximum at a stem diameter of approximately 60 cm or an age of about 100 years. Only then reaches the species the senescence stage (Bowman et al., 2013). It confirms the species as long-living, as also observed by Fichtler et al. (2004) for the Oshakati and Ondwanga regions of Namibia, and recorded for other parts of the distribution area (Therrell et al., 2007). The longevity and constant growth rate is not a typical pattern for an early succession species, as it was described by Von Breitenbach (1973). It places the species, also considering the medium wood density, more towards the late successional stages.

6.4 Biotic factors influencing the occurrence and abundance *Pterocarpus angolensis*

The dissertation set out to determine the environmental conditions that influence the occurrence and productivity of *P. angolensis*. Next to abiotic site conditions, biotic variables such as anthropogenic disturbances showed important patterns.

High fire frequencies affect the species

Most fires in southern Africa have an anthropogenic origin, especially in the study area where most fires occur outside the rainy and thus lightning season (Stellmes et al., 2013b). The species is known to tolerate fire (Banda et al., 2006; Von Breitenbach, 1973), but the regional SDM illustrates that its presence decreases in areas with fire frequencies larger than 23% and that it is absent in areas with fire frequency larger than 46%. Such high fire frequencies occur especially in north-western Angola and the southern DRC. They are less common in the *Baikiaea – Pterocarpus* forests, which have an annual fire frequency of about 14 to 24% (De Cauwer et al., 2016; Schelstraete, 2016; Siljander, 2009). The *Pterocarpus angolensis – Dialium englerianum* community has a significantly higher annual fire frequency (24% or on average a fire every 4 years) than all other communities except the *Guibourtia coleosperma* community. The results show no evidence of a negative effect of fire frequency on the presence of the species (Chapters 3 and 4).

There are however indications that the fire frequency negatively affect both small and larger trees. Tree seedlings need a gap of about 6 years between fires to reach minimum escape heights (Bond, 2008) and such conditions are rare for the tree communities on the sandy plateaux (De Cauwer et al., 2016; Pröpper et al., 2015). Trees with a reference DBH of 30 cm show a negative relation between fire damage and tree height. Trees accumulate fire damage with each fire (Schelstraete, 2016) at the stem base, causing a gradual decline in health and stability (Figure 6.1). This explains to a large extent why there are hardly any trees with DBH over 50 cm and why there was a higher proportion of smaller stems (60%) in the DBH class 10 – 20 cm compared to tree communities that had less fires in the past.

Human presence decreases abundance of species

Our study gives several indications of negative human impact on the abundance of *P. angolensis* in the study area. The *Pterocarpus angolensis – Dialium englerianum* community is mainly situated far away (> 35 km) from the Okavango river along which most settlement is concentrated, and outside walking distance from agricultural fields (> 7 km) or villages (> 9 km). The highest proportional basal area of *P. angolensis* is in areas more than 10 km away from main roads, showing the impact and location of commercial harvesting. Forest clearing for agriculture took mainly place next to roads and the Okavango River during the last decades, however within the forest, no decline in the basal area of *P. angolensis* over the last 40 years can be demonstrated. More data near the historical forest inventory plots is however needed to give a more complete picture.



Figure 6.1 – Fire damage at stem base of *Pterocarpus angolensis* (left). Trees topple over when a large part of the stem base is affected (middle). Local villagers often remove the logs immediately after the fire (right).

Competitive advantage in drier areas

P. angolensis may have a lower competitive ability in the most productive areas of its environmental range but does well in areas where other species struggle due to less favourable environmental conditions. The SDM model showed that *P. angolensis* co-occurred with the Miombo tree species *Brachystegia boehmii* and *Dalbergia melanoxylon* at a regional level and that it has a competitive advantage over *Schinziophyton rautanenii* and *Julbernardia paniculata*. The only species that seemed to have a clear competitive advantage over *P. angolensis* in less favourable conditions was *Burkea africana*, both at a regional and a local level. It is the indicator species of another sandy plateaux community in the study area, the *B. africana* community; an open and earlier succession stage forest.

6.5 Impacts of climate change and rising atmospheric CO₂

The SDM model shows that projected climate change can decrease the species' distribution area with 20% to 50% by 2080. The species is most sensitive in Namibia and Botswana because of a predicted decrease of early wet season rainfall and increased temperature seasonality. High temperature seasonality has also a negative effect on the abundance of the species in the study area (Chapter 4). A northward shift of the distribution in south-western Africa is a realistic scenario by the end of 21st century whereas a high emission scenario predicts the species to disappear from Namibia and Botswana. Our results fit in with a study of Midgley et al. (2005) that showed that tree cover and biomass in northern Namibia, southern Angola, and eastern Botswana will decrease. The other results for the study area

confirm the negative impact of higher summer temperatures and temperature seasonality on the growth rate of the species (Box 2). Moreover, of all tree communities, the *Pterocarpus angolensis* – *Dialium englerianum* community shows the least resilience towards climate change. The low proportion of small trees (DBH 5 – 10 cm) observed in this study, the low seedling density recorded in the same study area (Kabajani, 2016), and some of the reported die-back cases of *P. angolensis* in the region (Mehl et al., 2011; Mmolotsi et al., 2012; Strohbach and Petersen, 2007) may be early warning signs of climate change effects on *P. angolensis*. More data to disentangle impacts of climate change, high fire frequencies in the late dry season, and their interaction may be needed. On the other hand, *B. africana*, a species that is more resistant to climate change in the study area but is also earlier in the succession, showed a better regeneration in the areas with high fire frequencies while there was no evidence that the *B. africana* community is more resistant than the *Pterocarpus angolensis* – *Dialium englerianum* community to late season fires (De Cauwer et al., 2016; Kabajani, 2016; Schelstraete, 2016).

Contrary to the decreasing biomass in northern Namibia and southern Angola, Midgley et al. (2005) predicted an increase of biomass in the border area of Namibia, Zambia, and Zimbabwe because of the fertilisation effect of rising atmospheric CO₂. This study found also evidence of the increasing CO₂ levels improving diameter growth of *P. angolensis* where mean summer rainfall is larger than 135 mm. It demonstrates that CO₂-induced growth in the study area is limited by the availability in moisture as indicated by other studies (Cole et al., 2010; Laubhann et al., 2009).

The B1 climate change scenario predicts that the distribution area of *P. angolensis* will increase considerably in Zambia (+78%), which is in accordance with other studies (Midgley and Thuiller, 2011; Scheiter and Higgins, 2009) that predicted a gain of forest or woodland cover in that area. However, Zambia has a tradition of shifting cultivation (unlike e.g. Namibia) and high fire frequencies may counterbalance the advantages created by changing climate conditions.

6.6 Implications for sustainable management of southern African dry forests

The results of this dissertation allow formulating implications and recommendations for the sustainable management of the species. They target forest managers, land use planners, decision-makers, and conservationists in the region.

Upscaling models with predictive mapping

The optimal site factors derived for the study area allow predicting and mapping the presence and productivity of the species based on data derived from forest inventories and environmental data. Satellite images can assist in the mapping, e.g. *P. angolensis* was mainly found in areas with EVI below 0.29 in the study area. The forest attribute maps can assist forest managers and planners who aim to maximize wood production of *P. angolensis*. It allows them to focus interventions, such as fire prevention, thinning or assisted regeneration, on stands with the highest abundance and performance. Silvicultural treatments are hardly achievable in all parts of the forests because of logistic difficulties caused by limited resources and access and it is worth investing in the most productive

areas. Even mere presence of forest management has an effect as is illustrated by the protected state forest of Hamoye in north-eastern Namibia, where mean basal area is double that of a nearby community forest (Schelstraete, 2016). Forest management in Hamoye consists of regularly cleared fire breaks, more rapid firefighting and a stricter policing of illegal harvesting. No thinning, pruning or assisted regeneration is performed.

Wood with a higher portion of heartwood in the driest parts of the study area

The heartwood portion was significantly higher at the lower latitudes of the study area and similar to the values obtained in eastern Africa (Shackleton, 2002; Therrell et al., 2007). To obtain heartwood with a diameter of minimum 30 cm at stem base, it is necessary to harvest trees with minimum DBH of 40 cm. However, at higher latitudes in Namibia, DBH would have to increase to 47 cm for the same amount of heartwood making high quality timber harvesting less interesting, especially because not many trees of that size remain.

Forest management interventions

Variations in annual growth and heartwood portion within the study area were large and to a large extent at individual tree level. It points to the large impact of forest structure and/or genetic differences, both of which can be improved with silvicultural treatments. Pruning and thinning can address the negative effect of tree competition in the juvenile phase. It is advisable to remove low quality timber trees of all species with DBH < 25 cm near good timber quality trees of *P. angolensis* under supervision of forest management. This will also remove low quality genetic material from the forest. Stand basal area should however be kept at a minimum of approximately 5 m² per ha (Figure 4.5). Pruning should be done early on, preferably when trees are within the DBH classes of 10 – 20 cm as a lot of trees have short boles caused by one lower side branch. Shrubs, grasses and dead plant material should be removed near trees to lower the fire fuel load and reduce fire damage at stem bases. Seeds for assisted regeneration should be collected from the individuals with fast growth and high heartwood portions (Therrell et al., 2007). This can be checked through increment borings, however it is necessary to plug the hole afterwards to avoid entry of pathogens or fire.

The current minimum harvest size of *P. angolensis* in Namibia is 45 cm and it takes on average 88 years, including the seedling phase, for the tree to reach this size. However, many trees do not reach this size because of accumulated fire damage and their economic value is lost. Reducing the minimum harvest rate is difficult considering the lower heartwood portion, although it may be considered for the Otjozondjupa region where the heartwood portion is higher. It is therefore relevant to keep investing in fire prevention for the most valuable stands. This is normally done through the creation of 15 m wide fire breaks, but can be complemented by reducing the fuel load in the forest through thinning, pruning and removal of grass.

Yield prediction

The models for total wood biomass, total wood volume, wood volume of stem and branches, and timber wood volume (with portion of heartwood) in combination with the growth

model allow to predict yield at a national level in Namibia. They are easy to use as they are based on one easy to measure predictor: stem diameter. The age-diameter model is the easiest to use for application of sustainable harvest guidelines, showing times of passage of about 19 years for each 10 cm DBH class. In fact, growth appeared so constant in the study area, that it is also possible to calculate diameter growth with an average of 5.5 mm per year for all DBH classes. The BAI model in combination with the biomass model allows to derive annual biomass yield for *P. angolensis*, which is approximately 190 kg per ha in the natural forests of the Kavango regions. The models contribute to one of the forest research strategy topics for Namibia; growth and yield of forest resources (Ministry of Agriculture, Water and Forestry, 2011).

Climate change adaptation strategies

The study showed that climate change is another threat to *P. angolensis*, on top of deforestation and too frequent fires in the late dry season. Climate adaptation strategies need to be developed to prepare for the effects on an important timber species and on the local population, craftsmen and industries that depend on it. A strategy that could be considered for Namibia (and Botswana, Angola) is assisted regeneration with fire protection in the part of the distribution area that has the lowest temperature seasonality and highest rainfall. In Namibia, these areas are in the Ohangwena, Oshikoto and the north of the Kavango regions. As they are often densely populated and deforested, planting in an agroforestry context may offer the best opportunities. The protection and creation of more refuges for the species may allow it to better adapt to a changing climate (Liu and Yin, 2013).

Suited for agroforestry

The preference of *P. angolensis* for open forest, its fairly open and small crown, and its nitrogen fixing abilities (Hogberg and Pearce, 1986) make it a good candidate for agroforestry in an area where nitrogen is a limiting factor for subsistence agriculture (Pröpper et al., 2015). The seedlings are difficult to grow (De Cauwer and Younan, 2015; Vander Heyden, 2014) and often do not survive the establishment phase after planting out, but a more intensive agroforestry environment with watering and protection from predators and fire may provide seedlings with enough care to ensure sufficiently high success rates.

Comparison with other land uses

The yearly sustainable yield that can be calculated with the volume, biomass, and growth models will assist land use managers and economists in comparing the direct economic potential of the forest with that of other land uses. The economic value of both timber and carbon sequestration can be calculated. This knowledge may possibly assist to prevent land use changes. In several African countries, including Namibia, large areas are under pressure to convert to cash-crop agriculture, such as tobacco, maize, and *Jatropha curcas* plantations (Jew et al., 2016; Jull, 2007; Namwoonde, 2010). Plantations of the species in agroforestry context has the potential to produce more biomass per year on the nutrient poor soils than traditional agriculture methods (250 - 600 kg per ha) (Pröpper et al., 2015). This is illustrated by the annual yield of approximately 190 kg per ha (Table 5.6) in natural forests in the

Kavango regions with *P. angolensis* representing a fraction, approximately 16%, of the total tree yield. The yield in natural conditions is probably lower than in plantation conditions and could be increased when thinning and pruning is applied, a labour extensive investment compared to traditional agriculture.

6.7 Prospects for future research

This study gives insight in mainly general ecological patterns on regional and local level. Some of those patterns can be investigated in further detail. They are summarised here:

- The SDM map can be improved by adding more occurrences, especially for Zambia and Mozambique, which were underrepresented in databases and literature. Validation can be improved by having more absences confirmed for the DRC and Angola. A wider range of climate change scenarios can be explored by evaluating more climate models in combination with the recently developed RCPs (IPCC, 2014).
- Wood density is an important factor in biomass models. As the values of wood density in Namibia vary a lot, more data are needed to understand what causes this variation.
- The trend between heartwood portion and latitude should be investigated further in Namibia and south-western Africa.
- Follow-up studies that focus on succession and short-term dynamics are necessary, especially with the numerous threats to the open forests in southern Africa, such as increasing fire occurrences, ongoing deforestation, conversion to cash-crops and commercial cattle farms, and climate change. Monitoring of mortality and regeneration near the edges of the transition zone between dry forest and scrubland, in particular in south-western Africa, can give more insight in possible trends of climate change. This would contribute to global predictions on the distribution of dry forests, that are currently lacking (Liu and Yin, 2013). Currently, no evidence is available of a decrease of *P. angolensis* in the southwest of its distribution area or of an increase in Zambia. Policy makers and managers in the region need more research based facts to support their decisions and interventions with regard to potential climate effects on dry forests (Midgley and Thuiller, 2011).
- The use of site form to determine tree productivity showed promising results in this study. Creating more site form data for *P. angolensis* through age-diameter relations and linking site form at a DBH of 30 cm to geo-climatic variables may be a way to objectively classify the production potential of the *Baikiaea – Pterocarpus* forests. Linking biomass equations to site quality would contribute to the Namibian forest research strategy (Ministry of Agriculture, Water and Forestry, 2011).
- Future studies on diameter increment should aim at collecting more stand-level information and be spread over more locations with similar geo-climatic variables to provide more insights in growth variations between trees.
- Past die-back incidences of *P. angolensis* (e.g. Pearce, 1979) should be related to fire frequencies and climate change on a regional scale.

This study showed that *P. angolensis* is a long-living, late successional species that has weak competitive abilities, especially during the juvenile phase. It therefore performs well in open, dry forests such as the *Baikiaea – Pterocarpus* forests of Namibia and Angola. However, natural regeneration is poor in the *Baikiaea – Pterocarpus* forests and few trees make it to the senescence phase because of high fire frequencies and possibly climate change. Sustainable forest management needs to include increased fire prevention measures, assisted regeneration and silvicultural treatments to improve juvenile growth rates. The proposed follow-up topics may encourage more researchers to contribute to our understanding of an important timber species and to the tropical dry forests of southern Africa.

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Annex A – Glossary

Annual Mean Temperature (°C)	The mean of the monthly temperature averages averaged over a year and across the data period.
Annual Precipitation (mm)	Sum of all total monthly precipitation values as averaged across the data period.
Aridity Index	Quantification of the precipitation deficit over atmospheric water demand. Mean annual precipitation divided by mean annual evapotranspiration.
Aspect (°)	Compass direction that a terrain slope faces.
Basal area	Sum of the cross sectional areas of trees at DBH (diameter at breast height) in a stand and expressed per unit ground area (i.e. 1 ha).
Climatic water deficit (CWD)	Long-term water deficit, water lost by the environment during dry months.
Competition index (CI)	Index reflecting individual tree competition, calculated as the tree DBH divided by the quadratic mean diameter of the plot or stand. The quadratic mean diameter is the DBH of the tree with mean plot/stand basal area.
Enhanced Vegetation Index (EVI)	A vegetation index based on spectral signals of the vegetation that is related to vegetation cover, density and condition. It is designed to enhance the vegetation signal with improved sensitivity in high biomass regions while minimising soil and atmosphere influences. It is a standard product derived from amongst others MODIS satellite images.
Environmental stress factor (E)	Environmental factor based on CWD, temperature, and rainfall seasonality that has an important impact on the diameter-height relationship of trees.
Fire frequency (%)	The probability that a fire returns on an annual basis. This is calculated by dividing the amount of years with a fire by the amount of years the location was monitored.
Isothermality (%)	Mean diurnal range divided by annual temperature range and multiplied by 100. Quantifies how large the day-to-night temperatures oscillate relative to the summer-to-winter (annual) oscillations.
Length of growing period (days)	Average length of the period when temperature regime and moisture supply are conducive to crop growth and development. It refers to the number of days when average daily temperature is above 5°C and the evapotranspiration is above a specific fraction of a reference evapotranspiration.
Maximum Temperature Warmest Month (°C)	The maximum of the maximum monthly temperatures over a year and averaged across the data period.
Mean Diurnal Range (°C)	The mean of the monthly temperature ranges over a year. The monthly temperature range is the mean of the daily temperature ranges (temperature maximum - temperature minimum) calculated per month and across the data period.
Mean Temperature Coldest Quarter (°C)	The mean of the monthly temperature averages of the three consecutive months with the lowest summed mean temperatures.
Mean Temperature Driest Quarter (°C)	The mean of the monthly temperature averages of the three consecutive months with the lowest cumulative precipitation total.
Mean Temperature Warmest Quarter (°C)	The mean of the monthly temperature averages of the three consecutive months with the highest summed mean temperatures.

Mean Temperature Wettest Quarter (°C)	The mean of the monthly temperature averages of the three consecutive months with the highest cumulative precipitation total.
Minimum Temperature Coldest Month (°C)	The minimum of the minimum monthly temperature over a year and averaged across the data period.
Monthly maximum temperature (°C)	Maximum temperature within a month and averaged across the data period.
Monthly mean temperature (°C)	Mean of the daily maximum and minimum temperature calculated for a month and averaged across the data period.
Monthly minimum temperature (°C)	Minimum temperature within a month and averaged across the data period.
Monthly mean precipitation (mm)	Sum of the precipitation within a month and averaged across the data period.
Open forest	Land spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 % or trees able to reach these thresholds in situ.
Potential evapotranspiration (mm)	Evapotranspiration of a reference crop in optimal conditions.
Precipitation Coldest Quarter (mm)	Sum of the monthly precipitations of the three consecutive months with the lowest summed mean temperatures in a year and averaged across the data period.
Precipitation Driest Month (mm)	Lowest monthly precipitation over a year and averaged across the data period.
Precipitation Driest Quarter (mm)	Sum of the monthly precipitations of the three consecutive months with the lowest precipitation total in a year and averaged across the data period.
Precipitation Seasonality (%)	Coefficient of variation (relative standard deviation) of the monthly precipitation totals over the course of the year and averaged across the data period.
Precipitation Warmest Quarter (mm)	Sum of the monthly precipitations of the three consecutive months with the highest summed mean temperatures in a year and averaged across the data period.
Precipitation Wettest Month (mm)	Highest monthly precipitation over a year and averaged across the data period.
Precipitation Wettest Quarter (mm)	The sum of the total monthly precipitations of the three consecutive months with the highest cumulative precipitation total.
Priestley-Taylor alpha coefficient	A measure of water stress and the annual ratio of actual to potential evapotranspiration.
Quadratic mean diameter	The DBH of the tree with mean basal area in the plot/stand.
Rainfall ...	See: Precipitation ...
Site form	Tree height of a tree with a given reference DBH.
Site index	Mean height of the dominant trees at a reference age at the site.
Suffrutex	Low-growing woody shrub (dwarf shrub) or perennial with a woody base.
Temperature Annual Range (°C)	Maximum Temperature of the warmest month - Minimum Temperature of the coldest month. A measure of temperature variation over the data period.
Temperature Seasonality (°C)	The amount of temperature variation over the year within the data period. Standard deviation of monthly temperature averages.

Sources: (Chave et al., 2014; Eid and Tuhus, 2001; FAO, 2014; Fischer et al., 2008; Hijmans et al., 2005; Huete et al., 2002; Jiang et al., 2008; O'Donnell and Ignizio, 2012; Pokharel and Froese, 2009; Stellmes et al., 2013a; Trabucco, 2010; Zomer et al., 2007)

Annex B – Sources of occurrences for *Pterocarpus angolensis*

Source	Number of occurrences
National Botanic Garden of Belgium (BR)	55
Tropicos, Missouri Botanical Garden (MO)	42
Jardim Botânico Tropical, Instituto de Investigação Científica Tropical, Lisboa (LISC)	35
Flora of Zimbabwe - Hyde, M.A. & Wursten, B.	26
SABIF - SANBI PRECIS, South Africa	22
Royal Botanic Gardens, Kew (K) - most through GBIF	20
Directorate of Forestry, Namibia, Forest Inventories	14
Dondeyne, University of Leuven – unpublished data	10
Tree Atlas Project Namibia	10
De Cauwer, 2006-2013, Polytechnic of Namibia - unpublished data	9
Revermann, 2011-2013, University of Hamburg – unpublished data	9
Burke and Strohbach, 2000	8
Therrell et al., 2007	7
Amri and Mamboya, 2012	6
Finckh, 2011, University of Hamburg – unpublished data	6
Flora of Mozambique - Hyde, M.A., Wursten, B.T., Ballings, P. & Dondeyne, S.	6
Shackleton, 2002	6
Svendsen and Hansen, 1995	6
Timberlake et al., 2009	4
Muller et al., 2012	3
Netherlands Centre for Biodiversity Naturalis, section National Herbarium of the Netherlands	3
van Daalen et al., 1992	3
Clarke, 1995	2
Frost, 2000	2
Mmolotsi et al., 2012	2
Real Jardín Botánico, Madrid (MA) - through GBIF	2
Timberlake and Mapaure, 2007	2
Abbot et al., 1997	1
Backeus et al., 2006	1
Bracebridge, 2006	1
Burgess et al., 1992	1
Campbell et al., 1996	1
Chidumayo, 1994	1
Coates Palgrave et al., 2007	1
Dowsett-Lemaire and Dowsett, 2009; Spottiswoode et al., 2008	1
Hogberg and Pearce, 1986	1
Holdo, 2006	1
Luoga et al., 2004	1
Lynam et al., 2003	1
Scholes et al., 2004	1
Schwartz et al., 2002	1
Shackleton and Scholes, 2011	1
Stromgaard, 1985	1
Syampungani, 2009	1
Timberlake et al., 2007	1
Vyamana et al., 2007	1
Xylarium, Royal Museum for Central Africa, Belgium	1

Annex C – Absences of *Pterocarpus angolensis* used in the presence-absence validation

Sources of the 20 absence points based on literature:

- Arrestad et al., 2011
- Howell et al., 2012
- Lovett and Norton, 1989
- Lötter and Beck, 2004
- Malaisse et al., 1999
- Murray hudson et al., 2011
- Saad et al., 2012
- Steyn and Stalmans, 2001
- Timberlake and Childes, 2004
- Timberlake and Mapaure, 2007
- Timberlake et al., 2010

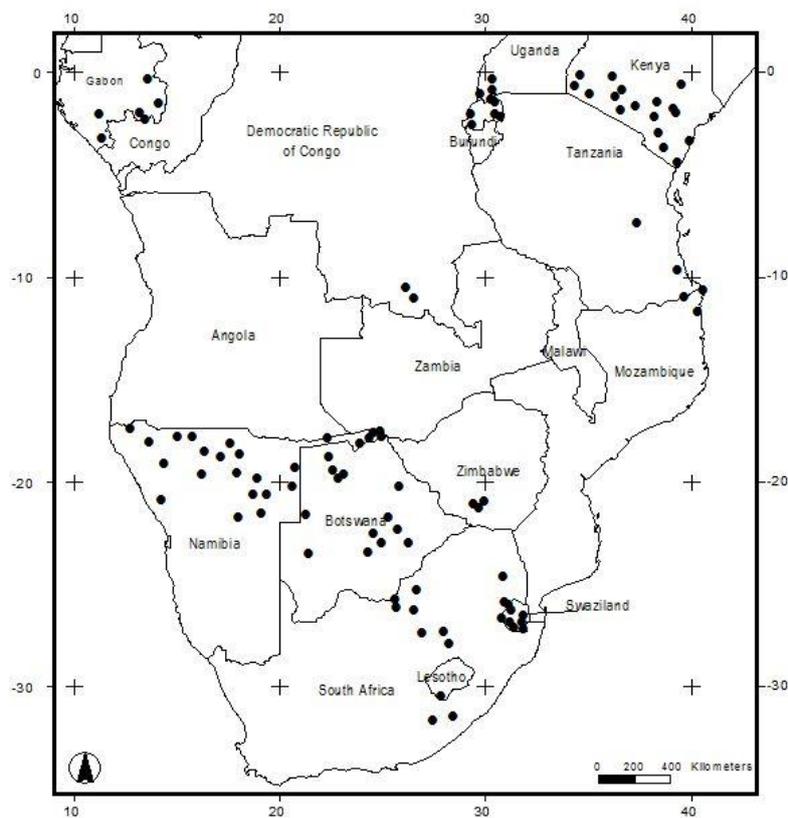
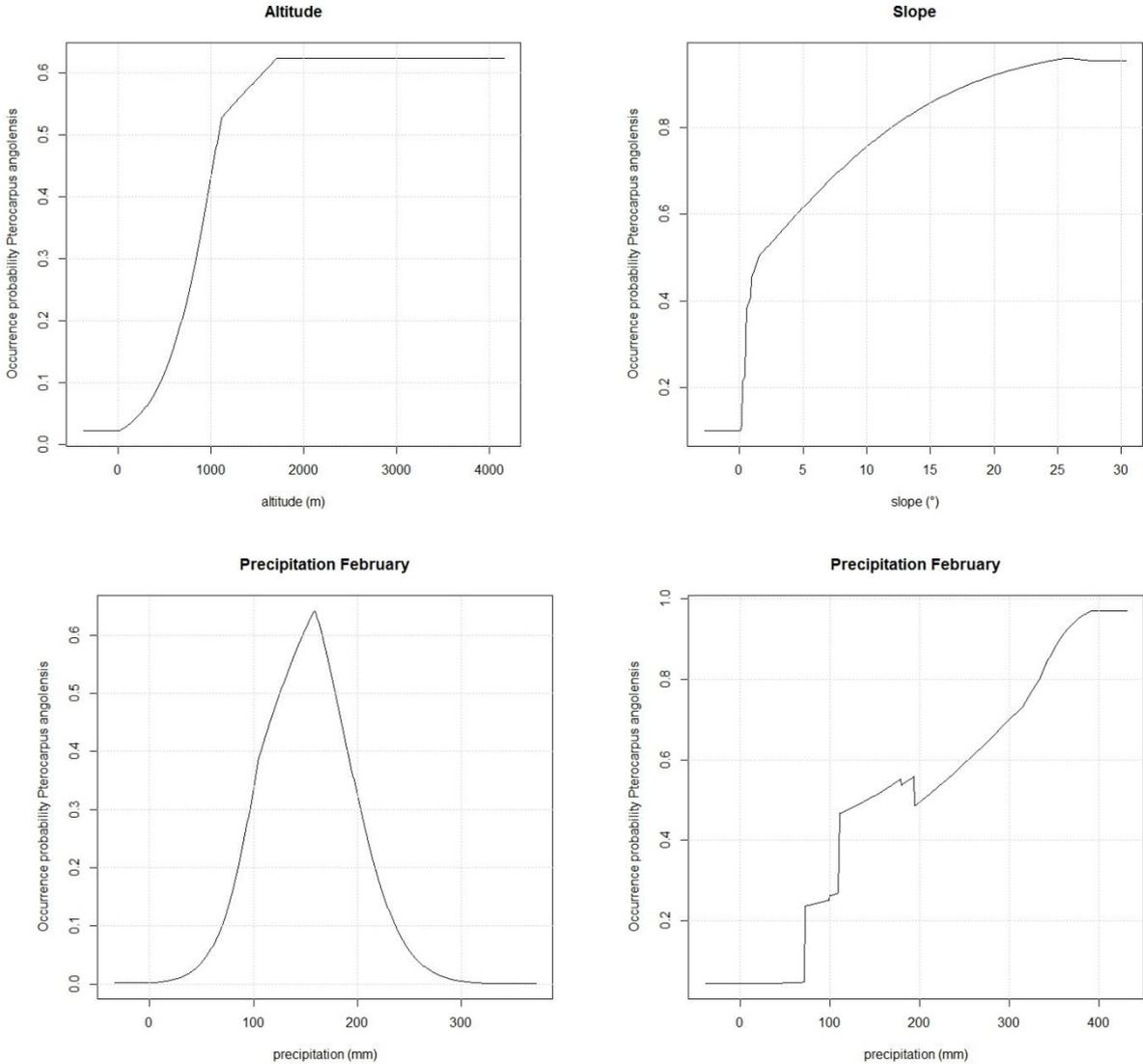


Figure C.1 – Location of all absence points used in the presence-absence validation.

Annex D – Response curves of environmental variables created by Maxent during the potential distribution modelling of *Pterocarpus angolensis*

The study area was divided in two zones: the Kalahari basin and the area outside (Figure 2.2). The Kalahari basin was considered as a group of sediments of the same age (Mendelsohn and el Obeid, 2004). The SDM of this study was applied with the training points of each of the two zones. Response curves of the models are shown for variables with the largest contributions to each model (Figure D.1).



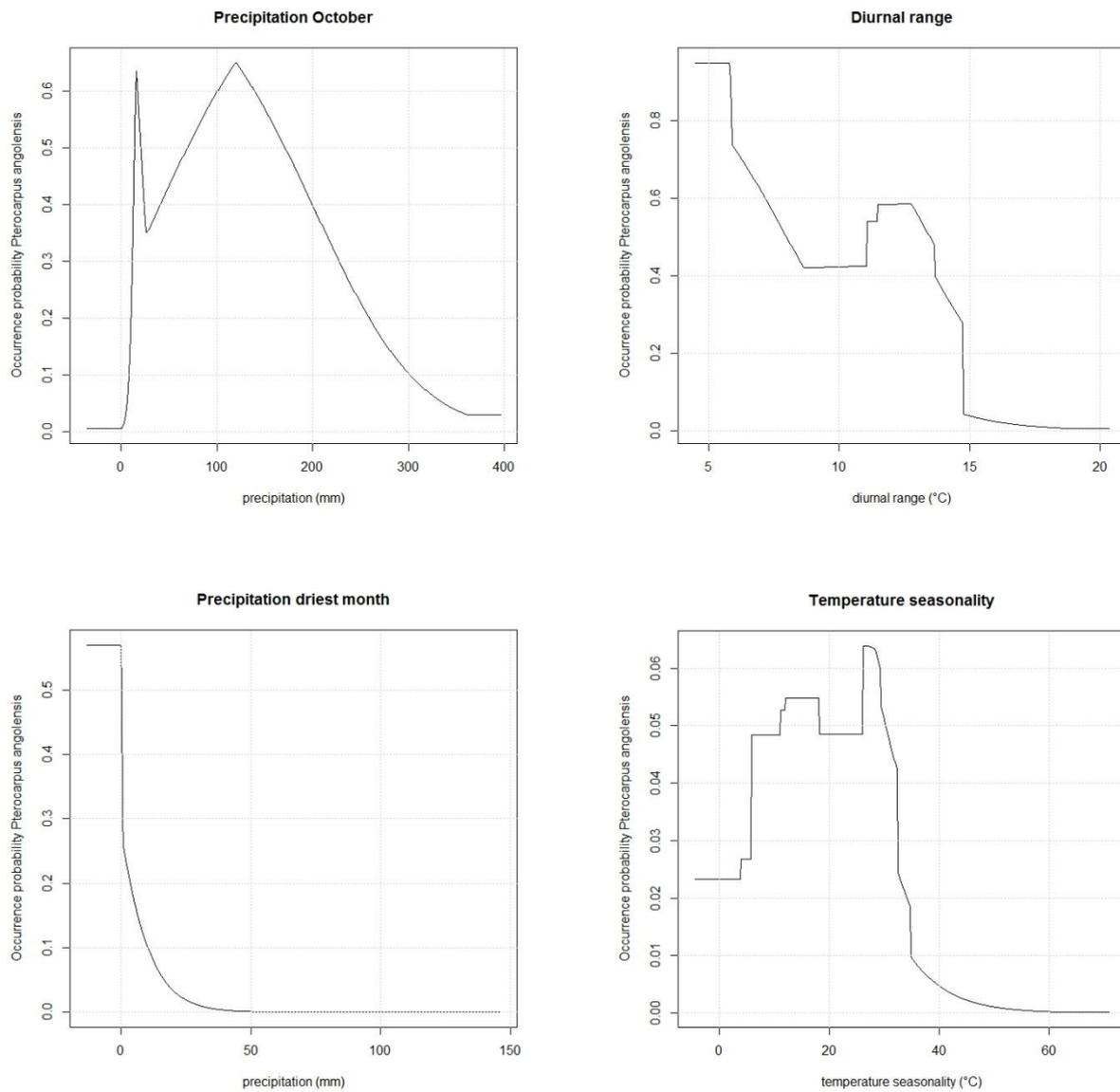


Figure D.1 – Response curves of SDM R for two zones: the Kalahari basin (left) and the area outside the Kalahari basin (right).

Annex E – Sample design of forest inventories

Sample design used for the research data:

Sample plots were systematically or randomly positioned along transects perpendicular to the Okavango river and major roads or fire breaks. The sample plot design used is based on that of the national forest inventory method of the Namibian Directorate of Forestry (Burke, 2002). It uses a circular design with three nested circles (Figure E.1):

- **Circle 1 with radius 10 m:** all trees and shrubs with circumference at breast height (CBH) ≥ 15.7 cm (= DBH of 5 cm) are measured;
- **Circle 2 with radius 20 m:** all trees and shrubs with CBH ≥ 62.8 cm (DBH of 20 cm) in the area outside circle 1 are measured;
- **Circle 3 with radius 30 m:** all trees and shrubs with CBH ≥ 141.4 cm (DBH of 45 cm) in the area outside circle 2 are measured;
- **Subplot with radius 5 m:** count all woody vegetation (seedlings, saplings, shrubs) with CBH < 15.7 cm.

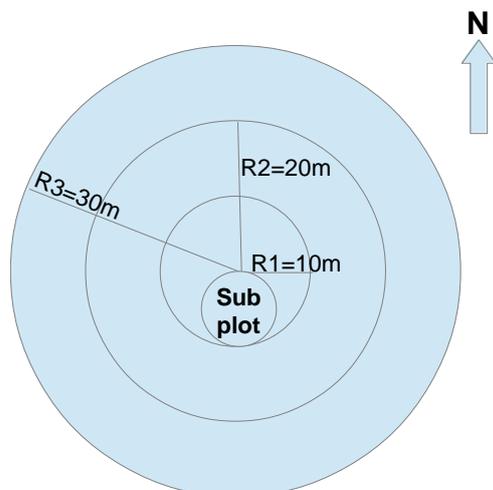


Figure E. 1 – Sample plot design for research data.

Sample design used for forestry data, except the inventory of Likwaterera community forest:

The sample method is based on a systematic grid design. The plot design is the same as for the research data, except that it has two subplots (Burke, 2002).

Sample design used for Likwaterera community forest:

Data was collected with a systematic grid design. The sample plots are circular with a radius of 20 m in which all trees with a DBH \geq 10 cm were recorded (Rechberger, 2008).

Sample design used for historical data:

Sample points were randomly selected from a systematic grid design. The selection was in proportion to the representation of three forest types determined during a preliminary survey. Four sample plots were established per sample point. They were located at randomly selected distances of 100, 200, 300, 400 and 500 m from the sample point and at randomly selected compass directions of 0, 45, 90, 135, 180, 225, 270, and 315 °. Sample plots were circular with a radius of 30 m in which all trees with a DBH \geq 10 cm were recorded (Geldenhuys, 1992).

Annex F – Tree species in the *Baikiaea* – *Pterocarpus* forests

Table F.1 – Tree species contributing most to the total basal area in the *Baikiaea* - *Pterocarpus* forests as determined by all inventory data

Species	Contribution to basal area (%)
<i>Burkea africana</i>	23
<i>Baikiaea plurijuga</i>	16
<i>Pterocarpus angolensis</i>	16
<i>Schinziophyton rautanenii</i>	12
<i>Guibourtia coleosperma</i>	11
<i>Dialium englerianum</i> ^a	6
<i>Terminalia sericea</i>	3
<i>Combretum collinum</i>	2
<i>Ochna pulchra</i>	1
<i>Combretum</i> spp.	1
<i>Combretum psidioides</i>	1
<i>Combretum zeyheri</i>	1
<i>Diplorhynchus condylocarpon</i>	1
<i>Erythrophleum africanum</i>	1
<i>Strychnos pungens</i>	1
<i>Philenoptera nelsii</i>	0.5
<i>Strychnos cocculoides</i>	0.4
<i>Commiphora</i> spp.	0.4
<i>Acacia erioloba</i>	0.4
<i>Combretum albopunctatum</i>	0.4
<i>Strychnos</i> spp.	0.4
<i>Acacia nigrescens</i>	0.2
<i>Peltophorum africanum</i>	0.2
<i>Swartzia madagascariensis</i>	0.2
<i>Combretum imberbe</i>	0.1
Total	99

^a *Dialium englerianum* in Namibia

Annex G – Performance of boosted regression tree models for the five tree communities of the *Baikiaea* – *Pterocarpus* forests

Table G.1 – Predictive performance of the boosted regression tree (BRT) models for each tree community and relative importance of the predictor variables (%). Deviance and correlation are calculated using 10-fold cross-validation. Distance to the Okavango River is a proxy for both abiotic and anthropogenic variables and was not included in the total contribution. *Burafr* = *Burkea africana*, *Schrau* = *Schinziophyton rautanenii*, *Baiplu* = *Baikiaea plurijuga*, *Guicol* = *Guibourtia coleosperma*, *Pteang-Diaeng* = *Pterocarpus angolensis-Dialium engleranum*.

	Range of predictor	<i>Burafr</i>	<i>Schrau</i>	<i>Baiplu</i>	<i>Guicol</i>	<i>Pteang-Diaeng</i>	Mean contribution
% Deviance explained		17	17	26	5	9	
Correlation		0.40	0.43	0.53	0.22	0.30	
Temperature seasonality	30.2 - 35.7 °C	12	11	6	10	19	12
Elevation	1077 - 1173 m	11	13	4	12	12	10
Aspect	0 - 359°	11	11	8	7	13	10
Distance to Okavango river	0 - 49 km		16	5	8	11	8
Distance to main roads	0 - 35 km	9	10	5	8		6
Distance to towns	4 - 84 km		15	3		12	6
Annual rainfall	531 - 625 mm	12	15	2			6
Distance to tracks	0 - 14 km	17		2	7		5
Ground waterlevel	20 - 80 m		10	16			5
Distance to non-perennial rivers	0 - 22 km	10		8	7		5
Distance to villages	0 - 17 km	10		2		11	5
Distance to agricultural fields	0 - 15 km				5	12	3
Slope	0 - 4.3°			7	10		3
Rainfall in February	119 - 141 mm			4	10		3
Cattle density	0 - 14 km-2	7		5			3
Landscape curvature	-0.1 - 0.14			4	7		2
Soil class	-			11			2
Fire frequency 1981 - 2004	0 - 10 years					10	2
Rainfall seasonality	102 - 111%				9		2
Rainfall warm quarter	144 - 195 mm			3			1
Nutrient availability class	2 - 4			2			0
Dune class	0 - 1			2			0
TOTAL CONTRIBUTION							
Abiotic factors		56	59	78	71	44	62
Anthropogenic factors		44	25	18	20	45	30

Annex H - Kruskal-Wallis tests of site variables for the tree communities

Table H.1 - Relation of communities with site variables. Only variables with significant differences ($p < 0.05$) are shown. Standard error of the mean is between brackets. Damage is expressed on a scale from 0 to 4 with 0 no, 1 mild, 2 moderate, 3 severe and 4 fatal damage.

	<i>Schinziophyton rautanenii</i>	<i>Baikiaea plurijuga</i>	<i>Burkea africana</i>	<i>Guibourtia coleosperma</i>	<i>Pterocarpus angolensis - Dialium engleranum</i>
BASED ON ALL DATA					
Annual rainfall (mm)	570 (19) ^a	561 (16) ^b	562 (11) ^b	563 (12) ^{bc}	564 (12) ^{ac}
Temperature seasonality (°C)	33.4 (1.8) ^a	33.5 (1.5) ^a	34.6 (1.0) ^b	34.4 (1.0) ^b	34.5 (1.01) ^b
Minimum temperature coldest month (°C)	6.5 (0.7) ^a	6.6 (0.6) ^a	6.1 (0.4) ^b	6.1 (0.4) ^b	6.1 (0.4) ^b
Sand in topsoil (%)	94 (2) ^a	93 (7) ^b	95 (2) ^c	95 (1) ^{ac}	95 (1) ^c
CEC in topsoil (cmol kg ⁻¹)	0.31 (0.85) ^a	0.97 (2.29) ^b	0.17 (0.69) ^c	0.17 (0.5) ^{ac}	0.13 (0.47) ^c
Ground water level (m)	35 (19) ^{ac}	47 (23) ^b	34 (13) ^a	34 (15) ^{ac}	31 (14) ^c
Distance to fossil rivers (km)	3.6 (3) ^a	2.7 (2.4) ^b	8.0 (5.7) ^c	5.9 (4.7) ^d	6.6 (4.9) ^{cd}
Distance to agricultural fields (km)	3.3 (2.3) ^{ac}	2.6 (2.1) ^b	3.0 (2.7) ^{bc}	3.3 (2.5) ^c	4.0 (2.8) ^a
Distance to main roads (km)	6 (5) ^a	10 (9) ^b	8 (4) ^b	8 (6) ^b	8 (5) ^b
Distance to towns (km)	35 (22) ^a	45 (20) ^b	42 (18) ^b	48 (21) ^{bc}	51 (22) ^c
BASED ON RECENT DATA					
Annual rainfall (mm)	571 (14) ^a	570 (13) ^a	561 (10) ^b	566 (10) ^a	567 (11) ^a
Precipitation seasonality (%)	107 (3) ^a	105 (3) ^a	108 (1) ^b	108 (2) ^b	108 (2) ^b
Temperature seasonality (°C)	33.6 (1.8) ^a	33.0 (1.8) ^{ab}	34.7 (0.7) ^c	34.6 (1.0) ^c	34.5 (1.1) ^{bc}
Sand in topsoil (%)	94 (2) ^a	92 (9) ^b	95 (1) ^c	95 (1) ^c	95 (1) ^c
Organic carbon in topsoil	0.08 (0.13) ^a	0.18 (0.19) ^b	0.01 (0.06) ^c	0.02 (0.08) ^c	0.03 (0.09) ^c
Dune (0,5=near;1=on)	0.25 (0.39) ^a	0.28 (0.40) ^a	0.04 (0.17) ^b	0.04 (0.16) ^b	0.06 (0.22) ^b
Valley (0=no;1=yes)	0.16 (0.37) ^a	0.22 (0.42) ^a	0.08 (0.27) ^b	0.02 (0.14) ^b	0.05 (0.22) ^b
Distance to fossil rivers (km)	3.4 (2.6) ^a	3.0 (2.3) ^a	8.7 (5.7) ^b	6.9 (4.5) ^{bc}	6.9 (4.9) ^c
Cattle density (km ⁻²)	6 (4) ^a	7 (4) ^a	3 (2) ^a	4 (2) ^b	3 (3) ^b
Fire frequency 1981-1991 (%)	23 (21) ^a	18 (20) ^a	33 (18) ^b	33 (20) ^b	34 (20) ^b
Fire frequency 1991-2004 (%)	19 (10) ^{ab}	16 (11) ^b	21 (10) ^a	21 (11) ^{ac}	24 (11) ^c
Distance to agricultural fields (km)	2.4 (2.0) ^{ab}	1.8 (1.6) ^b	2.9 (2.5) ^{ac}	2.8 (2.3) ^{ac}	3.3 (2.3) ^c
Distance to tracks (km)	1.0 (1.0) ^a	0.6 (0.7) ^b	2.9 (3.4) ^c	2.0 (2.6) ^c	2.2 (2.7) ^c
Distance to villages (km)	5.4 (3.1) ^{ab}	4.3 (2.4) ^b	6.7 (3.9) ^{ac}	6.3 (3.5) ^{ac}	7.2 (3.5) ^{ac}

Annex I – Description of the tree communities in the *Baikiaea* – *Pterocarpus* forests

1. Slope communities

The slope communities were closer to the Okavango and fossil rivers than the sandy plateau communities, but the average distance was still 2 to 3 km. They were often in areas with slightly lower temperature seasonality, which is mainly in the west of the study area (69% of plots). The communities had a higher mean DBH, basal area, tree cover and enhanced vegetation index. They showed more signs of anthropogenic impact as they were situated closer to villages and tracks and in areas with a cattle density higher than 5 animals km⁻². They were often found near dunes or (dry) river valleys with slight slopes (>1.5 °) mainly exposed to the north.

1.1 *Schinziophyton rautanenii* community

This community was characterised by the presence of *S. rautanenii* and to a lesser extent by the uncommon tree *Erythrophleum africanum*. It had the highest stem density of all communities, as well as the largest maximum DBH and basal area because of the large diameters of mature *S. rautanenii* trees. Annual rainfall was significantly higher than that of other communities with a threshold of 580 mm. The community was closer to the Okavango river, main roads and major towns than any other community and showed most signs of cattle and human disturbances.

1.2 *Baikiaea plurijuga* community

B. plurijuga is a good indicator species for this community, assisted by the fact that it tends to grow in clusters (Graz, 2006). Next to the valuable timber tree *B. plurijuga*, *Philenoptera nelsii* and *Commiphora* species were typical for this community but much less common. It concerns a denser forest type with a significantly lower amount of small or dead trees. It was found in the least sandy areas with a significantly higher amount of organic carbon and higher CEC in the topsoil and closest to agricultural fields. It was the community closest to fossil rivers.

2. Sandy plateau communities

The sandy plateau communities were often on flatter terrain and occurred under harsher conditions such as lower minimum temperature of the coldest month and higher temperature and rainfall seasonality. There was a higher fire frequency in the period 1981 – 2004 compared to the slope communities and fire was the major cause of tree damage. The proportion of small stems was larger than for the slope communities.

2.1 *Burkea africana* community

B. africana was a suitable indicator species of this community because of its abundance rather than its predictive value. The community had lower tree cover and less stems, as well as significantly lower DBH and basal area. It occurred in areas with slightly lower annual rainfall, was significantly further away from fossil rivers than other communities and in the

areas with lowest cattle density. It can often be found closer to the main road than the other sandy plateau communities, and sometimes also close to villages.

2.2 *Guibourtia coleosperma* community

G. coleosperma is a good indicator species for this community. Basal area and mean and maximum DBH were slightly higher than in the other sandy plateau communities. The community was found on plains or slight depressions in the landscape. The most common aspect was west, opposite of the major wind direction.

2.3 *Pterocarpus angolensis* – *Dialium englerianum* community

The community was characterised by the abundance of the valuable timber tree *P. angolensis* and also the less common *D. englerianum*. It was furthest away from agricultural fields and towns, but could sometimes be found close to villages. It is most likely to be found in areas with fire frequency higher than 33%.

Annex J – Predictor variables used for the productivity models

Table J.1 - Overview of predictor variables tested in the boosted regression tree models for presence, abundance, proportional abundance, and site form of Pterocarpus angolensis in Namibia and Angola. Data of damage classes and dunes were on an ordinal scale and all other data on an interval scale. A glossary of terms is given in Annex A.

Abiotic variables	Source
Bioclimatic variables: Temperature Seasonality, Max Temperature Warmest Month, Min Temperature Coldest Month, Precipitation Warmest Quarter, Annual Precipitation, Precipitation seasonality, Annual rainfall, Temperature annual range, Diurnal range, Precipitation wettest quarter	WorldClim (Hijmans et al., 2005)
Precipitation February, Prec. October, Prec. November	Shuttle Radar Topography Mission (SRTM), NASA
Altitude, Slope (derived in GIS), Aspect (derived in GIS), Landscape curvature (derived in GIS)	
Soil-pH, Sand fraction, Organic Carbon, CEC, base saturation	Harmonised World Soil Database (FAO/IIASA/ISRIC/ISSAS/JRC, 2009)
Frost days	Derived from Climatic Research Unit time-series datasets (CRUTS v.3.10.01) (Harris et al., 2013)
Regional biotic variables	Source
Occurrence of forest, cropland, pasture and browse	FAO, 2007
Disturbances	Source
Fire frequency for the period 1991 - 2012	Verlinden, 2004 - Landsat Quicklook
Distance to perennial and non-perennial rivers, distance to agriculture, tracks, main roads, towns and villages	Stellmes et al., 2013b - MODIS Burned Area
Dunes, Cattle density	GIS data digitised in Google Earth (2013, 2014) and derived from the Atlas of Namibia (Mendelsohn et al., 2002)
Fire damage class, Human damage class, Cattle damage class	Own forest inventory data in nested plots with maximum radius of 30 m (Annex E, research sample design)
Stand variables	Source
Enhanced Vegetation Index (EVI) for the year, EVI for the dry season, EVI for the wet season	Stellmes et al., 2013a - MODIS time series 2000-2012
Stand basal area (BA), Tree cover, Shrub cover, Grass cover, Competition index CI, Tree height.(Maximum tree height) ⁻¹ (H.Hmax) ⁻¹	Own forest inventory data in nested plots with maximum radius of 30 m (Annex E, research sample design)

